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Interactions Among Prescribed Fire, Soil Attributes, Fungal Mats, and Mycorrhizal Fungus Fruiting Patterns in an Old-Growth *Pinus ponderosa / Abies concolor*stand in Crater Lake National Park, Oregon, USA

Kermit Cromack
US Forest Service

Randy Molina
US Forest Service

Jane E. Smith
US Forest Service

James M. Trappe
US Forest Service

Efren Cazares-Gonzales
US Forest Service

See next page for additional authors

Authors
Kermit Cromack, Randy Molina, Jane E. Smith, James M. Trappe, Efren Cazares-Gonzales, Mary Rasmussen, and Matt Trappe

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Final Report to the Joint Fire Science Program

Project #03-3-2-05: "Effects of prescribed burning on mycorrhizal fungi in Crater Lake National Park."

Principal Investigators:

Dr. Kermit Cromack, Jr.

Dr. Randy Molina

Dr. Jane E. Smith

Dr. James M. Trappe

Dr. Efren Cázares-Gonzales

Mary Rasmussen

Matt Trappe

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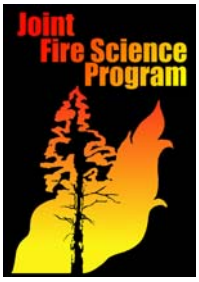
Oregon State University

U.S.D.A. Forest Service



Joint Fire Science Program

Executive Summary

The first of its kind

This study is the first of its kind to take a tripartite approach to the interactions among prescribed burn treatments, soil attributes, and fungal fruiting patterns. Our study site had been previously established with three different prescribed burn treatments, applied in the early spring, late spring, and fall of 2002, as well as non-burned control plots. We measured fuel levels and soil attributes two years post-treatment, and surveyed ectomycorrhizal fungal fruiting patterns between 2003 and 2006. Using multivariate statistics we were able to identify how the treatments affected specific soil attributes, which of those attributes affected fungal fruiting patterns, and how the burn treatments affected fungal fruiting patterns. The relationship between burn treatments and fungal fruiting patterns is not a simple one.

Soil characteristics tend to occur as a suite

We measured mineral soil bulk density, total soil C, δ^{13}C depletion, total soil N, δ^{15}N enrichment, C:N ratio, CWD mass, FWD mass, litter mass, and mineral soil pH in 24 plots. We found that many of these occurred as correlated suites of attributes. Above mean levels of δ^{13}C depletion, δ^{15}N enrichment, C:N ratios, and fuels tended to occur on the same plots, mostly on control and early spring burn treatments. Higher soil bulk density, total N, and pH occurred on a different set of plots, including most of the fall burn plots but also three control plots.

Pre-treatment patterns: a silver lining

We detected a spatial gradient of soil attributes across the study site, present prior to treatment. Plots on the east end of the study area generally had lower C:N ratios and higher soil bulk density, total N, and pH, grading to higher C:N ratios and lower soil bulk density, total N, and pH at the west end (a distance of 2 km). This gradient enabled us to separate the effects of the treatment on fungal fruiting patterns from the effects of the soil attributes. In fact, the fungal fruiting pattern was one of the clues that led us to examine spatial patterns beyond statistical correlations: we saw the same fruiting patterns on

some non-burned control plots as we did on fall-burned plots. Clearly the burn treatment itself is not the only factor at work.

Prescribed burn treatment effects on soil attributes

The different burn treatments did have measurable effects on soil attributes, even against the background gradient of soil attributes. All burn treatments significantly reduced litter mass and fine woody debris compared to controls, and the late spring and fall burns significantly reduced coarse woody debris. Fall burns were significantly more effective at fuels reduction than either spring burn treatment.

The fall burn treatment significantly reduced soil C:N ratios, but spring burn treatments had no measurable effect on them. Total C in the fall burn plots was slightly but not significantly lower than controls ($p = .12$); no treatment significantly affected total N. The fall burns also significantly increased soil pH.

Fruiting patterns primarily influenced by soil C:N ratios

Fungal fruiting patterns did not conform to burn treatments; they correlated more closely with the suites of soil characteristics. The single element that best predicted fungal fruiting patterns was the C:N ratio. Although the C:N ratio was correlated with other soil properties, the gradient of soil attributes and the mosaic of burn treatments endowed the plots with a diversity of attribute combinations, which enabled us to disentangle the soil attribute correlations and their relationships to fungal fruiting patterns.

Fungal indicator guilds

Our statistical analysis allowed us to identify certain fungal taxa that served as consistent indicators for soil attributes, most significantly C:N ratios. As with soil attributes, these taxa tended to occur as sets, or 'guilds.'

The guild of fungi indicating lower C:N ratios included *Amanita pantherina*, *Boletus chrysenteron, B. zelleri*, *Morchella angusticeps,* and *Sarcosphaera coronaria*. Indicating higher C:N ratios were *Cortinarius rigidus, Elaphomyces granulatus, Gautieria monticola, Gomphus floccosus, Hysterangium separabile, Hydnotrya variiformis,* and *Melanogaster tuberiformis.*

Of the low C:N guild, only *Morchella angusticeps* fruited exclusively on burned plots. All the rest of the low C:N indicator species were collected at least one non-burned control plot. Of the high C:N guild, 5 of the 7 indicator species were hypogeous. In 23 of 24 plots, the presence of one guild to the exclusion of the other was an accurate indicator of higher (26-31) vs. lower (18-25) C:N ratios.

Prescribed burn treatment effects on fungal fruiting patterns

Prescribed burn treatments affected fungal fruiting patterns to the extent that they changed soil C:N ratios. The fall burn treatment reduced soil C:N ratios by 2.4 to 4.6 points. All but one of the fall burn treatment plots had C:N ratios below 25, and all but that plot produced the low C:N fungal guild. Spatial correlation suggests that the anomalous fall burn plot likely had a relatively high C:N ratio prior to the burn application, and while the burn treatment reduced its C:N ratio the reduction was insufficient to shift fungal fruiting patterns.

Prescribed burn treatment effects on fungal mats

Using DNA sequencing, we identified 128 fungal mats representing 46 taxonomic groups at our study site. We have identified two fungal genera previously not known to form mats (*Alpova* and *Lactarius*), and identified the lichen *Trapeliopsis granulosa* as the predominant organism forming surface biotic crusts. The distribution of data limited statistical analyses, but several species were significantly correlated to the abundance of litter and coarse woody debris, notably *Gautieria monticola*, *Lepiota magnispora*, and *Piloderma fallax*. These taxa respond poorly to more intense burns and other activities disrupting the forest floor. Data from other sites at Crater Lake National Park indicate it

may take more than 15 years for fungal mats to re-establish after severe forest floor disturbance.

Summary and take-home message

Differing prescribed fire treatments have differing effects on soil chemistry and surface fuels. These effects influence the fruiting patterns and abundance of mycorrhizal and mat-forming fungi. The response of mycorrhizal fungal fruiting patterns to fire is primarily driven by the fire's effect on the soil C:N ratio. Prescribed burns implemented in the spring have very little effect on fungal communities; in fact more sporocarps were collected on spring-burned plots than on non-burned controls. Fires implemented in the fall significantly reduce fungal productivity and shift fungal fruiting patterns, but do not eliminate fungal communities. Fall prescribed burns also greatly reduce the abundance of fungal mats, primarily as a function of litter consumption.

Deliverables Crosswalk Table

Proposed	***Delivered***	***Status***
Annual progress reports	Annual progress reports completed	Done
Publication series	Two papers are currently in preparation and will be submitted for peer review by the end of 2007: Trappe MJ, Cromack K, Jr., Trappe JM, Perrakis DDB, Cazares-Gonzales E, Castellano MA, and Miller SL. 2008. Interactions Between Prescribed Fire, Soil Attributes, and Mycorrhizal Fungus Fruiting Patterns in an Old-Growth *Pinus ponderosa* / *Abies concolor* stand at Crater Lake National Park, Oregon, USA. Forest Ecology and Management, in preparation. Trappe MJ, Cromack K, Jr. 2008. A Survey of Filamentous and Mat Forming Soil Fungi at Crater Lake National Park, Oregon, U.S.A. Mycologia, in preparation.	In process
Regional meeting	Trappe MJ. 2005. Effects of prescribed fire on mycorrhizal fungi at Crater Lake National Park. Joint Fire Science Program 2005 annual meeting, San Diego, CA. Poster presentation.	Done
National meeting	Trappe MJ. 2005. Effects of prescribed fire on mycorrhizal fungi at Crater Lake National Park. AAAS 2005 annual meeting, Ashland, OR. Oral presentation.	Done
National meeting	Trappe MJ. 2008. Effects of prescribed fire on mycorrhizal fungi at Crater Lake National Park. AFE "Fire in the Southwest" Conference, Tucson, AZ. Abstract submitted for oral presentation.	Pending
Site tour	Led group of USFS and BLM silviculturalists and Park staff on tour of study site, July 2004.	Done
Crater Lake National Park staff presentation	We will present our findings to the ecology staff at Crater Lake National Park in the spring of 2008.	Pending
Ph.D. dissertation	Dissertation defense expected January 2008.	Pending

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Introduction

Ecological background

Prescribed fire is a valuable tool for returning forests of the western United States to their historic fire regimes and fuel levels after more than a century of fire suppression (Agee, 1993). Often the goal of prescribed fire is simply to reduce fine fuels and understory density, but prescribed fires affect other aspects of forest communities in many other, poorly understood ways. Fire affects not only the habitat of above-ground biota but also the below-ground habitat. This research examines relationships between prescribed burn treatments and selected soil and fuel attributes on mycorrhizal fungus fruiting patterns in a mixed ponderosa pine (*Pinus ponderosa* Doug.)/white fir (*Abies concolo*r [Gord. and Glend.] Lindl.) stand in Crater Lake National Park, Oregon, USA.

Mycorrhizal fungi are critical to survival and growth of all forest tree species in the Pacific Northwest by facilitating nutrient and water uptake through their symbiotic relationship with tree roots (Smith and Read, 1997). Most biomass of mycorrhizal fungi is in the top 10 cm of soil, a region likely to be affected by forest fire (Stendell et al., 1999). Even light-intensity burns can alter the mycorrhizal fungus community (Smith et al., 2004; Smith et al., 2005); intense fires may damage the mycorrhizal community (Baar et al., 1999; Jonsson et al., 1999; Grogan et al., 2000), impeding the plant community's survival, recovery, and growth. Therefore the implications of fire-induced changes in the mycorrhizal community can be significant to post-fire stand recovery or productivity.

The response of mycorrhizal fungus fruiting patterns to fire is important because fungal sporocarps are a significant food source for wildlife (North et al., 1997; Cazares et al., 1999; Claridge et al., 1999; Ashkannejhad and Horton, 2006) and hence are an important response variable to evaluate effects of fire on wildlife carrying capacity. Another management consideration is that several mycorrhizal fungi in southwestern Oregon produce sporocarps of gustatory and economic value for humans, such as matsutake

(*Tricholoma magnivelare* Peck [Redhead]), chanterelles (*Cantharellus* and *Craterellus* spp.), king bolete (*Boletus edulis* [Bull.]), and morels (*Morchella spp.*) (Molina et al., 1993; Pilz and Molina, 2002).

Some fungi form dense aggregations of hyphae in the soil, often referred to as "fungal mats." These mats often have greater concentrations soil nutrients, enzymes involved in decomposition, and soil biota than surrounding soils (Cromack et al 1979, Griffiths et al 1994). Another facet of our project was to study the effects of the burn treatments on fungal mats.

The timing of a prescribed burn affects fire severity, primarily as a function of fuel moisture (Kauffman and Martin, 1989). Burn severity can affect soil chemistry, fine roots, litter layer coverage and depth, and levels of coarse woody debris (CWD) in different ways (Agee, 1993; Cromack et al., 2000; Perrakis, 2004). Soil moisture may conduct heat deeper into the ground while simultaneously regulating maximum soil temperatures (Hartford and Frandsen, 1992; Campbell et al., 1995). All these factors have potential to affect the mycorrhizal community: soil chemistry and fine root survival influence the availability of energy resources and habitability of the immediate environment (Snith and Read, 1997; Smith et al., 2004; Smith et al., 2005); litter coverage and CWD influence soil moisture retention, and CWD is an important habitat feature for many small mammals that play a major role in distributing fungal spores (Maser and Trappe, 1984).

Many studies have examined effects of fire on soil attributes (reviewed in Johnson and Curtis, 2001; Certini, 2005), mycorrhizae (reviewed in Cairney and Bastias, 2007) and fungal fruiting patterns (Visser, 1995; Vernes et al., 2001; Dahlberg, 2002; Claridge and Trappe, 2004; Fujimura et al., 2005; Trappe et al., 2006), as well as the effect of soil attributes on fungal fruiting patterns (van der Heijden et al., 1999; Lilliskov et al., 2001). Here we explore the relations among seasonal prescribed burning, an array of soil attributes, and mycorrhizal fungus fruiting patterns over three years in an effort to separate the effects of fire treatment from the effects of soil attributes on fungal fruiting patterns.

Hypotheses

Our first hypothesis was that prescribed burning at different seasons influences belowground habitat differently, as measured by the soil attributes of total carbon (C) and nitrogen (N), mineral soil bulk density, C:N ratios, and $\delta^{13}C/^{15}N$ isotopic signatures, and on the aboveground habitat, as measured by surface fuels in the form of CWD, fine woody debris (FWD) and litter mass. Our second hypothesis was that burning at different times of the year affects the post-fire mycorrhizal fungus fruiting patterns differently, as measured by sporocarp inventories conducted over multiple years. We combined the fuels data of Perrakis (2004) with our soil attribute measurements to quantify many of the physical changes brought about by the different prescriptions and relate these to mycorrhizal fungus fruiting patterns. In the course of soil analyses we discovered a pre-existing gradient of soil attributes across the study area, which permitted us to separate effects of burn treatments from effects of soil attributes on mycorrhizal fungus fruiting patterns.

Methods

We collected data on ten habitat attributes for use as explanatory variables: mineral soil bulk density, total soil C, $\delta^{13}C$ depletion, total soil N, $\delta^{15}N$ enrichment, C:N ratio, CWD mass, FWD mass, litter mass, and mineral soil pH. We collected and identified mycorrhizal fungal sporocarps as dependent variables over three years in spring and fall. We analyzed these data in several ways to 1) determine the effect of the prescribed burn treatments on the habitat attributes and fungal fruiting and mat forming patterns, 2) seek relations within and between the habitat attributes and fungal fruiting and mat forming patterns, and 3) identify fungal community guilds as responses to prescribed burn treatments and habitat attributes.

Study site

The study site at the south border of Crater Lake National Park in southern Oregon (42° 48'N, 122° 50'W) was characterized by McNeil and Zobel (1980). The topography is fairly flat with an elevation gradient from 1460 to 1550 m. Average annual precipitation is

about 65-85 cm yr^{-1}, most falling between October and May. The soils resemble Lapine and Stieger series and are highly porous with the base mineral soil dominated by volcanic pumice mixed with basaltic cobble from the eruption of Mt. Mazama ca. 7000 years ago. The litter (O horizon) is a fairly thick (to 20 cm) layer of ponderosa pine and white fir needles, ranging in dry mass from about 3 to 6 kg m^{-2}. The humus layer (A horizon) is quite variable in thickness and has diffuse interfaces with the litter above and mineral soil below.

The forest overstory is dominated by ponderosa pine with some subdominant white fir. The midstory is primarily composed of white fir and lodgepole pine (*Pinus contorta* [Doug.]), and the minimal understory includes *Pyrola*, *Carex*, and a number of forbs. *Ceanothus* and *Arctostaphylos* were also present but restricted to forest edges. Fire scar analysis by McNeil and Zobel (1980) indicated that fires affecting substantial portions of the study area occurred in 1782-84, 1791, 1818, 1846, 1864, 1879, and 1902. The last is the year the area was designated as a National Park, and fire suppression from that year through 1978 was effective. Prior to 1902, the overall fire return interval ranged from 12.8 to 40 yrs with a mean of 21.1 yrs.

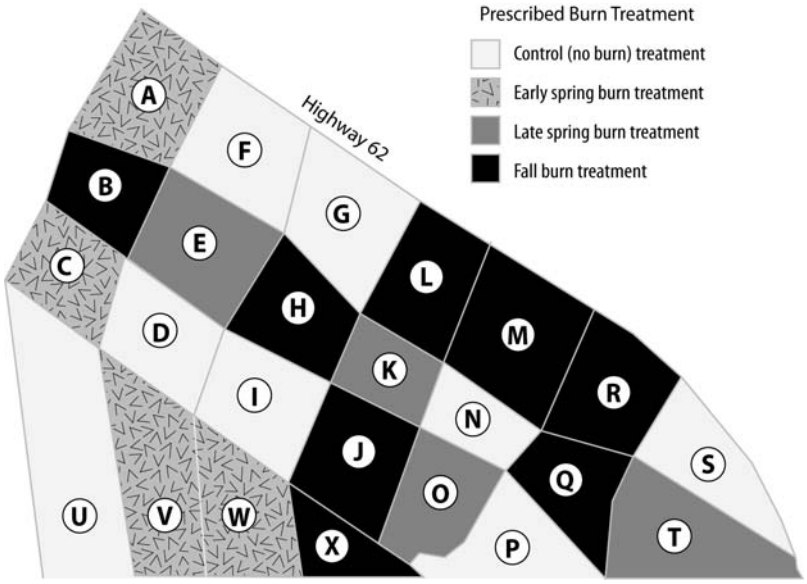

Figure 1. Map of prescribed burn treatments.

Prescribed burns

The prescribed burns were planned by Dr. James Agee and Dan Perrakis of the University of Washington. The site was divided into 24 treatment units averaging 2.8 ha in size, each of which was randomly assigned a burn prescription (Fig. 1). Four prescriptions were applied: control (non-burned; eight plots), early spring burn (ignited June 20, 2002; 4 plots), late spring burn (ignited June 28, 2002; 4 plots), and fall burn (ignited October 9-10, 2002; 8 plots). The fall burn initially was planned to be applied in two treatments (early and late fall), but weather and fire crew logistic constraints permitted only one ignition weekend for all eight fall burn treatment units. Similarly, the close timing of the spring burn prescriptions was necessitated by competing demands for the fire crew. All burn treatments were somewhat patchy in their intensity and severity.

Fungal sporocarp sampling

In the three years following the burn applications, fungal fruiting data were collected in the spring and fall by time-constraint sampling (Claridge et al., 2000). Time-constraint sampling entails sampling of plots of a standard area for a standard number of person-minutes, allowing surveyors to employ intuition and experience to look in diverse microhabitats and maximize data collection. The method has been used successfully to quantify fungal diversity and habitat associations over broad ecotypes in southeastern Australia. Field trials of time-constraint sampling conducted at Crater Lake indicated that 1000 m^2 (20 x 50 m) survey plots sampled for 100 person minutes captured the asymptotes of detected fruiting body diversity (M. Trappe, unpublished data).

In each sampling iteration, four of each spring burn treatment units were sampled and four each of the eight fall and non-burned control units were sampled. The same four fall burn treatment units consistently were sampled each spring and the remaining four were sampled each fall. This sampling schedule also applied to the control plots. Four treatment units of each prescription were sampled spring and fall for three years. At each sampling iteration, a 1000 m^2 survey plot was established within each of the 16 treatment units. The survey plots were randomly located and oriented and placed away from the edge of the treatment unit, and were moved each year within the treatment unit to

broaden the total area sampled and eliminate disturbance effects from previous sampling activities. Taxa collected in less than three treatment units in either spring or fall were not used in data analysis. All collection data were converted to presence/absence for each plot for analysis.

Several researchers have attempted to link belowground mycorrhizal communities with aboveground sporocarps (Gardes and Bruns, 1996a; Dahlberg et al., 1997; Chen and Cairney, 2002; Fujimura et al., 2004) with varying degrees of success, largely due to the fine spatial scale of mycorrhizal colonization on root tips and seasonal and annual variability in fruiting patterns. Because one of the main reasons for this study was to evaluate the impacts of prescribed burn treatments on sporocarps in the context of food webs, we decided to focus our sampling efforts on sporocarps rather than root tips. We recognize that sporocarp production responses to habitat conditions do not necessarily reflect belowground mycorrhizal community responses to habitat conditions (Horton and Bruns, 2001) and certainly a significant part of the mycorrhizal community in this ecosystem produced few or no sporocarps during our sampling, however inventory based on sampling mycorrhizal root tips was beyond the scope of this project. Due to tremendous variability in biomass between taxa and between seasons we focused on presence/absence of species rather than standing crop biomass as indicative of treatment effect on the food web.

Fungal species identification

Fungal collections were identified by standard morphological methods augmented by restriction fragment length polymorphism (RFLP) analysis and DNA sequencing of immature, degraded, or cryptic specimens. The ITS region of the nrDNA was used for all molecular analyses, and sequences were identified by matching with GenBank using the BLAST search tool.

Many of the taxa collected at Crater Lake were originally named as species in Europe, but recent work in molecular taxonomy suggests that many North American fungi that closely resemble European counterparts are, in fact, distinct species which have not yet

been described and named. In particular, the genera *Cortinarius* and *Russula* are taxonomically unresolved in North America, so the European species names used here represent the closest morphological fit to species or species complexes collected at Crater Lake. All collections were accessioned into the Oregon State University Mycological Herbarium (OSC).

A relatively small number of saprobic species were collected on the plots, but were not included in data analysis. These were *Cryptoporus volvatus* (Peck) Shear*, Gyromitra infula* (Schaeff.) Quél., *Pholiota carbonaria* A.H. Sm., *Flavoscypha cantharella* (Fr.) Harmaja, *Gastropila subcretacea* (Zeller) P. Ponce de León, *Ramaria stricta* (Pers.) Quél. and *Trappea darkeri* (Zeller) Castellano. Several mycorrhizal fungi were collected three times but two of those collections were from the fall and one from the spring or vice-versa; these failed to reach the threshold of at least three occurrences to be included in either spring or fall data sets. *Morchella angusticeps* Peck was included in the analysis as data about its trophic status is inconclusive (Dahlstrom et al., 2000; Hobbie et al., 2001), as was *Geopyxis vulcanalis* Peck whose close relative *G. carbonaria* (Alb. and Schwein.) Sacc. forms mycorrhizae with *Picea* (Vrålstad et al., 1998) and possibly *Pinus* (Egger and Paden, 1986).

Fungal mat sampling

We collected and sequenced soil fungi that formed aggregations of hyphae or rhizomorphs sufficiently dense to be visible to the naked eye and at least palm-sized. We did not attempt to distinguish between mycorrhizal and saprobic taxa in the field. Each of the 24 plots was sampled for a person-hour in July 2005 and again in September 2006. Sampling focused on microhabitats within each plot likely to support soil fungi, such as low areas, underneath fungal sporocarps and animal digs, and adjacent to decayed logs. The litter surface was gently raked back to reveal the upper layers of the A horizon. When soil macrofungi were observed a tissue sample was collected and notes were taken on the appearance of fungi in situ.

Fungal mat identification

DNA was extracted from the samples following Gardes and Bruns (1996b), and the ITS region of the nrDNA was amplified by PCR. In some cases the entire ITS region would not amplify; for these the ITS-2 region was amplified. Samples were sequenced and identified using the BLAST search tool on GenBank; those that did not provide a match with at least 90% similarity were discarded from the dataset. Names were assigned at the species level when unequivocal GenBank sequence similarity was ≥ 98%, at species group level when equivocal matches for 2 or more species ≥ 95% sequence similarity, and at genus level with sequence similarity of 90-98%. Samples failing to match ≥90% of nucleotides with GenBank sequences were discarded.

Soil cores and mineral soil bulk density

Six soil cores were taken with a 335 cm^3 corer from random locations throughout each treatment unit, labeled, and refrigerated in sealed plastic bags. Before coring, the litter layer was removed to expose the mineral soil surface. Cores were oven dried at 60° C for 12 h. The cores had variable amounts of either heavy basaltic rocks or very light pumice, the proportions of which strongly affected core bulk density. Because we were interested in the density of the finer mineral soil, the cores were weighed after drying, their volume was measured, then they were screened to remove >1 cm rocks and coarse organic debris, and volume and weight were measured again. The volume of large rocks and debris (as determined by volume prescreen minus volume post-screen) was subtracted from the original core volume to obtain a “rock-free” volume. This volume was divided by the post-screening weight to reach a rock-free bulk density.

Carbon, nitrogen, and isotopic analysis

The screened soil core samples were ground to a sand consistency and homogenized, then ca 10 g subsamples were further homogenized and ground to flour consistency in an analytical mill. This finely ground soil was further subsampled (sample size 50-70 mg), carefully weighed into 8 x 5 mm tin cups and sent to UC Davis Stable Isotope Facility for assay of total C content, total N content, and $\delta^{13}C/^{15}N$ isotopic signatures. Overall, the isotopic analysis of the mineral soils showed $\delta^{15}N$ enrichment by about 2.5‰

relative to IAEA standard (air) and $\delta^{13}C$ depletion by about 25.5‰ relative to IAEA standard (Vienna Peedee Belemnite).

Fuels: litter mass, fine and coarse woody debris

Fuels data were collected by Perrakis (2004) after application of the burn prescriptions. In each unit ten, 20 m long, fuel inventory transects were established for a total of 200 m of line transect. Coarse (>7.6 cm diameter) and fine (0.6 – 7.6 cm diameter) woody fuels were measured along these transects by Brown's (1974) line-intersect method, with the addition of litter depth measurements at three points along each transect. Woody debris mass was calculated by use of the values for Pacific Northwest mixed-conifer forests derived by van Wagtendonk et al. (1996), and litter mass was calculated by regression equations from Agee (1973).

Soil pH

The pH of mineral soil samples was measured by mixing 1 g of finely ground soil sample in 5 cl of deionized water. These were allowed to equilibrate for 1 h, and then measured with a digital pH meter.

Data analysis

Fungal sporocarp collections from spring and fall were analyzed separately, as different sets of treatment units were sampled between the seasons and there was little overlap in taxa. When correlating spring-fruiting fungal sporocarp data to habitat attribute data, only the habitat data from the 16 treatment units sampled in the spring were used; for fall-fruiting fungi, only the habitat data from the 16 treatment units sampled in the fall were used. When correlating habitat attributes overall, data from all 24 treatment units were used.

Pearson's correlation analysis was used to identify correlations between habitat attributes. Logistic regression was used to test relationships between habitat attributes and species occurrence. Linear regression was used to test for correlations between fungal mat abundance and habitat attributes. ANOVA was used to test for significant

differences between treatments. No variables required transformation. These analyses were performed with SAS 9.1 statistical analysis software (SAS, 2003).

Non-metric multidimensional scaling (NMS; Clark, 1993), a form of ordination statistics (PC-ORD 4.33; McCune and Mefford, 1999), was used to elucidate relationships among and between habitat attributes and the fruiting response of mycorrhizal fungi. NMS provides closeness-of-fit relationships between all explanatory and dependent variables for complex multivariate data sets, identifies potential indicator species, and produces scattergrams which spatially orient experimental units to minimize residuals between all variables.

Three data sets were used in ordination analysis. The first had habitat attribute data for all 24 plots, but no fungal collection data. The second had fungal collection and habitat attribute data for the 16 plots sampled in the spring. The third had fungal collection and habitat attribute data for the 16 plots sampled in the fall. Five different ordinations were performed: 1) habitat attributes for all plots; 2) habitat attributes of the plots sampled in the spring; 3) species collections of plots sampled in the spring; 4) habitat attributes of plots sampled in the fall; 5) species collections of plots sampled in the fall. Ordinations of habitat attributes show similarities in physical properties between plots, and ordinations of species collections show similarities in fungal fruiting patterns between plots. For consistency, all ordination scattergrams were rotated so the CWD vector is to the right.

The habitat attributes of litter mass, FWD, and CWD were highly correlated. Fine woody debris was eliminated from ordination analysis, as its presence disproportionally weighted the influence of the surface burn effects. Although still correlated, both CWD and litter mass were left in the ordination data sets as they represent quite different ecological functions. These will collectively be referred to as ‘fuels’ hereafter.

To identify groups of plots that were most similar, a cluster analysis using Sorensen’s distance measure and flexible beta group linkage of -0.25 was performed on each ordination, producing matrices of possible grouping combinations. Indicator species

analysis was then applied to these matrices, and the grouping combination with the lowest cumulative p-value was selected as the most robust (Dufrene and Legendre, 1997).

Row and column analysis was performed on the habitat attribute data set. With unmodified data the coefficient of variation of column totals was 146%, indicating that data transformation was necessary. A generalized relativization by column was chosen as the most appropriate method to normalize data on significantly different scales. An outlier analysis of the relativized data set indicated no outliers of > 2 s.d. Scree plot analysis indicated that a two-dimensional solution was optimal, so final ordination was performed in two-dimensional space with a random starting point using Sorensen's distance measure.

Because the spring and fall fungal collection data sets were binary (presence/absence), Beal's smoothing was applied to both matrices. Beal's smoothing is a transformation designed for data sets that contain a large number of zeros and replaces binary data with quantitative "favorability" values (Beals, 1984; McCune, 1994).

In the spring collection data set, *Elaphomyces granulatus* Fr. was identified as a multivariate outlier (2.5 s.d.) and was removed from the data set, as was *Cantharellus subalbidus* Morse from the fall collection data set (2.4 s.d.). Scree plot analysis indicated that a two-dimensional solution was optimal for both spring and fall datasets, so final ordination was performed in two-dimensional space with a random starting point using Sorensen's distance measure.

Results

Total sporocarps collected

A total of 566 collections representing 133 species of mycorrhizal fungi were collected over three years. A table of all collections is presented in Appendix A. Of these 133 species, 77 were found in only one or two plots in a collecting season (spring or fall) and were not used in data analysis, resulting in a final data set of 458 collections representing

56 species. The columns in Appendix A show how many plots over three seasons a taxon was collected per treatment (four plots for each treatment over three seasons give a maximum of 12 for each treatment). The taxa collected on at least three plots (and subsequently included in the data analysis) are listed first and are designated by the four-letter abbreviations used in the scattergrams.

The mean values and standard errors for each habitat attribute by prescribed burn treatment are presented in Appendix B, differences between treatments in Appendix C, and correlations between habitat attributes in Appendix D. In all tables a (-) symbol preceding the *p-value* indicates a negative correlation. Steel et al. (1997) suggest using an $\alpha = 0.10$ for field experiments having smaller numbers of replicates for each treatment, and we use this significance threshold in discussing our results.

Fungal sporocarp correlations with habitat attributes

Of the 16 taxa collected in the spring on three or more plots, eight correlated with habitat attributes at a $p < 0.10$ level of significance (Appendix E); of the 45 species collected in the fall on more than three plots, 19 correlated with habitat attributes at a $p < 0.10$ level of significance (Appendix F).

Ordination of habitat attributes for all plots

The habitat attributes ordination for all 24 plots is presented in Fig. 2. Cluster analysis identified five groups of plots within this ordination.

Group 1 contained three fall burn treatment plots (plots R, L, and M) and one late spring burn treatment plot (plot T). These plots had higher total N and lower C:N ratios than the other burn treatments found in group 2. Group 2 contained all of the remaining fall burn plots, unified by lower total N and higher C:N ratios. All of these plots had relatively low levels of fuels.

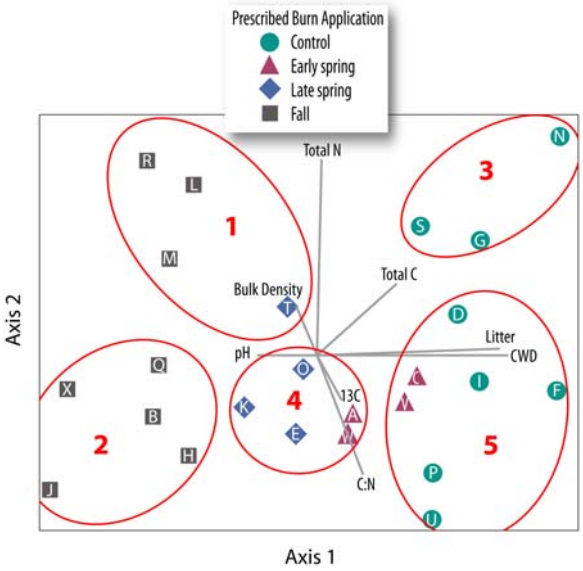

Figure 2. Ordination of habitat attributes for all plots.

Group 3 was formed by three control plots that differed from the rest of the controls by their high levels of total N and correspondingly lower C:N ratios. Groups 4 and 5 represented a continuum of fuel levels, and to a lesser extent soil pH. They share lower levels of total N and higher C:N ratios, and have higher fuel levels than the plots in the first and second groups. Group 4 (with lower fuel levels than group 5), contained the remaining three late spring burn plots and two of the early spring burn plots. In group 5 were five of the eight control plots and the remaining two early spring burn plots. Plot D had higher total N levels than other members of this group, but this was offset by correspondingly higher levels of total C, resulting in a higher C:N ratio than the other three high N control plots in group 3.

The fall burn plots all shared the trait of low fuel levels and were divided among two groups along axis 2: those that had high concentrations of total N and low C:N ratios, and those with lower total N and higher C:N ratios. Likewise, all of the control plots shared the trait of high fuel levels, but also were divided into two groups along axis 2 based on their total N concentrations and C:N ratios. These divisions assisted in teasing out the attributes behind the treatments that were driving the fungal fruiting patterns observed.

Ordination of habitat attributes for plots sampled in the spring

The ordination of habitat attributes of the 16 plots surveyed in the spring is presented in Figs. 3.1 and 3.2. Fungal collection data are displayed in the vector overlay in Fig. 3.2 but do not affect the position of the scattergram points. Cluster analysis identified four groups of plots within this ordination.

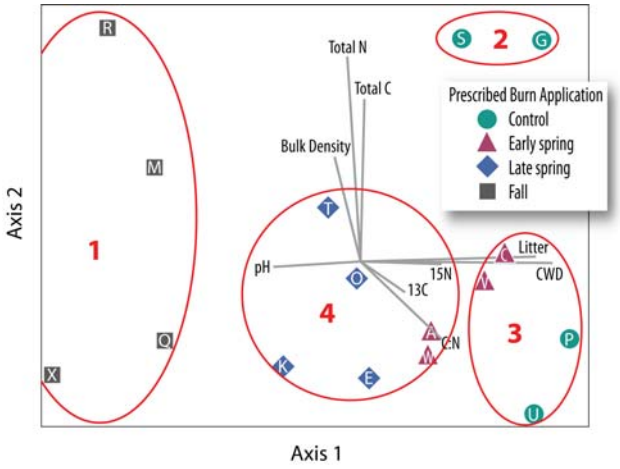

Figure 3.1. Ordination of habitat attributes for spring collection plots, with habitat attribute overlay.

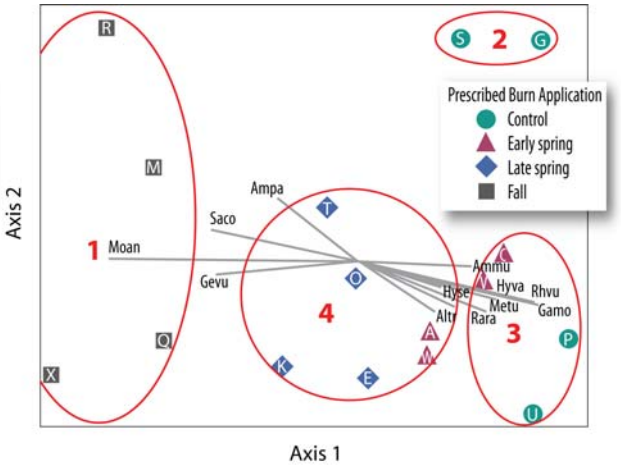

Figure 3.2. Ordination of habitat attributes for spring collection plots, with species collection overlay.

Group 1 contained all four fall burn plots, unified by higher soil pH and lower fuel levels (Fig. 3.1). This group was characterized by the presence of *Amanita pantherina* (DC.) Krombh., *Geopyxis vulcanalis* Peck, *Morchella angusticeps* Peck and *Sarcosphaera coronaria* (Jacq.) J. Schröt. (Fig. 3.2).

Group 2 contained two control plots. Consistent with the habitat attribute ordination of all the plots (Fig. 2), these were separated from the other control plots and all of the spring burn plots by their high total N and total C, and subsequently low C:N ratios. No species vectors pointed strongly in the direction of these two plots (Fig. 3.2).

Group 3 contained the remaining two control plots and two of the early spring burn plots. This group was associated with high C:N ratios and fuel levels. *Amanita muscaria* (Pers.)

Gonn. and Rabenh., *Gautieria monticola* Harkn., *Hydnotrya variiformis* Gilkey, *Melanogaster tuberiformis* Corda, *Ramaria rasilispora* Marr and D.E. Stuntz, and *Rhizopogon vulgaris* (Vitt.) M. Lange were associated with these plots.

Group 4 contained all late spring burn treatment plots and two early spring burn plots. It represents plots with habitat attributes intermediate between the first (low fuels and high pH) and third (high fuels and low pH) groups. They were unified by lower levels of total C and total N, and all but plot T had above mean C:N ratios. Most of these plots had *Morchella angusticeps* and *Sarcosphaera coronaria*, and plots O and T were more similar to group 1 in having *Amanita pantherina* and *Boletus zelleri* Murrill as well. Plots A, E, and W were more akin to group 3, all having *Hysterangium separabile* Zeller and most having *Gautieria monticola*, *Hydnotrya variiformis*, and *Melanogaster tuberiformis*.

Ordination of species collections for plots sampled in the spring

The ordination of species collected on the 16 plots surveyed in the spring is presented in Figs. 4.1 and 4.2. Soil attribute data are displayed in the vector overlay of Fig. 4.1 but do not affect the position of the scattergram points. Cluster analysis identified three groups of plots within this ordination.

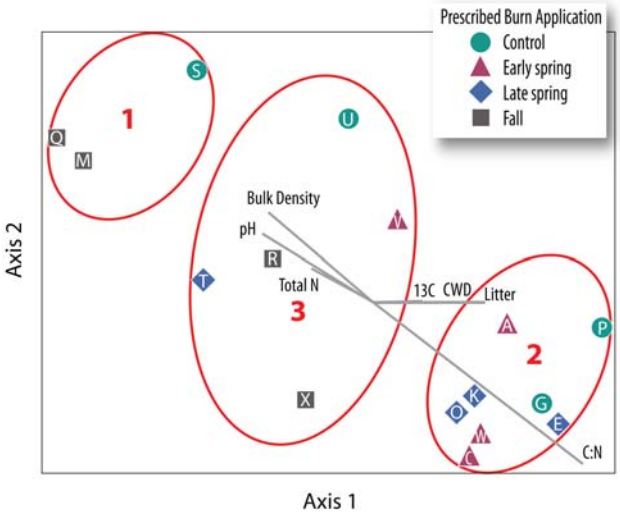

Figure 4.1. Ordination of species collections for spring collection plots, with habitat attribute overlay.

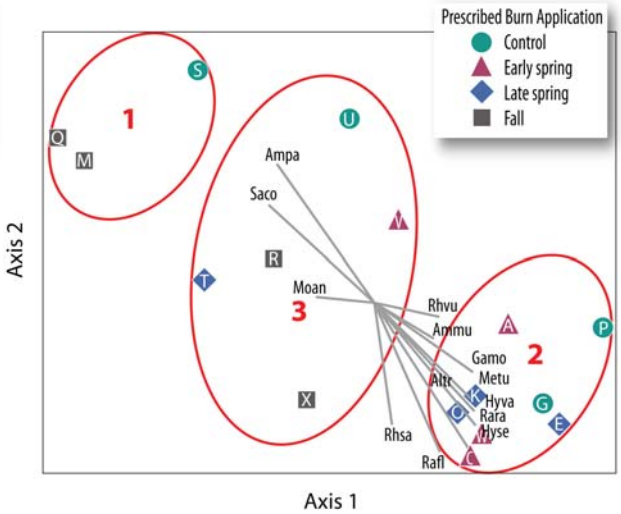

Figure 4.2. Ordination of species collections for spring collection plots, with species collection overlay.

Group 1 contains two fall burn plots and one control plot. The two fall burn plots have relatively high soil pH and total N, but average soil bulk density. Control plot S is an anomaly in this group, but one aspect it has in common with other group members over other control plots is its relatively high soil bulk density— the highest of all control plots by a substantial margin. All three plots have low C:N ratios as a consequence of their high total N levels, and all plots in this group produced *Amanita pantherina* and *Sarcosphaera coronaria* (Fig. 4.2).

Group 2 included three of each of the early and late spring burn plots as well as two control plots, but none of the fall burn plots. Of these six spring burn treatment plots, none had *Amanita pantherina* and only one had *Sarcosphaera coronaria*. Thirty-three of the 41 hypogeous species collections (excluding *Sarcosphaera*) in the spring were found in this group. Five of the six plots had *Hysterangium separabile* and *Ramaria rasilispora*, taxa absent from the other two spring burn plots (in group 3). All of the plots in group 2 had above above mean fuel levels and C:N ratios except plot G (a control plot), which had high levels of total N and a subsequently low C:N ratio. *Gautieria monticola, Hydnotrya variiformis, Hysterangium separabile, Melanogaster tuberiformis,* and *Ramaria flavobrunnescens* var. *aromatica* Marr and D.E. Stuntz were produced in group 2 (Fig. 4.2).

Group 3 is intermediate between groups 1 and 2, in both habitat attributes and sporocarp production, with several of the plots producing *Gautieria monticola, Melanogaster tuberiformis,* and *Ramaria flavobrunnescens* var. *aromatica* but not *Hydnotrya variiformis*. All of the plots except U (a control plot with a low C:N ratio) produced *Geopyxis vulcanalis* and *Morchella angusticeps*.

Ordination of habitat attributes for plots sampled in the fall

The ordination of habitat attributes of the 16 fall fruiting collection plots is presented in Figs. 5.1 and 5.2. Cluster analysis identified two groups of plots within this ordination.

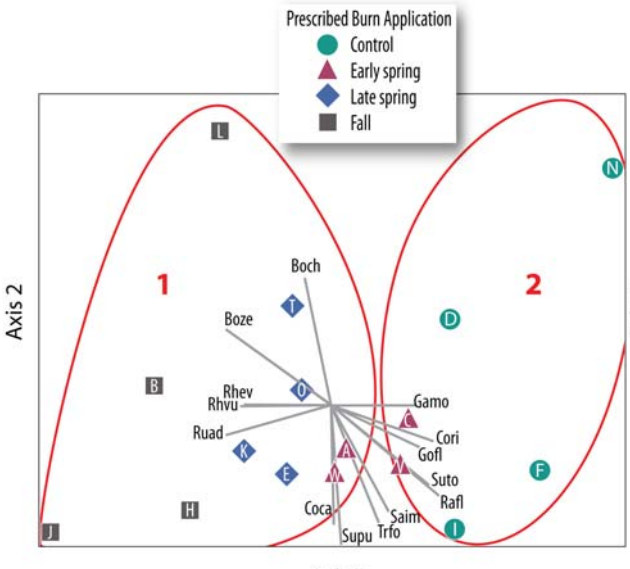

Figure 4.1. Ordination of species collections for spring collection plots, with habitat attribute overlay.

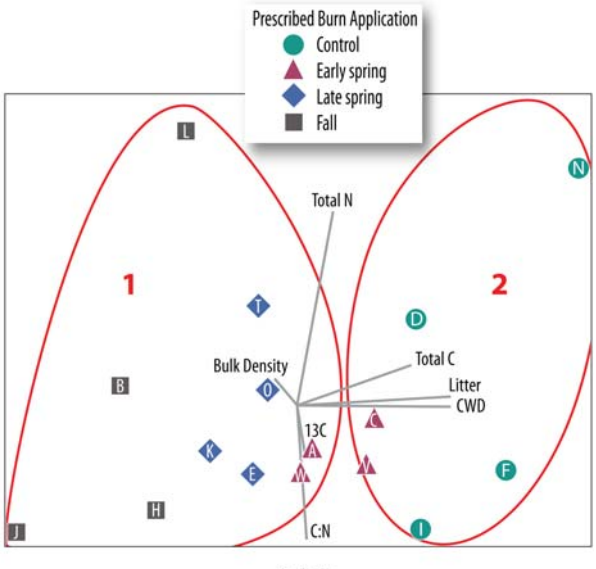

Figure 4.2. Ordination of species collections for spring collection plots, with species collection overlay.

Group 1 contained all fall burn and late spring burn plots, and two of the four early spring burn plots (plots A and W). This group had lower levels of fuels and total C, and somewhat higher levels of soil bulk density. These plots were widely distributed along axis 2, indicating a spectrum of C:N ratios. *Boletus chrysenteron* Bull. and *B. zelleri* were collected on plots with higher total N and lower C:N ratios in this group (plots B, L, and T); *Rhizopogon vulgaris* and *Russula adusta* (Pers.) Fr. were collected on plots with the lower total N and higher C:N plots (plots E, H, J, and K). The two early spring burn treatment plots (plots A and W) have the highest C:N ratios and CWD levels in this group and appear to support many taxa found in the group 2, but with the notable absence of *Cortinarius rigidus* (Scop.) Fr.

Group 2 contained all of the control plots and two of the four early spring burn plots (plots C and V). All of these plots had above mean levels of fuels, and all except plots D and N had above mean C:N ratios. Although plots D and N had above mean levels of total C, these were offset by high levels of total N, resulting in their lower C:N ratios. *Gomphus floccosus* (Schwein.) Singer and *Cortinarius rigidus* associated with higher CWD levels,

while *Cortinarius caperatus* (Pers.:Fr.) Fr., *Sarcodon imbricatus* (L.) P. Karst., *Suillus punctatipes* Singer, and *Tricholoma focale* (Fr.) Ricken were more closely associated with higher C:N ratios.

Ordination of species collections for plots sampled in the fall

The ordination of species collected on the 16 plots surveyed in the fall is presented in Figs. 6.1 and 6.2. Cluster analysis identified three groups of plots within this ordination. Most of the plots fell along a continuum from higher bulk density and pH on the left to higher C:N ratios and fuels on the right.

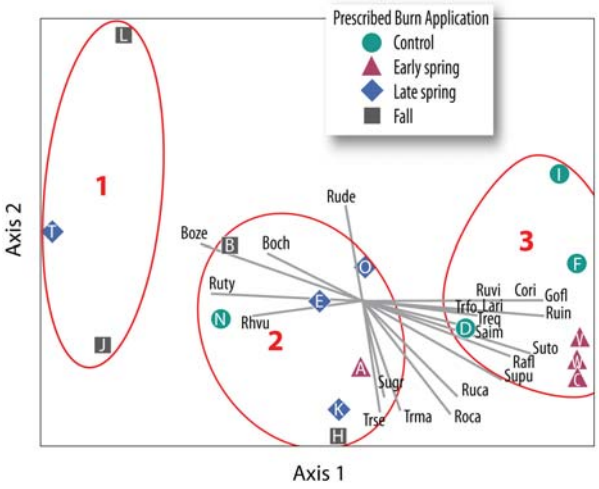

Figure 4.1. Ordination of species collections for spring collection plots, with habitat attribute overlay.

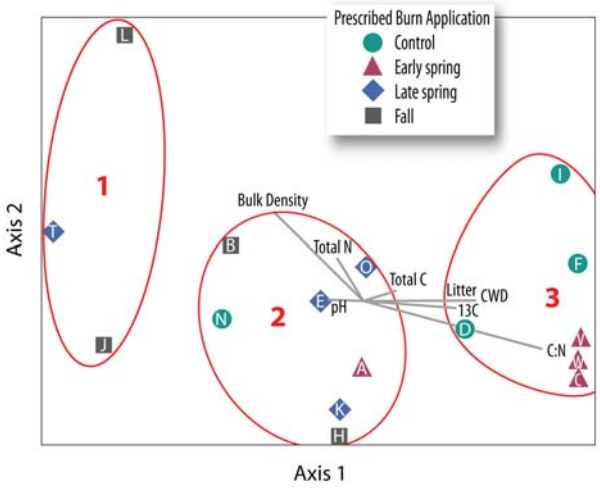

Figure 4.2. Ordination of species collections for spring collection plots, with species collection overlay.

Group 1 was composed of two fall burn plots and one late spring burn plot. These three plots had above mean soil bulk densities and below mean C:N ratios and fuels. *Boletus zelleri* was collected on all of these plots, and *B. chrysenteron* on two of them. *Boletus zelleri* was also collected on plots B, E, and O in group 2.

Group 2 contains the remaining fall and late spring burn treatment plots, as well as one early spring burn plot and two control plots. Except for plot N (the only control plot in the

group), all plots in this group had below mean levels of total C and total N. Plots A, H, and K were unified by their lower bulk density. Plot N had the lowest C:N ratio of any control plot, and the highest level of total N and fuel levels of all plots.

Groups 1 and 2 combined produced all collections of *Boletus zelleri*, as well as 17 of the 18 *Rhizopogon* collections (*R. evadens* A.H. Smith*, R. salebrosus* A.H. Smith, and *R. vulgaris*). They were also unified by the taxa absent— none of plots in these two groups produced *Cortinarius rigidus* or *Russula integra* (L.) Fr., and only plot E produced *Gomphus floccosus.*

Group 3 includes three early spring burn plots and three control plots. The members of this group all had above mean levels of CWD and below mean mineral soil bulk density. All these plots produced *Gomphus floccosus*, four produced *Russula integra*, three produced *Cortinarius rigidus* and three *Russula albonigra* (Krombh.) Fr.. The absence of any of these taxa and the presence of *Boletus chrysenteron* in control plot N is why it ordinated to the left of center on axis one in species space.

Fungal mats collected

150 fungal mat collections were made, and DNA was successfully amplified and sequenced from 110 of them, representing 28 taxonomic units (Appendix G). We were able to assign names at the species level to 19 taxa, and at the species complex level to 9 taxa. Members of the 4 most common genera (*Gautieria*, *Piloderma, Ramaria,* and *Rhizopogon*) comprised 73% of all collections. Ten taxa were collected only once.

Effect of burn treatment and soil attributes on fungal mat abundance

Sixty seven total (identified and unidentified) soil fungi collections were made in the 8 control plots ($\bar{x}$ = 8.4), 74 in the 8 spring burn plots ($\bar{x}$ = 9.3), and 9 in the 8 fall burn plots ($\bar{x}$ = 1.3). The habitat attributes most correlated with the most abundant soil fungi were C:N ratio, CWD, FWD, and litter mass. These attributes were largely intercorrelated and showed significant response to burn treatment (Appendices C and D).

Linear regression indicated that abundance of mat-forming taxa was positively correlated with soil C:N ratios and the mass fine woody debris and needle litter (Appendix H). Abundance was negatively correlated with soil pH. Significant interactions were detected between all of the significant variables; those between soil C:N ratios, fine woody debris, and litter mass had the highest adjusted R^2 values.

Ten taxa were collected on at least three plots, and logistic regression correlations with habitat attributes are displayed in Appendix I. *Gautieria monticola* mats were positively correlated with total C and C:N ratios. *Lepiota magnispora* Murrill was positively correlated with FWD and litter mass. *Piloderma fallax* (Lib.) Stalpers was positively correlated with C:N ratio, CWD levels, FWD levels, and litter levels, and negatively correlated with mineral soil bulk density and δ^{13}C depletion. *Piloderma sp* was also positively correlated with C:N ratio and negatively correlated δ^{13}C depletion; when all *Piloderma* were combined the correlations were identical to those of *P. fallax*. *Ramaria stricta* (Pers.) Quél. was positively correlated with C:N ratio, and when all of the species in the *R. stricta* complex were combined they were positively correlated with δ^{15}N, C:N ratio, and soil pH.

Discussion

We monitored mycorrhizal fungus sporocarp production over a period of three years, but several studies have suggested that as much as seven years of continuous monitoring may be required to document most (but probably not all) of the fungal fruiting species at a site (Luoma and Frenkel, 1991; Arnolds, 1992; Vogt et al., 1992). Although there is no doubt there are taxa at this site we did not observe due to the short duration of the project, we excluded rarer fungi from statistical analysis so their omission is unlikely to have substantially affected the results.

Many mycorrhizal fungus species typically fruit in a patchy pattern which can appear to favor one set of habitat attributes over another, when in fact they are just randomly fruiting in one place and not another (Hosford et al., 1997; Jonsson et al., 1999; Pilz and Molina, 2002). Nonetheless, the patterns we observed between certain soil properties

(most notably C:N ratio) and mycorrhizal fungus fruiting patterns were remarkably consistent, irrespective of burn treatment or location within the study site.

Because our project began after prescribed burns were applied, we do not have any pre-treatment data. The control plots were not uniform in their soil attributes or fungal fruiting patterns across the study site, and while this provided an opportunity to separate burn treatment effects from soil attribute effects we can only infer what the soil attributes were in the burned plots prior to treatment.

In this discussion and in the graphics presented, plots are represented as solid units with uniform characteristics. This is obviously a simplification, and there was often substantial variability of habitat attributes within a plot. Because the study was designed to examine burn treatment effects, the soil cores were collected randomly throughout each plot and not in a pattern designed to detect pre-existing soil gradients. Despite these limitations, the effects of the fall burn treatment had enough influence on soil attributes and fuels to produce a statistically significant signal. More subtle influences on soil attributes by the spring burn treatments may have occurred but were not detected.

Treatment effects on habitat attributes

Mineral soil bulk density might be expected to increase with fire intensity as a function of increased consumption of organic soil components. Here the bulk density was lowest in the spring burn plots (Appendix B) and was not correlated with total C (Appendix C). This pattern is difficult to explain until viewed spatially. Figure 7 depicts the treatment units by their bulk density, and shows that the units with the highest soil bulk densities were at the lower (eastern) end of the project area and concentrated adjacent to Highway 62. An artifact of random treatment assignment was that all of the early spring burn treatment units were placed in the western (least dense) end of the project area (Fig. 1), and half of the fall burn treatments were located in the densest end of the geographic gradient. As the control plots were not significantly different in their bulk density from the late spring

and fall burn treatment units (Appendix C), the observed patterns of mineral soil bulk density were likely an underlying pattern at the site and not strongly influenced by the burn treatments.

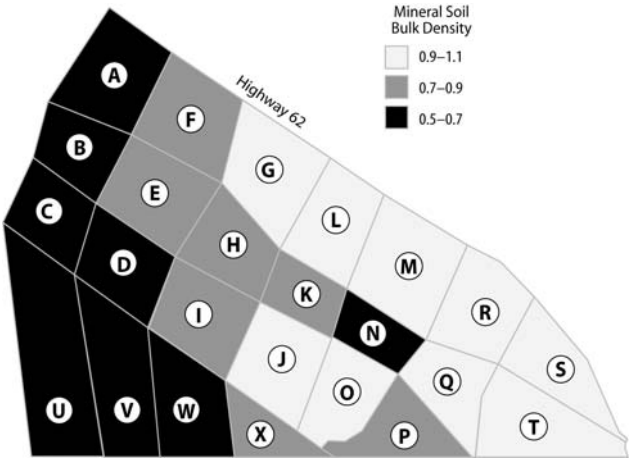

Figure 7. Map of mineral soil bulk density.

Monleon et al. (1997) found that levels of total C increased four months post fire, had a net decrease 5 yrs post-fire, and returned to control levels 12 yrs post-fire. Our sampling of total C thus provides only a snapshot of a temporally dynamic element. We found that while total C concentrations correlated with higher levels of surface fuels, two fall burn plots with below mean surface fuel levels had above mean total C (plots L and R). The five plots that had the highest total C all were controls, and the five plots that had the highest total N also had above mean levels of total C. $\delta^{13}C$ depletion in the mineral soil (Fig. 8) ranged from -24.82 to -26.65‰ and was not correlated with any burn treatment (Appendix C), but had a spatial pattern similar to that of soil bulk density (Fig. 7).

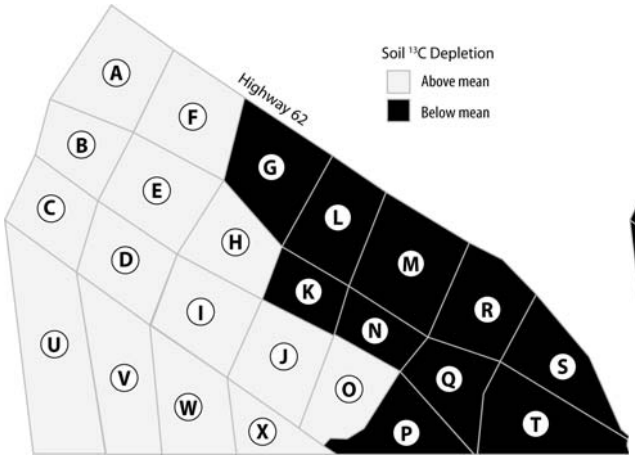

Figure 8. Map of $\delta^{13}C$ depletion.

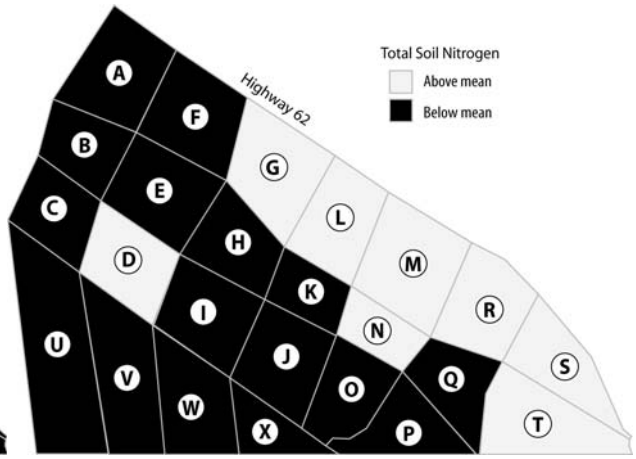

Figure 9. Map of soil N distribution.

Soil organic N normally decreases immediately post-fire due to volatilization and transformation into inorganic forms, particularly ammonium (NH_4^+). Ammonium can be held in the soil by cationic adsorption (Mroz et al., 1980), but some of it is biologically mineralized into more mobile forms such as nitrate (NO_3^-) (Covington and Sackett, 1992). This can result in a pulse of available inorganic nitrogen immediately after a fire.

Monleon et al. (1997) found that the initial pulse of inorganic N had dissipated by the end of the second growing season in a *P. ponderosa* system in central Oregon. Grogan et al. (2000) observed a similar pattern in a *Pinus muricata* D. Don system in coastal California. Our soil samples were taken after the second growing season post-treatment and presumably do not reflect this initial pulse of N. Indeed, levels of total N (organic plus inorganic) did not differ significantly between treatments. As with soil bulk density and $\delta^{13}C$ depletion, higher levels of N generally occurred in plots along the highway at the eastern end of the project area (Fig. 9). Snowbrush (*Ceanothus velutinus* Dougl.) can fix substantial amounts of N (Binkley et al., 1982) but at this site *C. velutinus* was restricted to the forest edge immediately adjacent to the highway, and was not found in the plot interiors where soil sampling occurred.

δ^{15}N enrichment levels did not correlate with any treatment or other habitat attribute variables and did not have any discernable spatial pattern. Notably, δ^{15}N enrichment did not correlate with total N, which might have provided insights to the spatial pattern of total N distribution (Fig. 9).

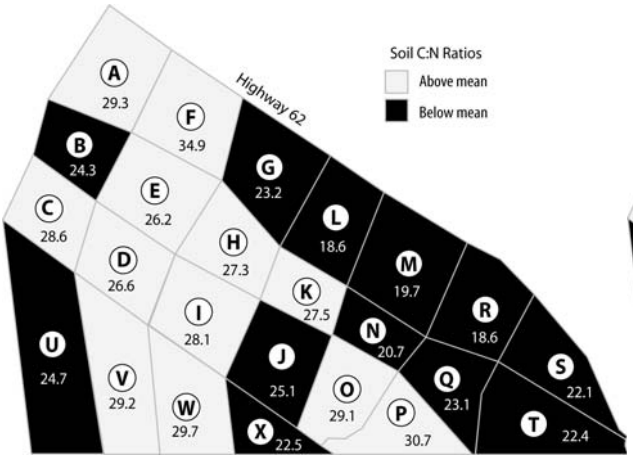

Figure 10. Map of C:N ratios.

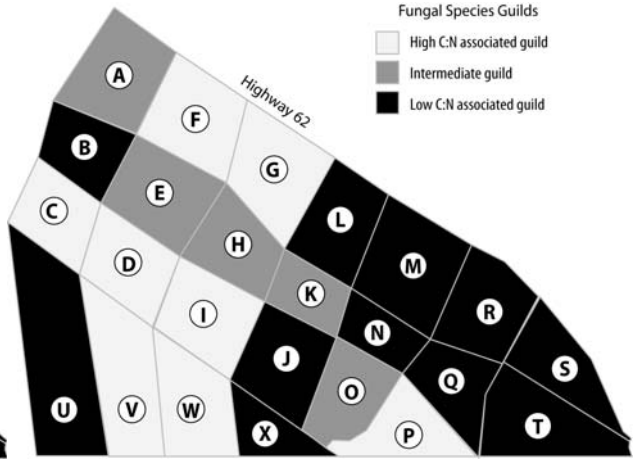

Figure 11. Map of mycorrhizal fungi guild indicator species fruiting patterns.

As with soil bulk density, total N, and δ^{13}C depletion, C:N ratios also had spatial pattern with lower values concentrated at the eastern end of the study area (Fig. 10). This may have biased the correlation between C:N ratio and fall burn treatments, however below mean C:N ratios were also measured on fall burn treatments elsewhere in the study area (plots B, J, and X).

Fuels responded significantly to burn treatments (Table 3), correlating positively with total C and negatively with soil pH. Total C was not correlated with any burn treatment, and soil pH differed only between non-burned controls and fall burns.

Correlations between habitat attributes

Above mean levels of δ^{13}C depletion, δ^{15}N enrichment, C:N ratios, and fuels tended to occur as a suite of characteristics, mostly on control and early spring burn treatments. In

contrast, higher soil bulk density, total N, and pH occurred on a separate suite of plots, including most of the fall burn plots but also three control plots. Most of the late spring burn plots had habitat attributes intermediate between these groups, except plot T (at the east end of the study area).

The association of fruiting patterns by groups of fungal taxa with discrete suites of habitat attributes in both spring and fall suggests the existence of fungal indicator species 'guilds'. Because these guilds correlate more closely with suites of habitat attributes than burn treatments, and most consistently with C:N ratios, we will refer to them hereafter as the 'high C:N guild' and the 'low C:N guild'. It is noteworthy that only about half of the species collected have these associations at $p < 0.10$; many taxa did not respond significantly to any habitat attribute or burn treatment.

Total C did not conform to these groupings; instead it correlated with fuels and total N, although no fuel was correlated with total N (Table 4). Total C was also uncorrelated with C:N ratios, indicating that the C:N ratios across this site are primarily a function of total N. Bulk density was negatively correlated with the C:N ratio (Table 5, Fig. 7). Plots G (control), O (late spring burn), and P (control) had above mean bulk density measurements but produced high C:N (plots G and P) or intermediate (plot O) fungal guilds. Plots B, N, U, and X had below mean bulk density measurements, but produced the low C:N fungal guilds. Thus the fungal fruiting patterns here correlate more closely with C:N ratios than bulk density.

Coarse woody debris levels were positively correlated with C:N ratios, and all of the high C:N fungal guild producing plots had above mean CWD levels. However, four of the plots producing the low C:N fungal guild (plots N, S, T, and U) had above mean CWD levels, and three of them (N, S, and U) also had above mean FWD and litter levels.

Spring collections: comparison of collections and habitat attributes ordinations

Most of the plots sampled in the spring were consistent in their groupings between the habitat attribute ordination (Fig. 3.1) and the collections ordination (Fig. 4.1). With the

exception of plots T (late spring) and U (control), the plots in groups 3 and 4 in the habitat attribute ordination combined into group 3 in the collections ordination. Plot T had the highest total N and lowest C:N ratio and litter levels of the group 4 in the habitat attribute ordination, and joined group 1 in the collections ordination.

The species vector overlays for both species space and habitat attribute space (Figs 3.2 and 4.2) agree that there are two distinct guilds of fungi in the spring collecting season. The vector of *Amanita pantherina*, *Geopyxis vulcanalis*, *Morchella angusticeps,* and *Sarcosphaera coronaria* associated with plots typified by higher pH and lower C:N ratios and fuel levels, which were primarily late spring and fall burn treatments. The opposing vector of *Elaphomyces granulatus, Gautieria monticola, Hysterangium separabile, Hydnotrya variiformis, Melanogaster tuberiformis,* and *Ramaria rasilispora* associated with plots of lower pH and higher C:N ratios and fuel levels; but not consistently with the control treatments. Many hypogeous taxa were not collected on any fall burn treatment.

The two control plots that grouped together (plots G and S) in habitat attribute space (group 2, Fig. 3.1) assumed quite different positions in species space (Fig. 4.1); plot S grouped with the plots typified by the presence of *Amanita pantherina* and *Sarcosphaera coronaria,* and the absence of *Elaphomyces granulatus, Gautieria monticola, Hysterangium separabile, Hydnotrya variiformis*, and *Ramaria flavobrunnescens* var. *aromatica*. Plot G was exactly the opposite, lacking *Amanita pantherina* and *Sarcosphaera coronaria* but having the others. Plots G and S were similar in their habitat attributes (Fig. 3.1) except that plot G had a lower soil bulk density.

Plots P and U (both controls) also grouped together in habitat attribute space, but separated in species space (Fig. 4.1), with plot P among the plots with higher C:N ratios and fuels, and plot U grouping among the plots with higher bulk density and pH. Plot U produced *Amanita pantherina, Geopyxis vulcanalis,* and *Sarcosphaera coronaria,* but not *Elaphomyces granulatus, Hydnotrya variiformis*, *Ramaria rasilispora*, or *Rhizopogon*

vulgaris, and plot P was opposite, lacking *Amanita pantherina, Geopyxis vulcanalis,* and *Sarcosphaera coronaria* but producing all the others. These two plots had similar fuel levels, but plot U had a lower bulk density and C:N ratio.

The relationship between plots T and K (both late spring burn plots) also is interesting. In the habitat attribute ordination (Fig. 3.1), they both fell on the left half of axis 1 with plot K somewhat more so than plot T. In both the spring and fall collection ordinations (Figs 4.1 and 6.1) plot K shifted to the right side of the ordination with the high C:N species guilds, and plot T moved in the other direction with the low C:N species guilds. Plot T had higher soil bulk density, total N, and CWD than plot K, and plot K had a higher C:N ratio.

The suites of attributes indicated by these groupings are consistent with what we might expect to separate burned from non-burned sites, however these fungi were collected over a continuum of burn intensities from non-burned controls to fall burns, suggesting the relationships are not as simple as "burned" vs. "not burned." For example, *Gautieria monticola*, correlated with higher C:N ratios and FWD levels (Table 5.1), was collected on four control plots but also on five spring burn treatment plots. Conversely, *Sarcosphaera coronaria*, negatively associated with FWD, was collected on two control plots as well as nine burned plots. Only *Morchella angusticeps* consistently fruited on burned plots to the exclusion of control plots; it was the only taxa more closely correlated with burn treatments than with C:N ratio.

Fall collections: comparison of collections and habitat attributes ordinations

In habitat attribute space (Fig. 5.2), species vector overlays again indicated two major fungal guilds in the fall collection season. A vector of *Boletus chrysenteron, B. zelleri, Rhizopogon evadens, R. vulgaris*, and *Russula adusta* associated with higher bulk density, lower C:N ratios, and lower fuel levels; an opposing vector of *Cortinarius rigidus, Gautieria monticola, Gomphus floccosus, Ramaria flavobrunnescens var. aromatica, Suillus punctatipes,* and *S. tomentosus* associated with higher C:N ratios and fuel levels.

In species collection space, species vector overlays (Fig. 6.2) generally agreed with those of the habitat attribute ordination (Fig. 5.2). The two main vectors in species collection space again were markedly opposed to each other, and the members of the vectors were largely the same taxa as in habitat attribute space, with the addition of *Russula integra* as a high C:N indicator. This ordination also suggested a third group: plots A (early spring burn), H (fall burn), and K (late spring burn) that may represent an intermediate set of soil attributes (Fig. 6.1). These plots tended to group with the other more disturbed plots in habitat attribute space due to their moderate to low fuel levels, but none of them produced *Boletus chrysenteron* or *B. zelleri*, and all three produced *Suillus punctatipes* and *S. tomentosus*.

Plots N and W are informative to the relationship between C:N ratios, fuel levels, and fungal guilds. Plot N is a control plot that ordinated to the right in habitat attribute space (Fig. 5.1) due to its high fuel levels, but produced indicator species consistent with its low C:N ratio (Fig. 6.2). Conversely, plot W ordinated with the late spring and fall burn plots in habitat attribute space due to its lower fuels levels, but produced indicator species consistent with its high C:N ratio. This suggests that the C:N ratio has more influence on fungal fruiting patterns than fuel levels.

Categorizing plots by species guilds

The plots can be grouped into three categories based on the indicator species they supported (Fig. 11): The low C:N guild in plots B, J, L, M, N, Q, R, S, T, U, and X; an intermediate guild in plots A, E, H, K, and O (inconsistent or without either high or low C:N indicator taxa); and the high C:N guild in plots C, D, F, G, I, P, V, and W. Four of the intermediate plots (A, E, K, and O) produced the high C:N guild in the spring (Fig. 4.2) and low C:N or intermediate guild in the fall (Fig. 5.2). Plot H was only sampled in the fall and did not produce any C:N ratio indicator taxa.

Of the late spring burn plots, only plot T produced a clearly low C:N guild both spring and fall, while the other late spring burn plots (E, K, and O) were intermediate. Three of the four early spring burn treatment plots (plots C, V, and W) produced high C:N-associated

guilds and the fourth (plot A) produced the intermediate guild. In total, more spring burn plots produced the high C:N guild than did control plots.

It is clear that there is some effect from burn prescription treatment; no fall burn plots produced the high C:N fungal guilds. However, three of the control plots produced the low C:N fungal guild. All but one of the plots (plot G; control) having above mean C:N ratios produced the high C:N guild. Plot G is spatially transitional between high and low C:N plots, and the apparent inconsistency between its C:N ratio and the fungal guild produced may be an artifact of the locations at which soil cores were taken within the plot. All of the intermediate fungal guild-producing plots also had above mean C:N ratios. Only one of the low C:N guild producing plots had an above mean C:N ratio (plot J, a fall burn). The three control plots (plots S, N, and U) that produced the low C:N guild all had below mean C:N ratios. The correlation between the C:N ratio (Fig. 10) and fungal guilds (Fig. 11) is much closer than that of burn treatment (Fig. 1) and fungal guild, and explains the occurrence of low C:N fungal guilds in control plots N, S, and U.

The seven plots at the east end of the study area all had low C:N ratios and produced low C:N guilds, irrespective of burn treatment. One clue to the effect of the fall burn treatment on the plots is to compare the C:N ratios from control plots G and S to those of proximate fall burn plots L, M, and R.

The C:N ratios of control plots G and S were 22.1 and 23.2 respectively, and fall burn plots L, M, and R ranged from 18.6 to 19.7. If we assume that the C:N ratio of the control plots did not change appreciably from before the burn treatments, then we can estimate that the fall burn treatment itself reduced the C:N ratio by 2.4 to 4.6 points in plots L, M, and R. By this estimate, it is quite possible that these plots were producing the low C:N fungal guild even before the burn prescriptions were applied. The contrast in C:N ratio between fall burn plots B, J, and X and their neighboring control and spring burn plots is also striking (Fig. 10).

Possible explanations for the spatial pattern of bulk density, total N, $\delta^{13}C$ depletion, and C:N ratios include the adjacent Highway 62, historic human use, or natural causes. Isotopic patterns do not support the effect of motor vehicle traffic as a source of C or N deposition. Both petrocarbon deposition (Andrews et al., 1999; Wilkes et al., 2000) and N fertilization (Ehleringer et al., 1993; Temple et al., 2005) would tend to increase $\delta^{13}C$ depletion, and at our site the low C:N plots are less $\delta^{13}C$ depleted.

From about 1925 to 1932 there was a park entry station and maintenance camp in the vicinity of plots Q, R, S, and T (pers comm., S. Mark). All of these plots had above mean bulk density, and plot S (a control) had the highest bulk density of the entire project area. It is possible that this area is still responding to an intense and prolonged disturbance from 75 years ago, either from the camp itself or from related highway construction activities.

Although many of the plots with the lowest C:N ratios are adjacent to the highway, the patterns of $\delta^{13}C$, total N, and C:N ratio across the landscape may be the consequence of some other unknown historic event. Plot U is a spatial anomaly, but we have no data on soil attributes adjacent to this plot outside the study area, and it may be at the edge of a larger pattern of soil attributes across the landscape. It is bounded within the study site by a group of five high C:N fungal guild producing plots, and although three of these five were spring burn treatment plots, they all had higher C:N ratios than the control plot U.

All five of the plots producing fungi intermediate between the high and low C:N guilds were in a line between plot O and plot A (Fig. 11). This line marked the transition from high C:N (to the west) to low C:N soils (to the east). Four of these five plots were spring burn treatments; one (plot H) was a fall burn treatment. Plot H was the only fall burn plot that did not clearly produce a low C:N fungal guild; it had the highest C:N ratio and CWD levels of the fall burn treatment plots.

Fall burn treatment plots B, J, and X all had below mean C:N ratios and produced the low C:N fungal guild, but in their case the lower C:N ratios were due to lower levels of total C,

rather than higher levels of total N. These plots were surrounded by control and spring burn treatment plots that maintained higher C:N ratios and produced high C:N or intermediate fungal guilds, suggesting that the fall burn treatment changed the soil C:N ratio enough to shift mycorrhizal fungus fruiting patterns. The fall burns may have reduced total C but the significance is marginal ($p = 0.123$).

All fall-burned plots produced low C:N guilds except plot H. Plot H was spatially associated with the group of plots with low total N levels (Fig. 11) and likely had a rather high C:N ratio before the treatment was applied. The burn treatment probably reduced the C:N ratio enough to produce the intermediate guild (perhaps by suppressing fruiting of high C:N guild species), but not enough to produce the low C:N guild.

Of all the early and late spring burn plots, only plot T produced the low C:N fungal guild. It was among the band of low C:N ratio plots along the highway, and also possibly produced the low C:N fungal guild before the burn treatment was applied.

One early spring burn plot and three late spring burn plots produced the intermediate fungal guild. As with plot H, all these plots were affected to some degree by the burn treatments, but not enough to drive down the C:N ratio sufficient to induce the fruiting of the low C:N fungal guild indicators. All control plots produced high C:N guilds except the three plots spatially predisposed to lower C:N ratios (plots N, S, and U).

It is unknown whether the fruiting patterns we observed are a consequence of spatial patterns of mycorrhizal thalli across the landscape, fruiting responses to environmental conditions, or a combination thereof. Sporocarp morphogenesis in saprobic fungi can be very sensitive to substrate chemistry (Moore, 1998), but very little is known about sporocarp initiation factors in mycorrhizal fungi. The C:N ratio might correlate with other unknown factors, such as soil water potential. Mycorrhizal fungi presumably have steady access to carbon, but relative levels of organic and inorganic forms of nitrogen may be influential.

Mat-forming fungi response to prescribed burn treatment

The distribution of mat-forming taxa limited our ability to correlate species occurrence with habitat variables to the more commonly occurring species. Additionally, habitat data was collected on a plot-level, and did not account for microhabitat. For example, while many collections were made in burned plots with patchy distributions of needle litter, the vast majority of collections were made in areas where the fire had left patches of unburned litter. It was highly apparent in the field that where there was sparse needle litter the likelihood of finding fungal mats decreased substantially.

Conclusions

For fungal sporocarp productivity, the plots were evaluated from three independent perspectives: by treatment, by habitat attributes, and by species guild. There was substantial agreement between these patterns, and the single most significant element corresponding to fungal fruiting patterns was the C:N ratio. With the exception of plot G, all plots with a C:N ratio below 26 produced a distinct guild of indicator fungal sporocarps. Most plots with a C:N ratio above 26 produced a distinctly different guild of indicator fungal sporocarps except those spatially transitional that produced an intermediate guild; these were influenced secondarily by fuel levels. C:N ratios were negatively correlated with mineral soil bulk density and total N, and positively correlated with $\delta^{13}C$ depletion.

The timing and consequent intensity of prescribed burn treatments can influence fungal communities by their effects on soil attributes. However, in this study the effects of the different treatments served more as adjustments to the pre-existing soil attributes rather than as primary drivers. The fall burn treatments were effective at pushing a plot toward production of the low C:N guild indicator species. Plots B, J, Q, and X were probably induced to switch fruiting guilds as a result of the treatment, and plot H probably responded with a shift from the high C:N guild to the intermediate guild. In no plot or treatment was mycorrhizal fungal fruiting suppressed entirely.

The abundance of fungal mats is highly correlated with needle litter mass, and where prescribed fire had removed the litter layer no mats were detected. Wildfire

chronosequence sites elsewhere at Crater Lake National Park indicate that mats may take in excess of 15 years to re-colonize after a sever fire event (M. Trappe, unpublished data).

We monitored mycorrhizal fungal fruiting and mat-forming patterns, not the mycorrhizal community on the root tips, and the fruiting patterns we observed may or may not be reflected in the rhizosphere. This site provides an opportunity to study relationships between above- and belowground interactions and fungal succession. The fact that it is in a National Park further increases the value of the project area for long-term research, due to its protection from activities that might confound future studies.

We have provided only a snapshot of the responses of mycorrhizal fungal fruiting patterns to prescribed burns and to pre-treatment habitat conditions. Having identified the species members of fungal guilds in each of these plots and their relationship to soil attributes and prescribed burn treatments, the logical follow-up is to continue monitoring this site over the ensuing years.

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Appendix A. Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

			Prescribed burn treatment				
Abbr.	Fungal species	Season collected	Control	Early spring	Late spring	Fall	Total
Altr	*Alpova trappei*	S	1	3	1	0	5
Ammu	*Amanita muscaria*	S	3	4	2	1	10
Ampa	*Amanita pantherina*	S/F	2	0	2	2	6
Bosu	*Boletopsis subsquamosa*	F	3	1	3	1	8
Boch	*Boletus chrysenteron*	F	1	1	1	2	5
Boze	*Boletus zelleri*	F	0	0	3	3	6
Casu	*Cantharellus subalbidus*	F	5	7	6	4	22
Coca	*Cortinarius caperatus*	F	1	5	2	2	10
Cocl	*Cortinarius claricolor*	F	2	3	2	2	9
Cori	*Cortinarius rigidus*	F	3	1	0	0	4
Cova	*Cortinarius variosimilis*	F	1	2	2	0	5
Elgr	*Elaphomyces granulatus*	S	2	0	1	1	4
Gasu	*Gastroboletus subalpinus*	F	1	1	2	0	4
Gamo	*Gautieria monticola*	S/F	4	3	2	0	9
Gevu	*Geopyxis vulcanalis*	S	1	3	1	4	9
Gofl	*Gomphus floccosus*	F	6	3	2	0	11
Hyva	*Hydnotrya variiformis*	S	2	1	2	0	5
Hyco	*Hysterangium separabile*	S/F	1	4	2	0	7
Inas	*Inocybe assimilata*	F	1	1	2	1	5
Lala	*Laccaria laccata*	F	2	3	2	3	10
Laka	*Lactarius kauffmanii*	F	1	0	1	1	3
Lari	*Lactarius riparius*	F	1	2	0	0	3
Laru	*Lactarius rufus*	F	3	0	3	0	6
Lasc	*Lactarius scrobiculatus*	F	3	2	5	3	13
Lege	*Leucopaxillus gentianeus*	F	2	1	1	0	4
Metu	*Melanogaster tuberiformis*	S/F	3	1	4	2	10
Moan	*Morchella angusticeps*	S/F	0	4	3	6	13
Raca	*Ramaria cartilaginea*	F	3	2	3	1	9

Appendix A (cont.). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

			Prescribed burn treatment				
Abbr.	Fungal species	Season collected	Control	Early spring	Late spring	Fall	Total
Rafl	*Ramaria flavobrunnescens v. aromatica*	S/F	8	7	9	3	27
Rara	*Ramaria rasilispora*	S	1	2	3	0	6
Rhev	*Rhizopogon evadens*	S/F	1	1	2	2	6
Rhpe	*Rhizopogon pedicellus*	S	0	1	1	1	3
Rhsa	*Rhizopogon salebrosus*	S/F	1	3	3	3	10
Rhvu	*Rhizopogon vulgaris*	S/F	1	3	3	2	9
Ruad	*Russula adusta*	F	0	2	1	3	6
Rual	*Russula albonigra*	F	3	1	0	0	4
Ruaz	*Russula azurea*	F	5	6	5	3	19
Rubrac	*Russula brevipes v. acrior*	F	3	0	1	1	5
Rubrbr	*Russula brevipes v. brevipes*	F	1	1	1	0	3
Ruca	*Russula cascadensis*	F	0	3	2	1	6
Rucl	*Russula claroflava*	F	2	3	3	3	11
Rude	*Russula densifolia*	F	2	1	1	1	5
Ruex	*Russula exalbicans*	F	5	1	0	1	7
Ruin	*Russula integra*	F	2	3	0	0	5
Ruty	*Russula tyrrhenica*	F	6	4	7	7	24
Ruvi	*Russula vinosa*	F	0	3	1	0	4
Saim	*Sarcodon imbricatus*	F	2	2	1	1	6
Saco	*Sarcosphaera coronaria*	S	2	2	3	4	11
Sugr	*Suillus granulatus*	F	1	1	2	1	5
Supu	*Suillus punctatipes*	F	5	5	2	4	16
Suto	*Suillus tomentosus*	F	4	5	2	1	12
Trfl	*Tricholoma equestre*	F	1	2	1	0	4
Trfo	*Tricholoma focale*	F	4	4	3	2	13
Trma	*Tricholoma magnivelare*	F	0	2	1	0	3
Trsa	*Tricholoma saponaceum*	F	3	0	1	1	5
Trse	*Tricholoma sejunctum*	F	1	4	2	1	8

Appendix A (cont.). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

			Prescribed burn treatment				
Abbr.	Fungal species	Season collected	Control	Early spring	Late spring	Fall	Total
	Albatrellus ovinus	F	0	1	0	0	1
	Arcangeliella crassa	F	0	1	0	0	1
	Boletus calopus	S	0	0	0	1	1
	Chroogomphus pseudovinicolor	F	1	0	0	0	1
	Chroogomphus vinicolor	F	1	0	0	1	2
	Cortinarius albobrunnoides	S/F	1	1	1	0	3
	Cortinarius biformis	F	1	0	1	0	2
	Cortinarius brunneus	F	0	0	1	0	1
	Cortinarius calochrous	F	0	0	1	0	1
	Cortinarius cinnamomeoluteus	S	0	0	1	0	1
	Cortinarius clandestinus	F	1	0	0	0	1
	Cortinarius coeruleolutescens	F	0	0	1	0	1
	Cortinarius delibutus	F	0	1	0	0	1
	Cortinarius depressus	S	0	1	0	1	2
	Cortinarius montanus	F	0	1	1	0	2
	Cortinarius muscigenus	F	0	0	2	0	2
	Cortinarius orichalceus	F	2	0	0	0	2
	Cortinarius (Thaxterogaster) pinguis	F	1	0	0	0	1
	Cortinarius prasinus	F	0	0	1	0	1
	Cortinarius sebaceus	F	0	2	0	0	2
	Cortinarius semisanguineus	S	0	1	0	0	1
	Cortinarius subfoetidus	F	0	0	2	0	2
	Dermocybe phoenicea v. occidentalis	F	0	1	0	0	1
	Elaphomyces muricatus	S/F	2	1	0	0	3
	Endogone lactiflua	F	1	0	0	1	2
	Gastroboletus turbinatus	F	0	0	1	0	1
	Gautieria gautierioides	F	0	0	1	0	1
	Gautieria pterosperma nom. prov.	F	0	0	1	0	1

Appendix A (cont.). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

			Prescribed burn treatment				
Abbr.	Fungal species	Season collected	Control	Early spring	Late spring	Fall	Total
	Genea gardneri	S	1	1	0	0	2
	Geopora cooperi	S	1	0	0	0	1
	Gymnomyces abietis	F	0	0	0	1	1
	Hebeloma crustuliniforme	F	0	1	1	0	2
	Hydnum repandum	F	0	1	0	0	1
	Hygrophorus bakerensis	F	0	1	0	0	1
	Hygrophorus chrysodon	F	0	0	1	0	1
	Hygrophorus erubescens	F	0	1	1	0	2
	Hygrophorus subalpinus	S	0	0	1	0	1
	Hymenogaster sublilacinus	S	0	0	1	0	1
	Inocybe geophylla	F	1	0	0	0	1
	Inocybe lanatodisca	F	0	1	0	0	1
	Inocybe mixtilis	F	1	0	0	0	1
	Inocybe rimosa	F	0	0	1	0	1
	Laccaria bicolor	F	0	1	0	1	2
	Lactarius deliciosus	F	1	0	0	0	1
	Leucogaster citrinus	S	0	1	1	0	2
	Leucogaster rubescens	S/F	0	2	1	0	3
	Leucophleps magnata	S	0	1	0	0	1
	Melanogaster variegatus	F	1	0	0	0	1
	Nolanea verna	S	0	0	1	0	1
	Peziza repanda	S	0	0	0	2	2
	Ramaria amyloidea	F	0	2	0	0	2
	Ramaria botrytis v. aurantiramosa	S	0	0	0	1	1
	Ramaria formosa	F	0	1	0	0	1
	Ramaria longispora	S/F	1	1	0	1	3
	Ramaria magnipes	S/F	0	0	2	1	3
	Ramaria rubrievanescens	S	0	0	1	0	1

Appendix A (cont.). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

			Prescribed burn treatment				
Abbr.	Fungal species	Season collected	Control	Early spring	Late spring	Fall	Total
	Rhizopogon brunneiniger	F	0	0	1	0	1
	Rhizopogon abietis	F	0	0	0	1	1
	Rhizopogon atroviolaceus	S	0	1	0	0	1
	Rhizopogon ellenae	F	0	1	0	0	1
	Rhizopogon fuscorubens	F	0	1	0	0	1
	Rhizopogon occidentalis	F	0	1	0	1	2
	Rhizopogon ochraceorubens	F	0	0	1	0	1
	Rhizopogon roseolus	F	0	1	0	0	1
	Rhizopogon truncatus	S	0	1	0	0	1
	Russula heterophylla	F	0	1	0	0	1
	Russula viscida	F	1	0	0	0	1
	Russula paludosa	F	0	1	0	0	1
	Sarcodon rimosus	F	1	1	0	0	2
	Suillus albidipes	F	1	0	0	1	2
	Suillus brevipes	F	0	0	1	1	2
	Tricholoma intermedium	F	0	0	1	0	1
	Tricholoma mutabile	F	0	0	0	1	1
	Tricholoma pessundatum	F	0	0	1	0	1
	Tricholoma portentosum	F	0	0	1	1	2
	Tricholoma virgatum	F	0	0	0	1	1
	Total Collections		144	165	154	103	566
	Total Species		69	81	81	55	133

Appendix B. Mean values of forest floor and soil habitat attributes by prescribed burn treatment. Standard errors are in parentheses.

	Control	Early spring	Late spring	Fall	Overall
Bulk density (g cm^{-3})	0.779 (0.145)	0.665 (0.139)	0.856 (0.192)	0.866 (0.109)	0.802
Total C (%)	3.64 (0.99)	2.97 (0.97)	2.69 (0.79)	2.57 (0.72)	3.01
$\delta^{13}C$ (‰)	-25.72 (0.42)	-25.97 (0.45)	-25.27 (0.32)	-25.41 (0.34)	-25.58
Total N (%)	0.130 (0.049)	0.101 (0.031)	0.104 (0.028)	0.119 (0.036)	0.149
$\delta^{15}N$ (‰)	2.26 (0.62)	2.61 (0.64)	2.46 (0.66)	2.07 (0.61)	2.29
C:N ratio	26.35 (3.04)	29.18 (2.50)	26.29 (3.02)	22.39 (2.58)	25.5
CWD (Mg ha^{-1})	122.38 (82.09)	105.43 (56.68)	71.25 (60.36)	36.06 (45.99)	82.13
FWD (Mg ha^{-1})	53.49 (22.91)	42.28 (19.06)	38.06 (11.37)	30.87 (13.08)	41.51
Litter mass (Mg ha^{-1})	103.11 (34.40)	73.72 (27.87)	60.23 (15.92)	31.98 (12.70)	67.36
Soil pH	5.78 (0.28)	5.93 (0.46)	5.87 (0.32)	6.25 (0.26)	6.0

Appendix C. ANOVA p - values for differences between prescribed burn treatments.

Total collections	Control	Early spring	Late spring
Early spring	0.810		
Late spring	0.966	0.986	
Fall	0.221	**0.033**	**0.080**

Total species	Control	Early spring	Late spring
Early spring	0.444		
Late spring	0.444	0.999	
Fall	0.305	**0.007**	**0.007**

Bulk density	Control	Early spring	Late spring
Early spring	0.305		
Late spring	0.555	**0.040**	
Fall	0.630	**0.027**	0.998

Total C%	Control	Early spring	Late spring
Early spring	0.894		
Late spring	0.145	0.510	
Fall	0.123	0.578	0.996

δ^{13}C depletion	Control	Early spring	Late spring
Early spring	0.940		
Late spring	0.418	0.233	
Fall	0.449	0.245	0.997

Total N%	Control	Early spring	Late spring
Early spring	0.777		
Late spring	0.552	0.986	
Fall	0.992	0.628	0.403

δ^{15}N enrichment	Control	Early spring	Late spring
Early spring	0.728		
Late spring	0.928	0.977	
Fall	0.713	0.219	0.411

C:N ratio	Control	Early spring	Late spring
Early spring	0.664		
Late spring	0.970	0.472	
Fall	**0.007**	**0.001**	**0.036**

CWD	Control	Early spring	Late spring
Early spring	0.430		
Late spring	**0.001**	**0.060**	
Fall	**<0.001**	**0.001**	**0.020**

Appendix C (cont.). ANOVA p - values for differences between prescribed burn treatments.

FWD	Control	Early spring	Late spring
Early spring	**0.040**		
Late spring	**0.004**	0.790	
Fall	**0.001**	**0.040**	0.290

Litter mass	Control	Early spring	Late spring
Early spring	**0.100**		
Late spring	**0.070**	0.990	
Fall	**0.050**	0.970	0.990

Mineral soil pH	Control	Early spring	Late spring
Early spring	0.790		
Late spring	0.960	0.980	
Fall	**0.040**	0.350	0.190

Appendix D. Pearson's correlations between habitat attributes. A negative sign preceding the p - value indicates a reverse correlation; values significant at p < 0.10 are bolded.

	Total collections	Total species	Bulk density	Total C %	δ^{13}C depletion	Total N %	δ^{15}N enrichment	C:N ratio	CWD	FWD	Litter mass
Total species	**-0.009**										
Bulk density	**-0.007**	**-0.009**									
Total C %	0.555	0.794	-0.783								
δ^{13}C depletion	**-0.061**	**-0.074**	**-0.001**	0.488							
Total N %	-0.111	-0.112	**0.089**	**0.003**	**-0.037**						
δ^{15}N enrichment	0.357	0.457	-0.369	0.827	-0.818	-0.397					
C:N ratio	**0.004**	**0.007**	**-0.006**	-0.869	**0.001**	**-0.001**	0.201				
CWD	0.241	0.268	-0.213	**0.005**	**0.070**	0.662	0.494	**0.015**			
FWD	0.642	0.657	-0.353	**0.060**	0.678	0.352	0.603	0.132	**0.001**		
Litter mass	0.401	0.417	-0.183	**0.003**	0.185	0.234	0.779	0.102	**0.001**	**0.001**	
Mineral soil pH	-0.240	-0.297	0.487	-0.302	0.778	0.870	-0.319	-0.110	**-0.014**	**-0.011**	**-0.015**

Appendix E. Logistic regression p - values of habitat attributes on fungal taxa collected on at least 3 plots in the spring. A negative sign preceding the p - value indicates a reverse correlation; values significant at $p < 0.10$ are bolded.

Species	Bulk Density	Total C %	$\delta^{13}C$ depletion	Total N %	$\delta^{15}N$ enrich	C:N ratio	CWD	FWD	Litter mass	Mineral soil pH
Alpova trappei	-0.259	-0.871	0.685	0.306	0.349	0.175	0.150	0.621	0.529	**-0.099**
Amanitia muscaria	-0.197	0.459	**0.085**	-0.791	0.724	0.246	0.195	0.182	**0.059**	0.867
Amanita pantherina	0.128	-0.925	-0.295	0.349	-0.676	-0.191	-0.563	-0.483	-0.797	-0.993
Elaphomyces granulatus	0.580	-0.315	-0.705	0.212	-0.761	-0.174	-0.647	-0.601	-0.896	0.546
Gautieria monticola	-0.175	-0.430	0.249	0.412	0.174	**0.057**	0.120	**0.078**	0.109	-0.223
Geopyxis vulcanalis	-0.669	-0.660	0.918	0.794	0.401	-0.253	-0.336	-0.196	-0.138	0.165
Hysterangium separabile	-0.1812	0.234	0.771	-0.840	0.332	0.207	0.206	0.240	0.246	-0.122
Hydnotrya variiformis	0.976	0.942	-0.541	-0.529	0.638	0.245	0.168	0.107	0.272	**-0.086**
Melanogaster tuberiformis	-0.381	-0.163	-0.500	-0.141	0.949	0.214	0.363	0.185	0.647	-0.112
Morchella angusticeps	-0.707	0.840	0.684	0.854	-0.325	-0.476	-0.110	**-0.082**	**-0.043**	0.139
Ramaria flavobrunnescens var. aromatica	-0.718	0.131	-0.452	0.455	0.547	0.565	-0.445	0.794	0.811	-0.118
Ramaria rasilispora	-0.298	-0.338	0.928	-0.114	0.928	**0.044**	0.528	0.341	0.483	-0.267
Rhizopogon pedicellus	-0.766	0.780	-0.435	0.585	-0.373	-0.574	-0.305	-0.837	-0.567	-0.808
Rhizopogon salebrosus	-0.367	0.784	0.509	-0.424	-0.331	0.400	-0.698	-0.635	-0.635	-0.763
Rhizopogon vulgaris	-0.190	-0.588	**0.092**	-0.243	0.968	0.249	0.139	0.605	0.517	0.508
Sarcospaera coronaria	0.202	-0.708	0.894	0.582	-0.194	-0.233	-0.250	**-0.099**	-0.175	0.156

Appendix F. Logistic regression p - values of habitat attributes on fungal taxa collected on at least 3 plots in the fall. A negative sign preceding the p - value indicates a reverse correlation; values significant at p < 0.10 are bolded.

Species	Bulk Density	Total C %	$\delta^{13}C$ depletion	Total N %	$\delta^{15}N$ enrich	C:N ratio	CWD	FWD	Litter mass	Mineral soil pH
Boletopsis subsquamosa	-0.717	0.324	-0.714	-0.905	-0.737	0.467	0.875	0.198	0.245	0.731
Boletus chrysenteron	0.573	-0.620	-0.628	0.210	-0.278	**-0.084**	-0.654	0.318	0.785	**0.064**
Boletus zelleri	**0.068**	-0.154	**-0.072**	-0.878	0.686	**-0.085**	**-0.042**	**-0.091**	**-0.054**	0.547
Cantharellus subalbidus	0.601	-0.824	0.350	-0.166	0.495	0.587	0.335	0.901	0.353	-0.297
Cortinarius claricolor	-0.678	0.504	-0.399	0.125	0.665	-0.163	0.488	0.381	0.494	0.383
Cortinarius rigidus	-0.257	**0.052**	0.209	-0.933	0.947	0.152	**0.082**	0.116	**0.095**	-0.103
Cortinarius variosimilis	0.803	0.568	-0.860	-0.298	0.288	0.127	0.307	0.327	0.392	-0.490
Gastroboletus subalpinus	0.713	-0.379	0.406	-0.383	-0.381	0.364	0.595	0.488	0.832	**-0.082**
Gautieria monticola	-0.228	0.669	0.625	0.327	-0.129	0.895	**0.100**	0.154	0.117	-0.287
Gomphus floccosus	-0.105	0.197	0.239	0.445	0.412	**0.095**	**0.059**	**0.084**	0.115	-0.115
Inocybe assimilata	-0.818	-0.758	-0.282	0.540	0.702	-0.537	0.976	0.728	0.664	0.949
Laccaria laccata	-0.753	-0.995	-0.632	0.317	-0.177	-0.439	-0.911	0.611	0.567	0.436
Lactarius kauffmanii	0.577	-0.739	0.458	-0.331	0.814	0.255	0.631	-0.914	-0.604	-0.651
Lactarius riparius	0.448	0.302	0.211	-0.280	0.492	0.327	0.195	0.717	0.546	-0.380
Lactarius rufus	0.568	0.320	-0.649	0.773	-0.218	0.418	0.181	**0.089**	**0.082**	-0.654
Lactarius scrobiculatus	-0.962	-0.923	0.863	-0.137	-0.796	0.146	-0.336	-0.703	-0.533	0.731
Leucopaxillus gentianeus	0.743	-0.793	0.845	0.987	-0.558	-0.945	0.446	-0.524	0.795	-0.544
Melanogaster tuberiformis	0.959	0.622	0.592	-0.261	0.432	0.347	-0.222	-0.369	-0.477	0.960
Morchella angusticeps	**-0.019**	0.841	-0.177	0.576	0.722	0.981	0.637	0.138	0.235	**-0.053**
Ramaria cartilaginea	-0.218	0.215	0.727	-0.899	0.832	**0.076**	0.402	0.109	0.123	-0.224
Ramaria flavobrunnescens v. aromatica	0.905	-0.392	-0.241	-0.487	-0.818	-0.407	-0.156	-0.340	-0.236	-0.939
Rhizopogon salebrosus	0.717	-0.164	-0.173	-0.574	-0.161	-0.854	-0.279	0.800	-0.659	0.984
Rhizopogon vulgaris	0.573	**-0.086**	-0.262	-0.205	-0.793	-0.738	**-0.072**	-0.117	-0.113	0.522
Cortinarius caperatus	-0.109	-0.526	0.361	-0.266	**0.100**	0.174	-0.691	-0.287	-0.349	-0.601
Russula adusta	0.965	-0.145	0.709	-0.186	0.880	0.643	-0.125	-0.102	-0.108	0.678
Russula albonigra	-0.167	0.264	0.647	0.680	-0.816	0.613	0.252	0.167	0.184	**-0.088**
Russula azurea	-0.130	0.646	0.710	-0.452	0.197	0.169	0.230	0.347	0.161	-0.230
Russula brevipes v. acrior	-0.316	0.940	-0.894	-0.712	-0.222	0.846	0.885	0.571	0.839	-0.246

Appendix F (cont.). Logistic regression p - values of habitat attributes on fungal taxa collected on at least 3 plots in the fall. A negative sign preceding the p - value indicates a reverse correlation; values significant at p < 0.10 are bolded.

Species	Bulk Density	Total C %	$\delta^{13}C$ depletion	Total N %	$\delta^{15}N$ enrich	C:N ratio	CWD	FWD	Litter mass	Mineral soil pH
Russula brevipes v. brevipes	0.540	0.242	**0.081**	-0.403	0.531	0.249	0.147	0.835	0.461	0.163
Russula cascadensis	-0.771	-0.282	0.624	-0.267	0.594	0.176	-1.000	-0.668	-0.548	-0.964
Russula claroflava	0.443	-0.781	-0.471	0.672	0.437	-0.269	-0.471	-0.758	-0.692	0.278
Russula densifolia	0.489	-0.647	-0.554	0.673	-0.249	-0.479	-0.935	0.601	-0.957	-0.893
Russula exalbicans	**-0.099**	0.233	0.502	0.180	-0.609	-0.511	0.331	0.399	0.183	-0.466
Russula integra	-0.109	**0.089**	0.115	-0.625	0.126	0.127	**0.080**	0.201	0.197	0.359
Russula tyrrhenica	0.743	-0.198	-0.322	0.257	-0.544	-0.366	-0.193	-0.497	-0.473	0.216
Russula vinosa	-0.217	-0.450	-0.894	-0.432	0.177	0.324	0.430	0.332	0.688	-0.408
Sarcodon imbricatus	-0.439	-0.235	-0.442	0.768	**0.055**	0.107	0.687	0.296	-0.751	0.263
Suillus granulatus	-0.262	-0.579	0.498	-0.834	-0.263	0.719	-0.900	-0.478	0.593	-0.249
Suillus punctatipes	**-0.044**	**-0.080**	0.433	-0.511	**0.089**	**0.050**	-0.682	-0.808	-0.724	-0.392
Suillus tomentosus	**-0.097**	-0.966	-0.586	0.162	**0.085**	**0.053**	**0.056**	**0.043**	0.102	-0.561
Tricholoma equestre	-0.457	-0.382	0.164	0.421	0.378	0.144	0.238	0.153	0.202	0.784
Tricholoma focale	-0.424	-0.200	-0.743	0.524	0.144	**0.067**	0.572	0.339	0.762	0.737
Tricholoma magnivelare	-0.405	-0.599	0.317	-0.642	-0.874	0.395	0.838	-0.859	0.851	-0.607
Tricholoma saponaceum	0.226	0.506	0.317	**0.071**	0.502	0.610	0.425	0.325	0.357	-0.677
Tricholoma sejunctum	-0.133	-0.254	0.356	-0.377	-0.373	0.442	-0.791	-0.330	0.594	-0.143

Appendix G. Mat-forming fungi abundance by burn treatment.

Fungal species	Control	Spring	Fall	Total
Alpova trappei	0	2	0	2
Cortinarius (Rozites) caperata	1	0	0	1
Cortinarius brunneus/gentilis	0	1	0	1
Cortinarius rigidus grp.	0	1	0	1
Gastropila subcretacea	2	0	0	2
Gautieria monticola	4	2	0	6
Hydnellum peckii	0	2	0	2
Lactarius scrobiculatus	1	0	0	1
Lepiota magnispora	2	3	0	5
Phlebiella vaga	0	2	0	2
Piloderma byssinum	0	1	1	2
Piloderma fallax	13	15	2	30
Piloderma sp.	2	2	0	4
Ramaria flavobrunnescens var. aromatica	2	0	0	2
Ramaria rasilispora	0	2	0	2
Ramaria stricta	3	3	1	7
Ramaria stricta OSC65995	1	2	0	3
Ramaria stricta/pinicola	4	6	0	10
Rhizopogon rubescens/roseolus	1	1	0	2
Rhizopogon salebrosus/subbadius grp.	1	5	1	7
Rhizopogon subg. Luteolus	1	0	0	1
Rhizopogon subpurpurascens/milleri	0	1	0	1
Rhizopogon vulgaris	3	1	0	4
Suillus tomentosus	1	0	0	1
Trechispora subsphaerospora	1	0	0	1
Tricholoma equestre	1	0	0	1
Tricholoma intermedium grp.	1	0	0	1
Tricholoma magnivelare	3	0	0	3
Tricholoma saponaceum/sejunctum	4	1	0	5
Total Collections	52	53	5	110
Total Species	21	19	4	30