AN ABSTRACT OF THE DISSERTATION OF

Matthew James Trappe for the degree of Doctor of Philosophy in Environmental Science presented on February 22, 2008.

Title: Effects of Disturbance Modes on Mycorrhizal Fungus Communities at Crater Lake National Park

Abstract Approved:

Kermit Cromack, Jr.

Crater Lake National Park presents an excellent opportunity for ecological research due to its relatively pristine landscape, the protection of its natural features, its infrastructure, and a Park administration supportive of scientific inquiry and restoration ecology. The research presented here examines the responses of fungi to various forms of perturbation. In the first chapter, we studied fruiting responses of mycorrhizal fungi to different prescribed applications in a ponderosa pine – white fir ecotype. We found that the most influential factor in fungal fruiting patterns was the soil C:N ratio, and identified corresponding "guilds" of fungal indicator species. Although more intense prescribed burns affected soil attributes, including C:N ratios, the fire served only as a modifier on an underlying landscape pattern of soil attributes. In the second chapter we examined the effects of past and current anthropogenic disturbance on mycorrhizal fungal fruiting patterns in a mountain hemlock – noble fir ecotype. At the microsite scale, intensive use had a detrimental effect on fungal diversity and productivity, but at the scale of the research plots there was no significant effect of anthropogenic disturbance on fungal fruiting patterns. In the third chapter, we studied the effects of the abovementioned disturbance types plus the effects of wildfires on mat-forming soil fungi. We identified 38 taxa of mat-forming fungi, and found that the presence of fungal mats is largely

correlated with needle litter. Several of these taxa were not previously known to form mats.

Effects of Disturbance Modes on Mycorrhizal Fungus Communities at Crater Lake National Park

by
Matthew James Trappe

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APPROVED:

Major Professor, representing Environmental Sciences

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Matthew James Trappe, Author

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CONTRIBUTION OF AUTHORS

Dr. Kermit Cromack, Jr. served as the Principal Investigator for all of these research projects, assisting with proposal preparation, and grant administration. He provided advice on methods of data collection and analysis, and provided direct field support, helping collect soil and fungal samples. Dr. James Trappe participated in most field excursions and was adept at recruiting field volunteers. He identified an enormous number of field specimens (many foul-tasting) and provided thorough manuscript reviews. Dan Perrakis assisted in establishing the prescribed fire research site and implementing the burn treatments. He performed pre- and post-treatment fuel inventories and shared his data for this research. Drs. Efren Cázares, Michael Castellano, and Steve Miller all provided assistance in the identification of cryptic taxa. Mary Rasmussen was instrumental in helping us to secure funding from the National Park Service, identify research sites, and clear administrative hurdles, as well as helping with field data collection. Dr. John Wilson helped to scout field sites and establish survey plots, and also shared his soil samples and fuels data with me. Bruce Caldwell and Dr. Robert Griffiths provided helpful input and manuscript review for the chapter on fungal mats.

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INTRODUCTION

Crater Lake National Park presents an excellent opportunity for ecological research due to its relatively pristine landscape, the protection of its natural features, its infrastructure, and a Park administration supportive of scientific inquiry and restoration ecology. The research presented here examines the responses of mycorrhizal fungi to various forms of perturbation and provides the first survey of mat-forming and filamentous soil fungi at the Park.

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. Mycorrhizal fungi are so important to the health of forest trees that most will not survive without fungal symbionts. Yet, most biomass of mycorrhizal fungi is in the top 10 cm of soil, a region vulnerable to disturbance by fire or human activity.

The response of mycorrhizal fungus fruiting patterns to disturbance is important because fungal sporocarps are a significant food source for wildlife and hence are an important response variable to evaluate effects of fire on wildlife carrying capacity. Several mycorrhizal fungi in southwestern Oregon and Crater Lake National Park produce sporocarps of gustatory and economic value for humans, including matsutake, chanterelles, king boletes, and morels.

Although a great deal of research has been done on the effects of prescribed burning and recreational use on various ecosystem components and functions, none have investigated the fruiting responses of mycorrhizal fungi to these perturbations. Additionally, we have little knowledge of the diversity of mat-forming and filamentous soil fungi at Crater Lake National Park, or the habitat associations of these fungi.

In the first chapter, we studied fruiting responses of mycorrhizal fungi to different prescribed applications in a ponderosa pine – white fir ecotype. The timing of a prescribed burn affects fire severity, primarily as a function of fuel moisture). Burn severity can affect soil chemistry, fine roots, litter layer coverage and depth, and levels of coarse woody debris (CWD) in different ways. Soil moisture may conduct heat deeper into the ground while simultaneously regulating maximum soil temperatures. 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; 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.

Many studies have examined effects of fire on soil attributes, mycorrhizae and fungal fruiting patterns, as well as the effect of soil attributes on fungal fruiting patterns. Here we explore the relationships among seasonal prescribed burning, an array of soil and fuel 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.

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 □13C/15N 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. In this work, we 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.

In the second chapter we examined the effects of past and current anthropogenic disturbance on mycorrhizal fungal fruiting patterns in a mountain hemlock – noble fir ecotype. Several researchers have examined effects of recreational use on forested sites. Soil compaction increases penetration resistance to water and slows the growth of adjacent trees, with implications for C and N cycling. Coarse-grained, highly porous, and sandy loam soils like those encountered at Crater Lake are more susceptible to compaction damage than silty clays. There is a loss of macropore space in compacted soils, resulting in an increase in soil moisture at the expense of soil air. Root damage may result from hypoxic conditions in compacted soils, and there may be reduced water potential in highly impacted sites. Soil compaction affects the ability of plants to propagate fine roots through the soil, and alters soil microbial communities in surface horizons. These conditions can persist for many years.

No studies to date have addressed the impacts of recreational use or soil compaction on mycorrhizal fungus fruiting patterns. We characterized soil properties and fuels levels, and surveyed mycorrhizal sporocarp fruiting patterns over a three year period at sites representing both past and current use areas paired with relatively undisturbed controls.

Our first hypothesis was that intense anthropogenic disturbance influences belowground habitat. Our second hypothesis was intense anthropogenic disturbance influences mycorrhizal fungus fruiting patterns, as measured by sporocarp inventories conducted over multiple years. In this chapter, we quantify many of the physical changes brought about by the both current and past site use and relate these to mycorrhizal fungus fruiting patterns.

In the third chapter, we studied the effects of the abovementioned disturbance types plus the effects of wildfires on mat-forming fungi with the first survey of those fungi at Crater Lake National Park.

Most fungal biomass exists as hyphae that permeate the soil. Often these are too fine to see, but sometimes they form rhizomorphs or aggregations of mycelial strands that are visible to the naked eye. Some taxa create discrete zones in the soil, where they appear to dominate soil biota, forming structures referred to as "fungal mats".

We collected soil fungal samples and by DNA sequencing identified 38 taxa of mat-forming soil fungi, several of which were not previously known to form mats. We also collected a suite of soil chemistry and surface fuels data and sought correlations between these factors and the abundance of soil fungi, and when possible, habitat preferences for specific taxa, finding that the presence of fungal mats is largely correlated with needle litter.

The first two chapters have direct applied value for resource managers trying to balance fuels reduction or recreational needs with an important element of forest ecosystems, mycorrhizal fungi. How different burn prescriptions might affect the mycorrhizal community is one consideration among many that managers should be informed of. Likewise the impact of human use (recreational or otherwise) that severely compacts soils on mycorrhizal communities is valuable information if planning conservation or intensive use areas. The third chapter adds to our nascent understanding of the biodiversity of mat-forming and filamentous soil fungi in the Pacific Northwest, and is the first such work in the mountain hemlock – noble fir or Ponderosa pine – white fir ecotypes.

INTERACTIONS AMONG PRESCRIBED FIRE, SOIL ATTRIBUTES, AND MYCORRHIZAL FUNGUS FRUITING PATTERNS AT CRATER LAKE NATIONAL PARK

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Interactions Among Prescribed Fire, Soil Attributes, and Mycorrhizal Fungus Fruiting Patterns at Crater Lake National Park

Abstract

We identified relationships between prescribed burn treatments and selected soil and fuel attributes on mycorrhizal fungus fruiting patterns in an old-growth ponderosa pine and white fir stand in Crater Lake National Park (CLNP), Oregon, USA. Three prescribed burn treatments (early spring, late spring, and fall burns) plus non-burned controls were applied to 24 ~3 ha units in 2002. We sampled mycorrhizal fungus sporocarp production in the spring and fall in the ensuing three years, and collected data on surface fuels, soil C and N concentrations, $\delta^{13}C$ and $\delta^{15}N$ signatures, pH, and bulk density. A gradient of C:N ratios and other soil attributes across the study area facilitated separation of effects of fire from effects of soil attributes on fungal fruiting patterns. Distinct guilds of fungal indicator species were identified, correlating more closely with soil C:N ratios than prescribed burn treatments. Although other habitat attributes (such as fuel levels) were correlated with C:N ratios, the C:N ratios were the most consistent predictor of fungal fruiting patterns. The fall burn treatment did reduce soil C:N ratios, and most of the fall burned units produced the fungal indicator species associated with lower C:N ratios, but the same fungal indicator species also fruited in the non-burned control units with lower C:N ratios. The spring burn treatments did not differ significantly from adjacent non-burned controls in fungal fruiting patterns or C:N ratios. Fall burn treatment units produced significantly fewer fungal species and collections than spring burn units, but did not differ significantly in fungal diversity and abundance from non-burned controls.

Introduction

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 CLNP, 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 fungal community (Smith et al., 2004; Smith et al., 2005); intense fires may change the mycorrhizal fungal 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 (Fogel and Trappe 1978; North et al., 1997; Cazares et al., 1999; Claridge et al., 1999; Mattson et al., 2002; Claridge and Trappe, 2004; Ashkannejhad and Horton, 2006; Jones et al., 2006) and hence are an important response variable to evaluate effects of fire on wildlife carrying capacity. Several mycorrhizal fungi in southwestern Oregon and CLNP produce sporocarps of gustatory and economic value for humans, including 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).

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 and Agee, 2006). 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 (Smith and Read 1997, 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., 2004; 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 relationships among seasonal prescribed burning, an array of soil and fuel 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.

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 and Agee (2006) 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 patterns, 2) seek relations within and between the habitat attributes and fungal fruiting patterns, and 3) identify fungal community guilds as responses to prescribed burn treatments and habitat attributes. Because our project began after prescribed burns were applied, we do not have any pre-treatment data. Interactions between applied burn treatments and a gradient of pre-existing soil chemistries were identified by ANOVA and spatial analysis.

Study site

The study site at the south border of CLNP 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 ca. 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* spp., *Carex* spp., and a number of forbs. *Ceanothus* spp. and *Arctostaphylos* spp. 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 in effect. Prior to 1902, the overall fire return interval ranged from 12.8 to 40 yrs with a mean of 21.1 yrs.

Prescribed burns

The prescribed burns were planned by Dr. James Agee and Daniel 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. 1.1). While these units were fairly large, they may not have been large enough to preclude possible edge effects or provide sufficient buffering between treatments. Four prescriptions were applied: control (non-burned; eight units, D, F, G, I, N, P, S, U), early spring burn (ignited June 20 - 22, 2002; 4 units, A, C, V, W), late spring burn (ignited June 28, 2002; 4 units, E, K, O, T), and fall burn (ignited October 9 - 10, 2002; 8 units, B, H, J, L, M, Q, R, X) (Perrakis and Agee, 2006). The fall burn initially was planned to be applied in two treatments (early and late fall), but weather and fire crew logistical 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. Because the interval between the two spring burn ignitions was during a period of rapid drying we decided to analyse the early and late spring burn treatments separately.

All burn treatments were somewhat patchy in their intensity and severity. In all treatments, damage to the ponderosa pine overstory was minimized, and all units remained well-stocked. The burn treatments reduced the mid-story of white fir by varying degrees; however it was present on all sample plots.

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 sporocarp detection. The method has been used successfully to quantify fungal diversity and habitat associations over broad ecotypes in southeastern Australia (Claridge et al., 2000). Field trials of time-constraint sampling conducted at CLNP indicated that 1000 m^2 (20 x 50 m) survey plots sampled for 100 person minutes captured the asymptotes of detected fruiting body diversity. Most of the sampling time was spent seeking hypogeous fungi; epigeous sporocarps were collected relatively quickly. All taxa were identified after unit sampling was complete.

All units of both spring burn treatments were sampled in the spring and again in the fall. Four each of the control units (G, P, S, U) and fall burn units (M, Q, R, X) were sampled in the spring and the remaining four each (control units D, F, I, N; fall burn units B, H, J, L) were sampled in the fall. At each sampling iteration, one 1000 m^2 survey plot was established within each of the 16 treatment units. The survey plots were placed away from the edge of the treatment unit, and were moved within the treatment unit at each sampling to broaden the total area sampled and eliminate disturbance effects from previous sampling activities.

Although the use of time-constraint sampling does not preclude comparisons of biomass and richness between species, this was not attempted because of great differences

between taxa in biomass and fecundity. The logistics of physically transporting all sporocarps from a unit (for biomass analysis) were also beyond the scope of this project.

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 CLNP 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 (Miller and Buyck, 2002; Frøslev et al., 2005). 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 CLNP. All collections were accessioned into the Oregon State University Mycological Herbarium (OSC).

A relatively small number of saprobic species were collected on the units, 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. &

Schwein.) Sacc. forms mycorrhizae with *Picea* (Vrålstad et al., 1998) and possibly *Pinus* (Egger and Paden, 1986).

Soil cores and mineral soil bulk density

Six soil cores were taken with a 335 cm^3 corer from random locations (by tossing a marker) throughout each treatment unit, labeled, and refrigerated in sealed plastic bags. Due to the patchy nature of fire in the burn treatments, some cores in the burned units were collected where the litter had not been consumed. 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.

Fuels: woody debris and litter mass

Fuels data were collected by Perrakis and Agee (2006) 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) planar 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, then measured with a digital pH meter.

Data analysis

Fungal 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. 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 unit for analysis.

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. 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 analysis (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 (bulk density, C, N, pH, fuels, etc.) for all 24 units, but no fungal collection data. The second had fungal collection and habitat attribute data for the 16 units sampled in the spring. The third had fungal collection and habitat attribute data for the 16 units sampled in the fall. Five different ordinations were performed: 1) habitat attributes for all units; 2) habitat attributes of the units sampled in the spring; 3) species collections of units sampled in the spring; 4) habitat attributes of units sampled in the fall; 5) species collections of units sampled in the fall. Ordinations of habitat attributes show similarities in physical properties (soil chemistry and fuels) between units, and ordinations of species collections show similarities in fungal species assemblages between units. 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 so FWD was eliminated from ordination analysis, as its presence disproportionally weighted the influence of the surface burn effects. Although FWD did not change the relative positions of units it tended to distort the scattergram horizontally, making it more difficult to read. 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 units 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 relativization was necessary, and generalized relativization by column was chosen as the most appropriate method to normalize data for ordination. 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), Beals smoothing was applied to both matrices. Beals 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 an multivariate outlier (2.5 s.d.) and was removed from the data set, as was *Cantharellus subalbidus* from the fall collection data set (2.4 s.d.). Again, scree plot analysis indicated that a two-dimensional solution was optimal for both spring and fall datasets and final ordination was performed in two-dimensional space with a random starting point using Sorensen's distance measure.

Results

A total of 566 collections representing 133 species of mycorrhizal fungi were collected over three years and are presented in Table 1.1. Of these 133 species, 77 were found in only one or two units 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 Table 1.1 show how many units over three seasons a taxon was collected per treatment (four units for each treatment over three seasons give a maximum of 12 for each treatment). The taxa collected on at least three units (and subsequently included in the data analysis) are listed first and are designated by the four-letter abbreviations used in the scattergrams.

Treatment effects on habitat attributes

The mean values and standard errors for each habitat attribute by prescribed burn treatment are presented in Table 1.2, differences between treatments in Table 1.3, and correlations between habitat attributes in Table 1.4. In all tables a (-) symbol preceding the *p* - value indicates a negative correlation. Steel et al. (1997) suggest using $\alpha = 0.10$ for field experiments having smaller numbers of replicates for each treatment and we use this significance threshold in discussing our results, but *p* - values above 0.05 should be interpreted with caution.

Bulk density was significantly lower in early spring burns than in late spring or fall burns. It was noticeably lower than in the controls as well but failed to make statistical significance due to high variability in controls. Bulk density was positively correlated with total N and negatively correlated with $\delta^{13}C$ depletion and C:N ratio.

Total nitrogen did not vary significantly between treatments. There was a very slight upward tendency in the control plots but well within the range of measurement variability. It was positively correlated with total C and bulk density and negatively

correlated with C:N ratio and $\delta^{13}C$ depletion. $\delta^{15}N$ enrichment was not significantly different between treatments, and $\delta^{15}N$ did not correlate significantly with any other habitat attribute variable.

Total carbon did not differ significantly between treatments. It trended downward with increasing burn intensity but the measurements were too variable to reach statistical significance. It was positively correlated with total N and fuels (litter mass, FWD, and CWD).

$\delta^{13}C$ depletion showed a slight tendency to decrease (become less negative) in late spring and fall burns compared to control and early spring burns, but even the upper and lower measurements (early spring and fall burns, respectively) did not differ significantly. $\delta^{13}C$ depletion was negatively correlated with bulk density and total N, and positively correlated with C:N ratio and CWD levels.

The C:N ratio was significantly lower in fall burns than all other treatments. It did not differ significantly between controls and either of the spring burns. It was negatively correlated with bulk density and total N and positively correlated with $\delta^{13}C$ depletion and all fuels measurements.

Litter mass differed significantly between controls and all burn treatments, despite substantial variability in the data. Litter mass decreased steadily with burn severity. Although the early spring burn treatment plots had almost twice as much mean litter mass as the fall burn treatment plots, the difference was not significant due to data variability. Litter mass was positively correlated with CWD and FWD, and was negatively associated with mineral soil pH.

Coarse woody debris responded dramatically to burning, with all treatments differing significantly from each other except controls and early spring burns. CWD correlated positively with total C, $\delta^{13}C$ depletion, C:N ratio, litter, and FWD levels and negatively with mineral soil pH.

Fine woody debris levels differed significantly between controls and all burn treatments. Among the burn treatments, only the early spring and fall burns differed. Fine woody debris correlated positively with total C, litter and CWD levels, and negatively with mineral soil pH.

Mineral soil pH trended upward from controls to the fall burns, but only those two extremes differed significantly. It correlated negatively with all fuel measurements (litter mass, CWD, and FWD).

Including all fungal collections with each treatment sampled equally, the total number of collections was significantly lower in fall burns than other treatments. Both spring burns produced more collections than controls but not significantly so.

Fungal species correlations with habitat attributes

Of the 16 taxa collected in the spring on three or more units, eight correlated with habitat attributes at $\alpha < 0.10$ level of significance; of the 45 species collected in the fall on more than three units, 20 correlated with habitat attributes at $\alpha < 0.10$ level of significance (Table 1.5).

Ordination of habitat attributes for all units

The ordination by habitat attributes for all 24 units is presented in Fig. 1.2. Cluster analysis identified five groups of units within this ordination (Fig. 1.3). In this ordination, the treatments are separated along the dominant horizontal axis, with the fall burn units to the left with higher bulk density and mineral soil pH, and the control units to

the right with higher fuel levels. There was a secondary stratification along the vertical axis, further separating units by the opposing attributes of total N and C:N ratio. This vertical stratification assisted in teasing out the habitat attributes underlying the treatments that influenced fungal fruiting patterns.

Groups 1 and 2 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 units in the first and second groups. Group 1 (with lower fuel levels than group 2), contained the remaining three late spring burn units and two of the early spring burn units. In group 2 were five of the eight control units and the remaining two early spring burn units. Unit 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 units in group 3. Group 3 was formed by three control units that differed from the rest of the controls by their high levels of total N and correspondingly lower C:N ratios.

Group 4 contained all of the remaining fall burn units, unified by lower total N and higher C:N ratios. All of these units had fuel levels well below the means. Group 5 contained three fall burn treatment units (units R, L, and M) and one late spring burn treatment unit (unit T). These units had higher total N and lower C:N ratios than the other burn treatments found in group 4.

Ordination of habitat attributes for units sampled in the spring

The ordination by habitat attributes of the 16 units surveyed in the spring is presented in Fig. 1.4. Fungal collection data are displayed in the vector overlay but do not affect the position of the scattergram points. Cluster analysis identified four groups of units within this ordination (Fig. 1.5).

Group 1 contained all late spring burn treatment units and two early spring burn units. It represents units 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 unit T had above mean C:N ratios. Most of these units had *Morchella angusticeps* and *Sarcosphaera coronaria*, and units O and T were more similar to group 4 in having *Amanita pantherina* and *Boletus zelleri* as well. Units A, E, and W were more akin to group 2, all having *Hysterangium separabile* and most having *Gautieria monticola*, *Hydnotrya variiformis*, and *Melanogaster tuberiformis*.

Group 2 contained the remaining two control units and two of the early spring burn units. This group was associated with high C:N ratios and fuel levels. *Amanita muscaria, Gautieria monticola, Hydnotrya variiformis, Melanogaster tuberiformis, Ramaria rasilispora*, and *Rhizopogon vulgaris* were associated with these units.

Group 3 contained two control units. Consistent with the habitat attribute ordination of all the units (Fig. 1.2), these were separated from the other control units and all of the spring burn units 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 units (Fig. 1.3).

Group 4 contained all four fall burn units, unified by higher soil pH and lower fuel levels. This group was characterized by the presence of *Amanita pantherina, Geopyxis vulcanalis, Morchella angusticeps*, and *Sarcosphaera coronaria*.

Ordination of species collections for units sampled in the spring

The ordination by species collected on the 16 units surveyed in the spring is presented in Fig. 1.6. Soil attribute data are displayed in the vector overlay but do not affect the position of the scattergram points. Cluster analysis identified three groups of units within this ordination (Fig. 1.7).

Group 1 included three of each of the early and late spring burn units as well as two control units, but none of the fall burn units. Of these six spring burn treatment units, 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 units had *Hysterangium separabile* and *Ramaria rasilispora*, taxa absent from the other two spring burn units (in group 3). All of the units in group 1 had above mean fuel levels and C:N ratios except unit G (a control unit), 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* were produced in group 1.

Group 2 contains two fall burn units and one control unit. The two fall burn units have relatively high soil pH and total N, but average soil bulk density. Control unit S is an anomaly in this group, but one aspect it has in common with other group members over other control units is its relatively high soil bulk density— the highest of all control units by a substantial margin. All three units have low C:N ratios as a consequence of their high total N levels, and all units in this group produced *Amanita pantherina* and *Sarcosphaera coronaria*.

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

Ordination of habitat attributes for units sampled in the fall

The ordination by habitat attributes of the 16 fall fruiting collection units is presented in Fig. 1.8. Fungal collection data are displayed in the vector overlay but do not affect the position of the scattergram points. Cluster analysis identified two groups of units within this ordination (Fig. 1.9).

Group 1 contained all fall burn and late spring burn units, and two of the four early spring burn units (units A and W). This group had lower levels of fuels and total C, and somewhat higher levels of soil bulk density. These units were widely distributed along axis 2, indicating a spectrum of C:N ratios. *Boletus chrysenteron* and *B. zelleri* were collected on units with higher total N and lower C:N ratios in this group (units B, L, and T); *Rhizopogon vulgaris* and *Russula adusta* were collected on units with the lower total N and higher C:N units (units E, H, J, and K). The two early spring burn treatment units (units 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*.

Group 2 contained all of the control units and two of the four early spring burn units (units C and V). All of these units had above mean levels of fuels, and all except units D and N had above mean C:N ratios. Although units 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* and *Cortinarius rigidus* associated with higher CWD levels, while *Cortinarius caperatus, Sarcodon imbricatus, Suillus punctatipes*, and *Tricholoma focale* were more closely associated with higher C:N ratios.

Ordination of species collections for units sampled in the fall

The ordination of species collected on the 16 units surveyed in the fall is presented in Fig. 1.10. Soil attribute data are displayed in the vector overlay but do not affect the position of the scattergram points. Cluster analysis identified three groups of units within this

ordination (Fig. 1.11). Most of the units fell along a continuum from higher bulk density and pH on the left to higher C:N ratios and fuels on the right.

Group 1 contains the remaining fall and late spring burn treatment units, as well as one early spring burn unit and two control units. Except for unit N (the only control unit in the group), all units in this group had below mean levels of total C and total N. Units A, H, and K are closely grouped due to their lower bulk density. Unit N had the lowest C:N ratio of any control unit, and the highest level of total N and fuel levels of all units.

Group 2 includes three early spring burn units and three control units. The members of this group all had above mean levels of CWD and below mean mineral soil bulk density. All these units produced *Gomphus floccosus*, four produced *Russula integra*, three produced *Cortinarius rigidus* and three *Russula albonigra*. The absence of any of these taxa and the presence of *Boletus chrysenteron* in control unit N explain the low axis one value of unit N in the species ordination.

Group 3 was composed of two fall burn units and one late spring burn unit. These three units had above mean soil bulk densities and below mean C:N ratios and fuels. *Boletus zelleri* was collected on all of these units, and *B. chrysenteron* on two of them. *Boletus zelleri* was also collected on units B, E, and O in group 1.

Groups 1 and 2 combined produced all collections of *Boletus zelleri*, as well as 17 of the 18 *Rhizopogon* collections (*R. evadens, R. salebrosus*, and *R. vulgaris*). They are also characterized by the taxa absent— none of units in these two groups produced *Cortinarius rigidus* or *Russula integra*, and only unit E produced *Gomphus floccosus.*

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 et al., 1991; Arnolds, 1992; Vogt et al., 1992). 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 their fruiting pattern may be random (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.

Several researchers have attempted to link belowground mycorrhizal communities with aboveground sporocarps (Gardes and Bruns, 1996; 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.

The control units 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 units prior to treatment.

In this discussion and in the graphics presented, units are represented as solid units with uniform characteristics. This is obviously a simplification, and there was often substantial variability of habitat attributes within a unit. Because the study was designed to examine burn treatment effects, the soil cores were collected randomly throughout each unit 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 some 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

Most of the treatment effects on soil properties and fuel levels were as expected with the exception of mineral soil bulk density. Bulk density might be anticipated to increase with fire intensity as a function of increased consumption of organic soil components, however here the bulk density was lowest in the spring burn units (Table 1.2) and was not correlated with total C (Table 1.4). This pattern is difficult to explain until viewed spatially. Figure 1.12 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. 1.1), and half of the fall burn treatments were located in the densest end of the geographic gradient. As the control units were not significantly different in their bulk density from the late spring and fall burn treatment units (Table 1.3), the observed patterns of mineral soil bulk density were likely an underlying pattern at the site and not strongly influenced by the burn treatments.

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 units with below mean surface fuel levels had above mean total C (units L and R). The five units that had the highest total C all were controls, and the five units that had the highest total N also had above mean levels of total C. $\delta^{13}C$ depletion in the mineral soil (Fig. 1.13) ranged from -24.82 to -26.65‰ and was not correlated with any burn treatment (Table 1.3), but had a spatial pattern similar to that of soil bulk density (Fig. 1.12).

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 (Table 1.3). As with soil bulk density and $\delta^{13}C$ depletion, higher levels of N generally occurred in units along the highway at the eastern end of the project area (Fig. 1.14). Snowbrush (*Ceanothus velutinus* Doug.) 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 unit interiors where soil sampling occurred.

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

As with soil bulk density, total N, and $\delta^{13}C$ depletion, C:N ratios also had spatial pattern with lower values concentrated at the eastern end of the study area (Fig. 1.15). 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 (units B, J, and X).

Fuels responded significantly to burn treatments (Table 1.3), and correlatied positively with total C and negatively with soil pH (Table 1.4). Total C was not correlated with any burn treatment, and soil pH differed only between non-burned controls and fall burns (Table 1.3).

Correlations between habitat attributes and fungal fruiting patterns

Above mean levels of $\delta^{13}C$ depletion, $\delta^{15}N$ enrichment, C:N ratios, and fuels tended to occur together as a suite of characteristics, mostly on control and early spring burn treatments. In contrast, higher soil bulk density, total N, and pH measurements occurred on a separate suite of units, including most of the fall burn units but also three control units. Most of the late spring burn units had habitat attributes intermediate between these groups, except unit T (at the east end of the study area), which was more similar to the fall burn treatments.

The association of fruiting patterns by discrete groups of fungal taxa with suites of habitat attributes in both spring and fall suggests the existence of fungal indicator species "guilds" (Root, 1967; Landers, 1983; Perry et al., 1989). 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' (Fig. 1.16). It is noteworthy that only about half of the species collected had habitat associations at $\alpha < 0.10$ (Table. 1.5), and fewer still were consistently identified as indicator species by ordination analysis; these few taxa may be more habitat-sensitive.

Many taxa did not respond significantly to any habitat attribute or burn treatment. Bulk density was negatively correlated with the C:N ratio (Table 1.4; Figs. 1.12 and 1.15). Units G (control), O (late spring burn), and P (control) had above mean bulk density measurements but produced high C:N (units G and P) fungal guilds or were intermediate (unit O). Units B, N, U, and X had below mean bulk density measurements, but produced the low C:N fungal guilds.

Coarse woody debris levels were positively correlated with C:N ratios, and all of the high C:N fungal guild producing units had above mean CWD levels. However, four of the units producing the low C:N fungal guild (units 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. Thus the fungal fruiting patterns here correlate more closely with C:N ratios than bulk density or CWD.

Spring collections: comparison of collections and habitat attributes ordinations
Most of the units sampled in the spring were consistent in their groupings between the habitat attribute ordination (Fig. 1.4) and the collections ordination (Fig. 1.6). With the exception of units T (late spring), U (control), and V (early spring), the units in groups 1 and 2 in the habitat attribute ordination combined into group 1 in the fungal species ordination. Unit T had the highest total N and lowest C:N ratio and litter levels of the group 1 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 4 and 6) 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 units 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 *Gautieria monticola, Hysterangium separabile, Hydnotrya variiformis,*

Melanogaster tuberiformis, and *Ramaria rasilispora* associated with units 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 units that grouped together (units G and S) in habitat attribute space (group 3, Fig. 1.4) assumed quite different positions in species space (Fig. 1.6); unit S grouped with the units typified by the presence of *Amanita pantherina* and *Sarcosphaera coronaria,* and the absence of *Gautieria monticola, Hysterangium separabile, Hydnotrya variiformis*, and *Ramaria flavobrunnescens* var. *aromatica*. Unit G was exactly the opposite, lacking *Amanita pantherina* and *Sarcosphaera coronaria* but having the others. Units G and S were similar in their habitat attributes (Fig. 1.4) except that unit G had a lower soil bulk density.

Units P and U (both controls) also grouped together in habitat attribute space, but separated in species space (Fig. 1.6), with unit P among the units with higher C:N ratios and fuels, and unit U grouping among the units with higher bulk density and pH. Unit U produced *Amanita pantherina, Geopyxis vulcanalis,* and *Sarcosphaera coronaria,* but not *Hydnotrya variiformis*, *Ramaria rasilispora*, or *Rhizopogon vulgaris*, and unit P was opposite, lacking *Amanita pantherina, Geopyxis vulcanalis,* and *Sarcosphaera coronaria* but producing all the others. These two units had similar fuel levels, but unit U had a lower bulk density and C:N ratio.

The relationship between units T and K (both late spring burn units) also is interesting. In the habitat attribute ordination (Fig. 1.4), they both fell on the left half of axis 1 with unit K somewhat more so than unit T. In both the spring and fall collection ordinations (Figs. 1.6 and 1.10) unit K shifted to the right side of the ordination with the high C:N species guilds, and unit T moved in the other direction with the low C:N species guilds. Unit T had higher soil bulk density, total N, and CWD than unit K, and unit 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 in the spring (Table 1.5), was collected on four control units but also on five spring burn treatment units. Conversely, *Sarcosphaera coronaria*, negatively associated with FWD, was collected on two control units as well as nine burned units. Only *Morchella angusticeps* consistently fruited on burned units to the exclusion of control units; it was the only indicator taxon 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. 1.8), 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. 1.10) generally agreed with those of the habitat attribute ordination (Fig. 1.8). 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 transitional group: units A (early spring burn), E (late spring burn), H (fall burn), K (late spring burn), and O (late spring burn). These units tended to group with the other more

disturbed units 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*.

Units N and W are informative to the relationship between C:N ratios, fuel levels, and fungal guilds. Unit N is a control unit that ordinated to the right in habitat attribute space (Fig. 1.8) due to its high fuel levels, but produced indicator species consistent with its low C:N ratio (Fig. 1.10). Conversely, unit W ordinated with the late spring and fall burn units in habitat attribute space due to its lower fuels levels, but produced indicator species consistent with its high C:N ratio, suggesting that the C:N ratio has more influence on fungal fruiting patterns than fuel levels.

Categorizing units by species guilds

The units can be grouped into three categories based on the indicator species they supported (Fig. 1.16): The low C:N guild in units B, J, L, M, N, Q, R, S, T, U, and X; intermediate or transitional units A, E, H, K, and O (inconsistent or without either high or low C:N indicator taxa); and the high C:N guild in units C, D, F, G, I, P, V, and W. Four of the intermediate units (A, E, K, and O) produced the high C:N guild in the spring (Fig. 1.6) and the low C:N guild in the fall (Fig. 1.8). Unit H was only sampled in the fall and did not produce any C:N ratio indicator taxa.

Of the late spring burn units, only unit T produced a clearly low C:N guild both spring and fall, while the other late spring burn units (E, K, and O) were intermediate. Three of the four early spring burn treatment units (units C, V, and W) produced high C:N-associated guilds and the fourth (unit A) was intermediate. In total, more spring burn units produced the high C:N guild than did control units.

It is clear that there is some effect from burn prescription treatment; no fall burn units produced the high C:N fungal guilds. However, three of the control units produced the

low C:N fungal guild. All but one of the units (unit G; control) having above mean C:N ratios produced the high C:N guild. Unit G is spatially transitional between high and low C:N units, 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 unit. All of the intermediate units also had above mean C:N ratios. Only one of the low C:N guild producing units had an above mean C:N ratio (unit J, a fall burn). The three control units (units 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. 1.15) and fungal guilds (Fig. 1.16) is much closer than that of burn treatment (Fig. 1.1) and fungal guild, and explains the occurrence of low C:N fungal guilds in control units N, S, and U.

The seven units 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 units is to compare the C:N ratios from control units G and S to those of proximate fall burn units L, M, and R.

The C:N ratios of control units G and S were 22.1 and 23.2 respectively, and fall burn units L, M, and R ranged from 18.6 to 19.7. If we assume that the C:N ratio of control units G and S did not change appreciably from before the burn treatments, then we can infer that the fall burn treatment itself reduced the C:N ratio by 2.4 to 4.6 in units L, M, and R. By this estimate, it is quite possible that these units were producing the low C:N fungal guild even before the burn prescriptions were applied. The contrast in C:N ratio between fall burn units B, J, and X and their neighboring control and spring burn units is also striking (Fig. 1.15), suggesting direct influence by the fall burn treatment.

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 units are less $\delta^{13}C$ depleted (Figs. 1.13 and 1.15).

From about 1925 to 1932 there was a park entry station and maintenance camp in the vicinity of units Q, R, S, and T (pers comm., S. Mark). All of these units had above mean bulk density, and unit 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 units 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. Unit U is a spatial anomaly, but we have no data on soil attributes adjacent to this unit 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 units, and although three of these five were spring burn treatment units, they all had higher C:N ratios than the control unit U. To the west of unit U an extension of the fall burn treatment outside the study area appears to have had severe effects on vegetation (and probably soils), and to the south is a regenerating ponderosa pine stands (ca. 10 yrs old) on the Winema National Forest. Both of these factors may have influenced edaphic conditions inside unit U.

All five of the units intermediate between the high and low C:N guilds were in a line between unit O and unit A (Fig. 1.16). This line marked the transition from high C:N (to the west) to low C:N soils (to the east). Four of these five units were spring burn treatments; one (unit H) was a fall burn treatment. Unit H was the only fall burn unit 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 units.

Fall burn treatment units 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. The fall burns may have reduced total C but the difference is non-significant ($p = 0.123$). These units were surrounded by control and

spring burn treatment units (Fig. 1.1) that maintained higher C:N ratios (Fig. 1.15), suggesting that the fall burn treatment changed the soil C:N ratio enough to shift mycorrhizal fungus fruiting patterns.

All fall-burned units produced low C:N guilds except unit H. Unit H was spatially associated with the group of units with low total N levels (Fig. 1.14) and likely had a rather high C:N ratio before the treatment was applied. The burn treatment may have reduced the C:N ratio enough to suppress 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 units, only unit T produced the low C:N fungal guild. It was among the band of low C:N ratio units along the highway, and based on the spatial pattern of soil properties also may have produced the low C:N fungal guild before the burn treatment was applied.

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. Primary elements in mycorrhizal morphogenesis are thought to be available energy, temperature patterns, and moisture availability. The C:N ratio probably influences nutrient (energy) availability but may also 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 to sporocarp morphogenesis.

Conclusions

The units 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 unit G, all units with a C:N ratio below 26 produced a distinct guild of indicator fungal sporocarps, indicated by the presence of *Amanita pantherina, Boletus chrysenteron, Boletus zelleri*, and *Sarcosphaera coronaria*. Most units with a C:N ratio above 26 produced a distinctly different guild of indicator fungal sporocarps, indicated by the presence of *Cortinarius rigidus, Hydnotrya variiformis, Hysterangium separabile, Lactarius rufus, Russula integra, R. albonigra*, and *Suillus tomentosus*. Units spatially transitional between higher and lower C:N soils produced fungal fruiting patterns intermediate between the high- and low-C:N guilds.

Our first hypothesis was that prescribed burning at different seasons influences belowground habitat differently. The fall burns in particular had significant effects on soil C:N ratios, pH, and surface fuel levels. Our second hypothesis was that prescribed burning at different seasons influences mycorrhizal fungus fruiting patterns differently. With the exception of *Morchella angusticeps*, which responded more to the treatment itself than the effects on soil properties, the timing and consequent intensity of prescribed burn treatments influenced fungal communities only indirectly, as a function of their effects on soil attributes. However, in this study the different treatments appeared to serve more as adjustments to the pre-existing soil attributes rather than as primary drivers. The fall burn treatments effectively promoted the fruiting of low C:N guild indicator species; units B, J, Q, and X were probably induced to switch fruiting guilds as

a result of the treatment, and unit H probably responded with a shift from the high C:N guild to an intermediate status, although lacking pretreatment data we cannot be sure. In no unit or treatment was mycorrhizal fungal fruiting suppressed entirely.

We monitored mycorrhizal fungal fruiting 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 units 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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Table 1.1. Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
Altr	*Alpova trappei*	Fogel	S	1	3	1	0	5
Ammu	*Amanita muscaria v. formosa*	(Pers.) Gonn. & Rabenh.	S	3	4	2	1	10
Ampa	*Amanita pantherina*	(DC.) Krombh.	S/F	2	0	2	2	6
Bosu	*Boletopsis subsquamosa*	(Fr.) Kotl. & Pouzar	F	3	1	3	1	8
Boch	*Boletus chrysenteron*	Bull.	F	1	1	1	2	5
Boze	*Boletus zelleri*	Murrill	F	0	0	3	3	6
Casu	*Cantharellus subalbidus*	A.H. Sm. & Morse	F	5	7	6	4	22

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
Coca	*Cortinarius caperatus*	(Persoon:Fr.) Fr.	F	1	5	2	2	10
Cocl	*Cortinarius claricolor*	(Fr.) Fr.	F	2	3	2	2	9
Cori	*Cortinarius rigidus*	(Scop.) Fr.	F	3	1	0	0	4
Cova	*Cortinarius variosimilis*	M.M. Moser & Ammirati	F	1	2	2	0	5
Elgr	*Elaphomyces granulatus*	Fr.	S	2	0	1	1	4
Gasu	*Gastroboletus subalpinus*	Trappe & Thiers	F	1	1	2	0	4
Gamo	*Gautieria monticola*	Harkn.	S/F	4	3	2	0	9

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
Gevu	*Geopyxis vulcanalis*	Peck	S	1	3	1	4	9
Gofl	*Gomphus floccosus*	(Schwein.) Singer	F	6	3	2	0	11
Hyva	*Hydnotrya variiformis*	Gilkey	S	2	1	2	0	5
Hyse	*Hysterangium separabile*	Zeller	S/F	1	4	2	0	7
Inas	*Inocybe assimilata*	Britzelm.	F	1	1	2	1	5
Lala	*Laccaria laccata*	(Scop.) Cooke	F	2	3	2	3	10
Laka	*Lactarius kauffmanii*	Hesler & A.H. Sm.	F	1	0	1	1	3

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
Lari	*Lactarius riparius*	Methven	F	1	2	0	0	3
Laru	*Lactarius rufus*	(Scop.) Fr.	F	3	0	3	0	6
Lasc	*Lactarius scrobiculatus*	(Scop.) Fr.	F	3	2	5	3	13
Lege	*Leucopaxillus gentianeus*	(Quél.) Kotl.	F	2	1	1	0	4
Metu	*Melanogaster tuberiformis*	Corda	S/F	3	1	4	2	10
Moan	*Morchella angusticeps*	Peck	S/F	0	4	3	6	13
Raca	*Ramaria cartilaginea*	Marr & D.E. Stuntz	F	3	2	3	1	9

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
Rafl	*Ramaria flavobrunnescens v. aromatica*	Marr & D.E. Stuntz	S/F	8	7	9	3	27
Rara	*Ramaria rasilispora*	Marr & D.E. Stuntz	S	1	2	3	0	6
Rhev	*Rhizopogon evadens*	A.H. Sm.	S/F	1	1	2	2	6
Rhpe	*Rhizopogon pedicellus*	A.H. Sm.	S	0	1	1	1	3
Rhsa	*Rhizopogon salebrosus*	A.H. Sm.	S/F	1	3	3	3	10
Rhvu	*Rhizopogon vulgaris*	(Vittad.) M. Lange	S/F	1	3	3	2	9
Ruad	*Russula adusta*	(Pers.) Fr.	F	0	2	1	3	6

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
Rual	*Russula albonigra*	(Krombh.) Fr.	F	3	1	0	0	4
Ruaz	*Russula azurea*	Bres.	F	5	6	5	3	19
Rubrac	*Russula brevipes v. acrior*	Shaffer	F	3	0	1	1	5
Rubrbr	*Russula brevipes v. brevipes*	Peck	F	1	1	1	0	3
Ruca	*Russula cascadensis*	Shaffer	F	0	3	2	1	6
Rucl	*Russula claroflava*	Grove	F	2	3	3	3	11
Rude	*Russula densifolia*	Secr. ex Gillet	F	2	1	1	1	5

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
Ruex	*Russula exalbicans*	(Pers.) Melzer & Zvára	F	5	1	0	1	7
Ruin	*Russula integra*	(L.) Fr.	F	2	3	0	0	5
Ruty	*Russula tyrrhenica*	Sarnari	F	6	4	7	7	24
Ruvi	*Russula vinosa*	Lindblad	F	0	3	1	0	4
Saim	*Sarcodon imbricatus*	(L.) P. Karst.	F	2	2	1	1	6
Saco	*Sarcosphaera coronaria*	(Jacq.) J. Schröt.	S	2	2	3	4	11
Sugr	*Suillus granulatus*	(L.) Roussel	F	1	1	2	1	5

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
Supu	*Suillus punctatipes*	(Snell & E.A. Dick) Singer	F	5	5	2	4	16
Suto	*Suillus tomentosus*	(Kauffman) Singer	F	4	5	2	1	12
Trfl	*Tricholoma equestre*	(L.) P. Kumm.	F	1	2	1	0	4
Trfo	*Tricholoma focale*	(Fr.) Ricken	F	4	4	3	2	13
Trma	*Tricholoma magnivelare*	(Peck) Redhead	F	0	2	1	0	3
Trsa	*Tricholoma saponaceum*	(Fr.) P. Kumm.	F	3	0	1	1	5
Trse	*Tricholoma sejunctum*	(Sowerby) Quél.	F	1	4	2	1	8

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Albatrellus ovinus	(Schaeff.) Kotl. & Pouzar	F	0	1	0	0	1
	Arcangeliella crassa	Singer & A.H. Sm.	F	0	1	0	0	1
	Boletus calopus	Pers.	S	0	0	0	1	1
	Chroogomphus pseudovinicolor	O.K. Mill.	F	1	0	0	0	1
	Chroogomphus vinicolor	(Peck) O.K. Mill.	F	1	0	0	1	2
	Cortinarius albobrunnoides	M.M. Moser & McKnight	S/F	1	1	1	0	3
	Cortinarius biformis	Fr.	F	1	0	1	0	2

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Cortinarius brunneus	(Pers.) Fr.	F	0	0	1	0	1
	Cortinarius calochrous	(Pers.) Gray	F	0	0	1	0	1
	Cortinarius cinnamomeoluteus	P.D. Orton	S	0	0	1	0	1
	Cortinarius clandestinus	Kauffman	F	1	0	0	0	1
	Cortinarius coeruleolutescens	Rob. Henry	F	0	0	1	0	1
	Cortinarius delibutus	Fr.	F	0	1	0	0	1
	Cortinarius depressus	Fr.	S	0	1	0	1	2

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Cortinarius montanus	Kauffman	F	0	1	1	0	2
	Cortinarius muscigenus	Peck	F	0	0	2	0	2
	Cortinarius orichalceus	(Batsch) Fr.	F	2	0	0	0	2
	Cortinarius (Thaxterogaster) pinguis	(Zeller) Singer & A.H. Sm.	F	1	0	0	0	1
	Cortinarius prasinus	(Schaeff.) Fr.	F	0	0	1	0	1
	Cortinarius sebaceus	Fr.	F	0	2	0	0	2
	Cortinarius semisanguineus	(Fr.) Gillet	S	0	1	0	0	1

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Cortinarius sect. phlegmacium sp. nov.		F	1	0	0	0	1
	Cortinarius subfoetidus	A.H. Sm.	F	0	0	2	0	2
	Dermocybe phoenicea v. occidentalis	(A.H. Sm.) Ammirati	F	0	1	0	0	1
	Elaphomyces muricatus	Fr.	S/F	2	1	0	0	3
	Endogone lactiflua	Berk.	F	1	0	0	1	2
	Gastroboletus turbinatus	(Snell) A.H. Sm. & Singer	F	0	0	1	0	1
	Gautieria gautierioides	(Lloyd) Zeller & C.W. Dodge	F	0	0	1	0	1

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Gautieria pterosperma nom. prov.	States	F	0	0	1	0	1
	Genea gardneri	Gilkey	S	1	1	0	0	2
	Geopora cooperi	Harkn.	S	1	0	0	0	1
	Gymnomyces abietis	Trappe & Castellano	F	0	0	0	1	1
	Hebeloma crustuliniforme	(Bull.) Quél.	F	0	1	1	0	2
	Hydnum repandum	L.	F	0	1	0	0	1
	Hygrophorus bakerensis	A.H. Sm. & Hesler	F	0	1	0	0	1

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Hygrophorus chrysodon	(Batsch) Fr.	F	0	0	1	0	1
	Hygrophorus erubescens	(Fr.) Fr.	F	0	1	1	0	2
	Hygrophorus subalpinus	A.H. Sm.	S	0	0	1	0	1
	Hymenogaster sublilacinus	A.H. Sm.	S	0	0	1	0	1
	Inocybe geophylla	(Pers.) P. Kumm.	F	1	0	0	0	1
	Inocybe lanatodisca	Kauffman	F	0	1	0	0	1
	Inocybe mixtilis	(Britzelm.) Sacc.	F	1	0	0	0	1

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Inocybe rimosa	Britzelm.	F	0	0	1	0	1
	Laccaria bicolor	(Maire) P.D. Orton	F	0	1	0	1	2
	Lactarius deliciosus	(L.) Gray	F	1	0	0	0	1
	Leucogaster citrinus	(Harkn.) Zeller & C.W. Dodge	S	0	1	1	0	2
	Leucogaster rubescens	Zeller & C.W. Dodge	S/F	0	2	1	0	3
	Leucophleps magnata	Harkn.	S	0	1	0	0	1
	Melanogaster variegatus	(Vittad.) Tul. & C. Tul.	F	1	0	0	0	1

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Nolanea verna	(S. Lundell) Kotl. & Pouzar	S	0	0	1	0	1
	Peziza repanda	Pers.	S	0	0	0	2	2
	Ramaria amyloidea	Marr & D.E. Stuntz	F	0	2	0	0	2
	Ramaria botrytis v. aurantiramosa	Marr & D.E. Stuntz	S	0	0	0	1	1
	Ramaria formosa	(Pers.) Quél.	F	0	1	0	0	1
	Ramaria longispora	Marr & D.E. Stuntz	S/F	1	1	0	1	3
	Ramaria magnipes	Marr & D.E. Stuntz	S/F	0	0	2	1	3

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Ramaria rubrievanescens	Marr & D.E. Stuntz	S	0	0	1	0	1
	Rhizopogon brunneiniger	A.H. Sm.	F	0	0	1	0	1
	Rhizopogon abietis	A.H. Sm.	F	0	0	0	1	1
	Rhizopogon atroviolaceus	A.H. Sm.	S	0	1	0	0	1
	Rhizopogon ellenae	A.H. Sm.	F	0	1	0	0	1
	Rhizopogon fuscorubens	A.H. Sm.	F	0	1	0	0	1
	Rhizopogon occidentalis	Zeller & C.W. Dodge	F	0	1	0	1	2

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Rhizopogon ochraceorubens	A.H. Sm.	F	0	0	1	0	1
	Rhizopogon roseolus	(Corda) Th. Fr.	F	0	1	0	0	1
	Rhizopogon truncatus	Linder	S	0	1	0	0	1
	Russula heterophylla	(Fr.) Fr.	F	0	1	0	0	1
	Russula viscida	Kudřna	F	1	0	0	0	1
	Russula paludosa	Britzelm.	F	0	1	0	0	1
	Sarcodon rimosus	(K.A. Harrison) K.A. Harrison	F	1	1	0	0	2

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

				Prescribed burn treatment				
Abbr.	Fungal species	Authority	Season collected	Control	Early spring	Late spring	Fall	Total
	Suillus albidipes	(Peck) Singer	F	1	0	0	1	2
	Suillus brevipes	(Peck) Kuntze	F	0	0	1	1	2
	Tricholoma intermedium	Peck	F	0	0	1	0	1
	Tricholoma mutabile	Shanks	F	0	0	0	1	1
	Tricholoma pessundatum	(Fr.) Quél.	F	0	0	1	0	1
	Tricholoma portentosum	(Fr.) Quél.	F	0	0	1	1	2
	Tricholoma virgatum	(Fr.) P. Kumm.	F	0	0	0	1	1

Table 1.1 (Continued). Mycorrhizal fungus sporocarps collected. Abbreviations provided for those taxa included in data analysis.

	Prescribed burn treatment				
	Control	Early spring	Late spring	Fall	Total
Total Collections	144	165	154	103	566
Total Species	69	81	81	55	133

Table 1.2. Mean values of forest floor and soil habitat attributes by treatment. Standard errors are in parentheses.

	Control	Early spring	Late spring	Fall	Overall
Total collections	144	165	154	103	n/a
Total species	69	81	81	55	n/a
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

Table 1.3. ANOVA *p* - values for differences between 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

Table 1.3 (Continued). ANOVA *p* - values for differences between treatments.

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	**<0.0001**	**0.000**	**0.020**

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

Table 1.4. Pearson's correlations between habitat attributes. Estimates are above *p* – value. A negative sign preceding the *p* - value indicates an inverse correlation; values significant at $\alpha < 0.10$ are bolded.

	Bulk density	Total C %	δ^{13}C depletion	Total N %	δ^{15}N enrichment	C:N ratio	CWD mass	FWD mass	Litter mass	Mineral Soil pH	Collections *
Total C %	-0.5926										
	-0.7833										
δ^{13}C depletion	0.6000	-0.1487									
	-0.0019	0.4881									
Total N %	0.3552	0.5702	0.4222								
	0.0892	**0.0030**	**-0.0378**								
δ^{15}N enrichment	-0.1918	0.0469	0.0495	-0.1794							
	-0.3693	0.8277	-0.8183	-0.3970							
C:N ratio	-0.5008	0.0756	-0.6379	-0.6954	0.1736						
	-0.0065	-0.8699	**0.0004**	**-0.0001**	0.2016						

Table 1.4 (Continued). Pearson's correlations between habitat attributes. Estimates are above *p* – values. A negative sign preceding the *p* - value indicates an inverse correlation; values significant at $\alpha < 0.10$ are bolded.

	Bulk density	Total C %	$\delta^{13}C$ depletion	Total N %	$\delta^{15}N$ enrichment	C:N ratio	CWD mass	FWD mass	Litter mass	Mineral Soil pH	Collections*
CWD mass	-0.2772	0.5580	-0.3842	0.1304	0.1491	0.4811					
	-0.2134	**0.0059**	**0.0702**	0.6629	0.4949	**0.0154**					
FWD mass	-0.1979	0.3883	-0.0890	0.2560	0.1117	0.2022	0.7458				
	-0.3539	**0.0608**	0.6789	0.3529	0.6033	0.1324	**0.0001**				
Litter mass	-0.2813	0.5716	-0.2798	0.2947	0.0604	0.2771	0.8911	0.8928			
	-0.1830	**0.0035**	0.1855	0.2345	0.7792	0.1024	**0.0001**	**0.0001**			
Mineral soil pH	0.1772	-0.2076	-0.0673	0.0745	-0.2037	-0.3766	-0.4623	-0.5109	-0.4762		
	0.4874	-0.3025	0.7784	0.8700	-0.3191	-0.1105	**-0.0147**	**-0.0115**	**-0.0154**		
Collections*	-0.5979	0.1333	-0.4795	-0.3219	0.1366	0.5962	0.2336	0.1167	0.1943	-0.2776	
	-0.0070	0.5558	**-0.0618**	-0.1117	0.3573	**0.0047**	0.2412	0.6428	0.4014	-0.2401	
Species*	-0.5861	0.0950	-0.4737	-0.3222	0.1009	0.5818	0.2293	0.1223	0.1989	-0.2535	0.9963
	-0.0098	0.7940	**-0.0744**	-0.1126	0.4571	**0.0072**	0.2677	0.6577	0.4174	-0.2975	**0.0098**

Table 1.5. Logistic regression *p* - values of habitat attributes on fungal taxa collected on at least 3 units in either spring or fall. A negative sign preceding the *p* - value indicates an inverse correlation; values significant at $\alpha < 0.10$ are bolded.

Species	Season	Bulk Density	Total C %	‰ $\delta^{13}C$ depletion	Total N %	‰ $\delta^{15}N$ enrichment	C:N ratio	CWD	FWD	Litter mass	Mineral soil pH
Alpova trappei	S	-0.259	-0.871	0.685	0.306	0.349	0.175	0.150	0.621	0.529	**-0.099**
Amanitia muscaria	S	-0.197	0.459	**0.085**	-0.791	0.724	0.246	0.195	0.182	**0.059**	0.867
Boletus chrysenteron	F	0.573	-0.620	-0.628	0.210	-0.278	**-0.084**	-0.654	0.318	0.785	**0.064**
Boletus zelleri	F	**0.068**	-0.154	**-0.072**	-0.878	0.686	**-0.085**	**-0.042**	**-0.091**	**-0.054**	0.547
Cortinarius caperatus	F	-0.109	-0.526	0.361	-0.266	**0.100**	0.174	-0.691	-0.287	-0.349	-0.601
Cortinarius rigidus	F	-0.257	**0.052**	0.209	-0.933	0.947	0.152	**0.082**	0.116	**0.095**	-0.103
Gastroboletus subalpinus	F	0.713	-0.379	0.406	-0.383	-0.381	0.364	0.595	0.488	0.832	**-0.082**
Gautieria monticola	S	-0.175	-0.430	0.249	0.412	0.174	**0.057**	0.120	**0.078**	0.109	-0.223
Gautieria monticola	F	-0.228	0.669	0.625	0.327	-0.129	0.895	**0.100**	0.154	0.117	-0.287
Gomphus floccosus	F	-0.105	0.197	0.239	0.445	0.412	**0.095**	**0.059**	**0.084**	0.115	-0.115
Hydnotrya variiformis	S	0.976	0.942	-0.541	-0.529	0.638	0.245	0.168	0.107	0.272	**-0.086**
Lactarius rufus	F	0.568	0.320	-0.649	0.773	-0.218	0.418	0.181	**0.089**	**0.082**	-0.654
Morchella angusticeps	S	-0.707	0.840	0.684	0.854	-0.325	-0.476	-0.110	**-0.082**	**-0.043**	0.139

Table 1.5 (Continued). Logistic regression *p* – values of habitat attributes on fungal taxa collected on at least 3 units in either spring or fall. A negative sign preceding the *p* - value indicates an inverse correlation; values significant at $\alpha < 0.10$ are bolded.

Species	Season	Bulk Density	Total C %	‰ $\delta^{13}C$ depletion	Total N %	‰ $\delta^{15}N$ enrichment	C:N ratio	CWD	FWD	Litter mass	Mineral soil pH
Morchella angusticeps	F	**-0.019**	0.841	-0.177	0.576	0.722	0.981	0.637	0.138	0.235	**-0.053**
Ramaria cartilaginea	F	-0.218	0.215	0.727	-0.899	0.832	**0.076**	0.402	0.109	0.123	-0.224
Ramaria rasilispora	S	-0.298	-0.338	0.928	-0.114	0.928	**0.044**	0.528	0.341	0.483	-0.267
Rhizopogon vulgaris	S	-0.190	-0.588	**0.092**	-0.243	0.968	0.249	0.139	0.605	0.517	0.508
Rhizopogon vulgaris	F	0.573	**-0.086**	-0.262	-0.205	-0.793	-0.738	**-0.072**	-0.117	-0.113	0.522
Russula albonigra	F	-0.167	0.264	0.647	0.680	-0.816	0.613	0.252	0.167	0.184	**-0.088**
Russula brevipes v. brevipes	F	0.540	0.242	**0.081**	-0.403	0.531	0.249	0.147	0.835	0.461	0.163
Russula exalbicans	F	**-0.099**	0.233	0.502	0.180	-0.609	-0.511	0.331	0.399	0.183	-0.466
Russula integra	F	-0.109	**0.089**	0.115	-0.625	0.126	0.127	**0.080**	0.201	0.197	0.359
Sarcodon imbricatus	F	-0.439	-0.235	-0.442	0.768	**0.055**	0.107	0.687	0.296	-0.751	0.263

Table 1.5 (Continued). Logistic regression *p* – values of habitat attributes on fungal taxa collected on at least 3 units in either spring or fall. A negative sign preceding the *p* - value indicates an inverse correlation; values significant at $\alpha < 0.10$ are bolded.

Species	Season	Bulk Density	Total C %	‰ $\delta^{13}C$ depletion	Total N %	‰ $\delta^{15}N$ enrichment	C:N ratio	CWD	FWD	Litter mass	Mineral soil pH
Sarcosphaera coronaria	S	0.202	-0.708	0.894	0.582	-0.194	-0.233	-0.250	**-0.099**	-0.175	0.156
Suillus punctatipes	F	**-0.044**	**-0.080**	0.433	-0.511	**0.089**	**0.050**	-0.682	-0.808	-0.724	-0.392
Suillus tomentosus	F	**-0.097**	-0.966	-0.586	0.162	**0.085**	**0.053**	**0.056**	**0.043**	0.102	-0.561
Tricholoma focale	F	-0.424	-0.200	-0.743	0.524	0.144	**0.067**	0.572	0.339	0.762	0.737
Tricholoma saponaceum	F	0.226	0.506	0.317	**0.071**	0.502	0.610	0.425	0.325	0.357	-0.677

Figure 1.1. Map of prescribed burn treatments.

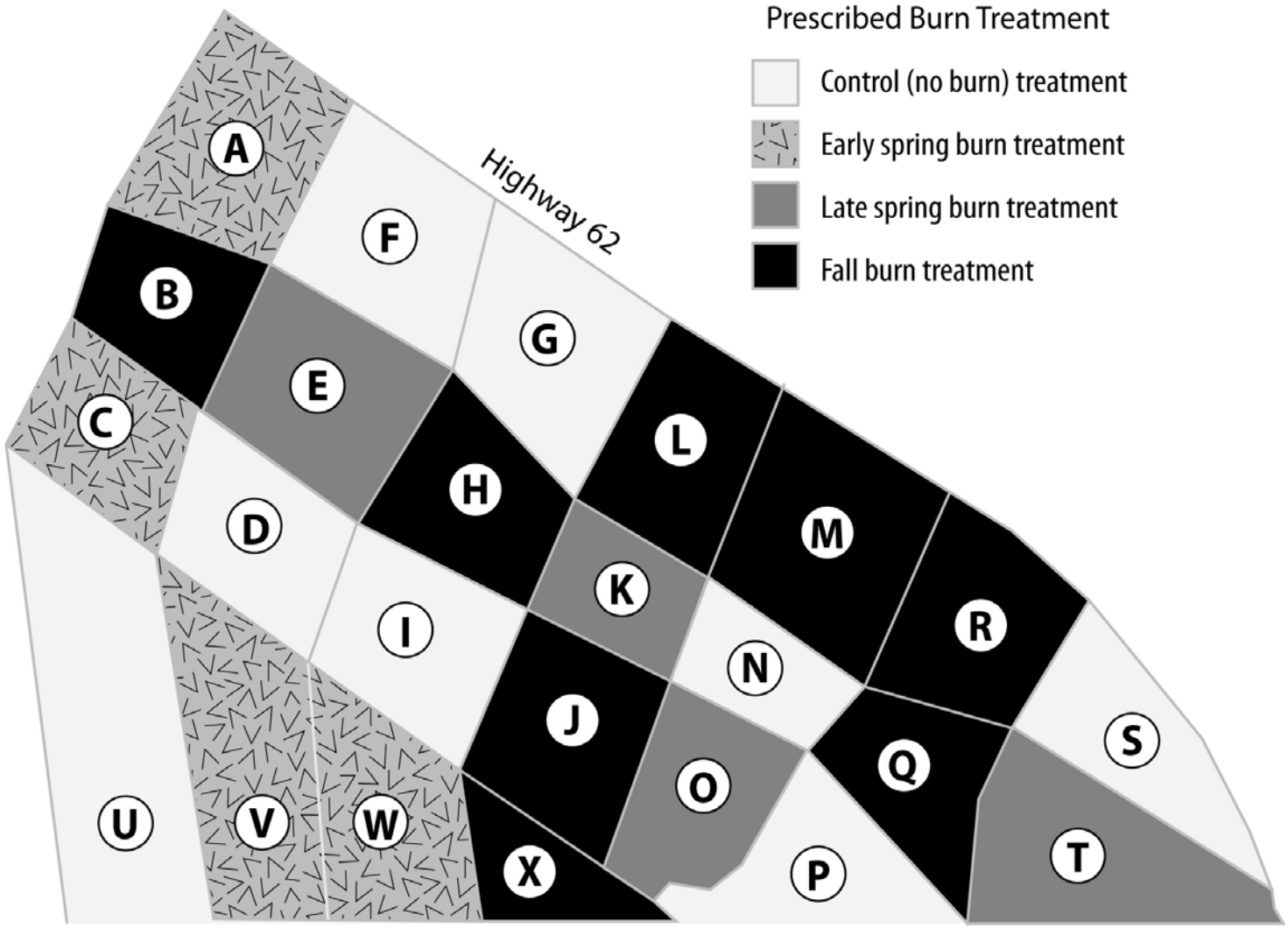


Figure 1.2. Ordination of habitat attributes for all units.

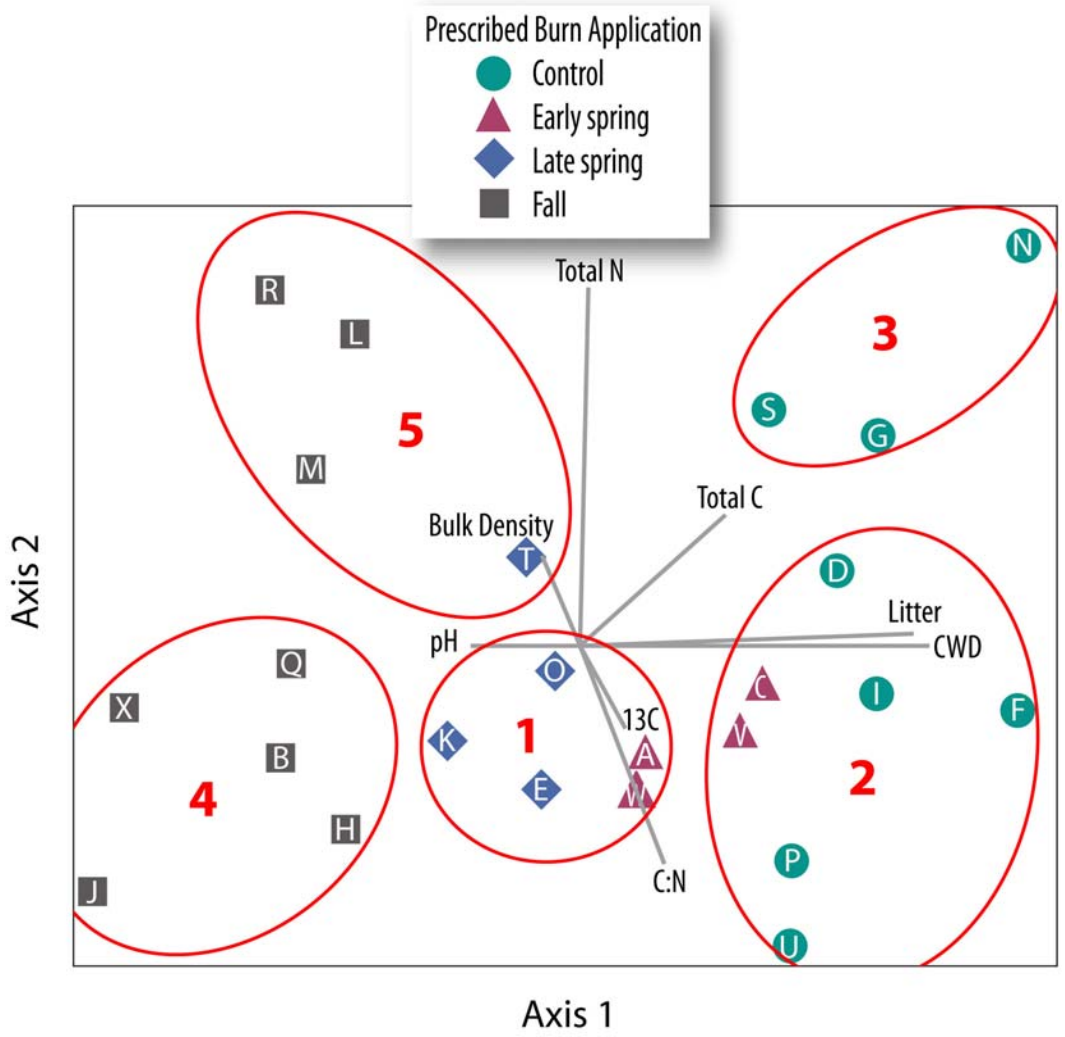


Figure 1.3. Dendrogram for the ordination of all treatment units, by habitat attributes.

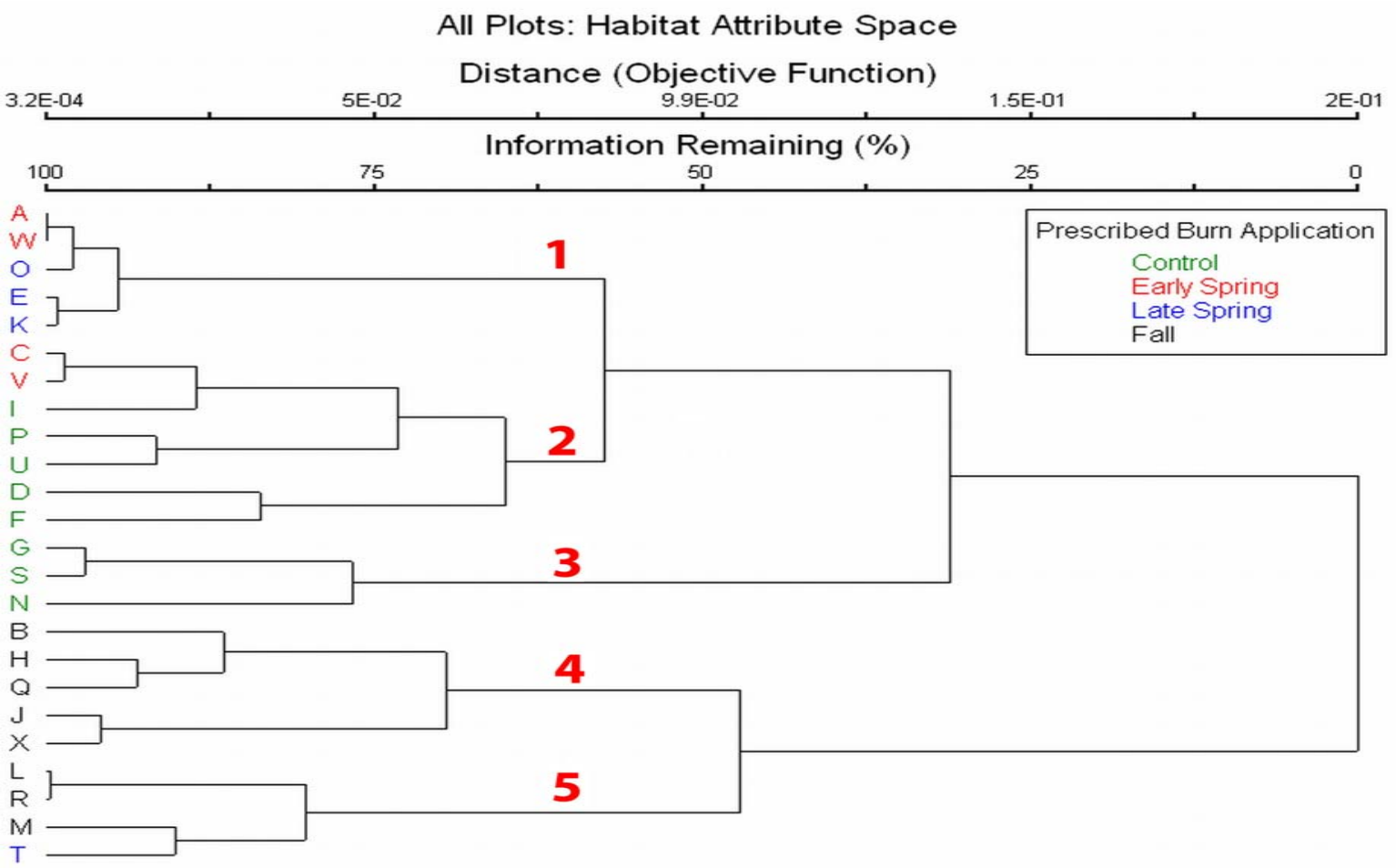


Figure 1.4. Ordination of spring collection units by habitat attributes.

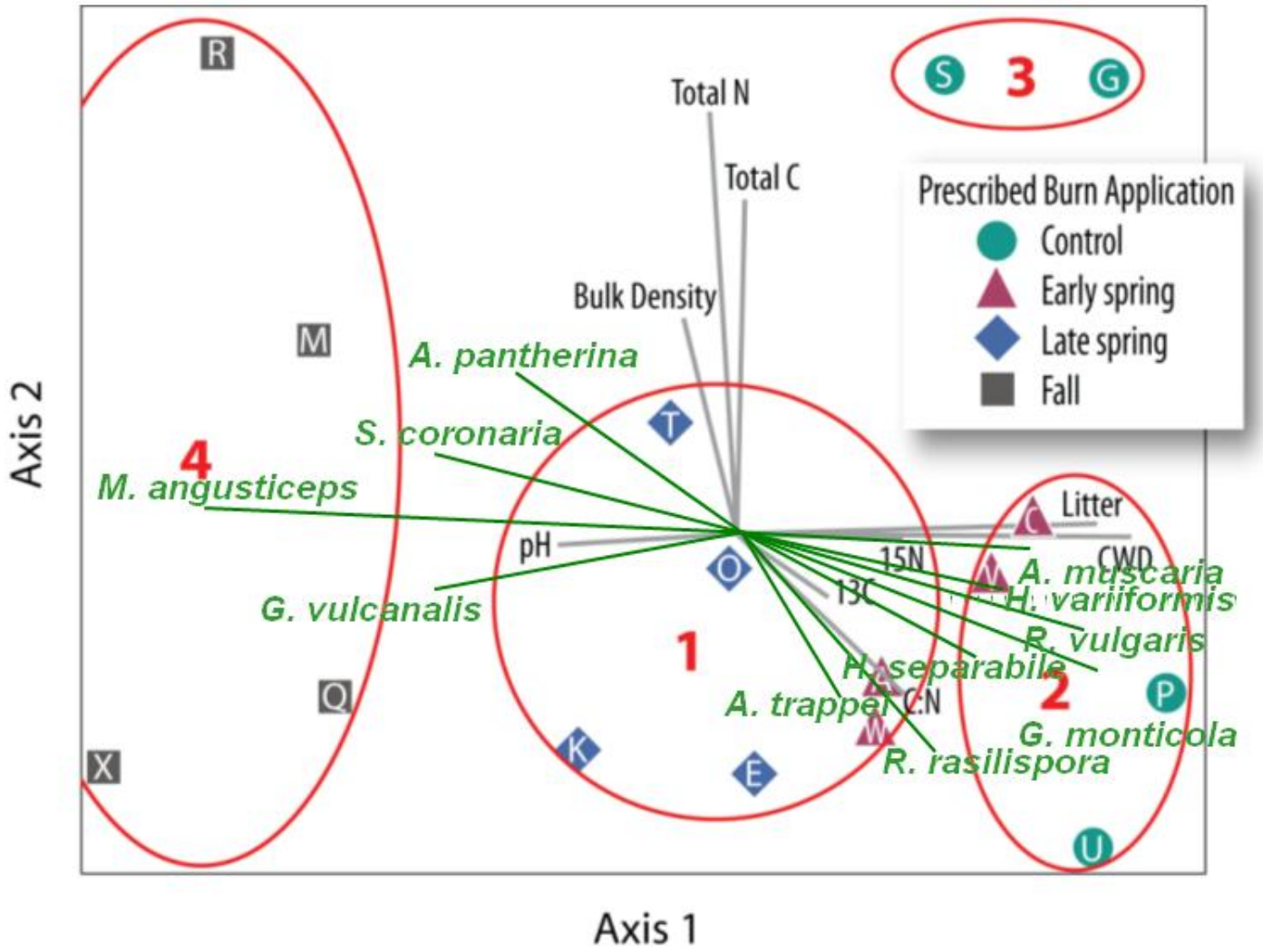


Figure 1.5. Dendrogram for the ordination of spring collection units by habitat attributes.

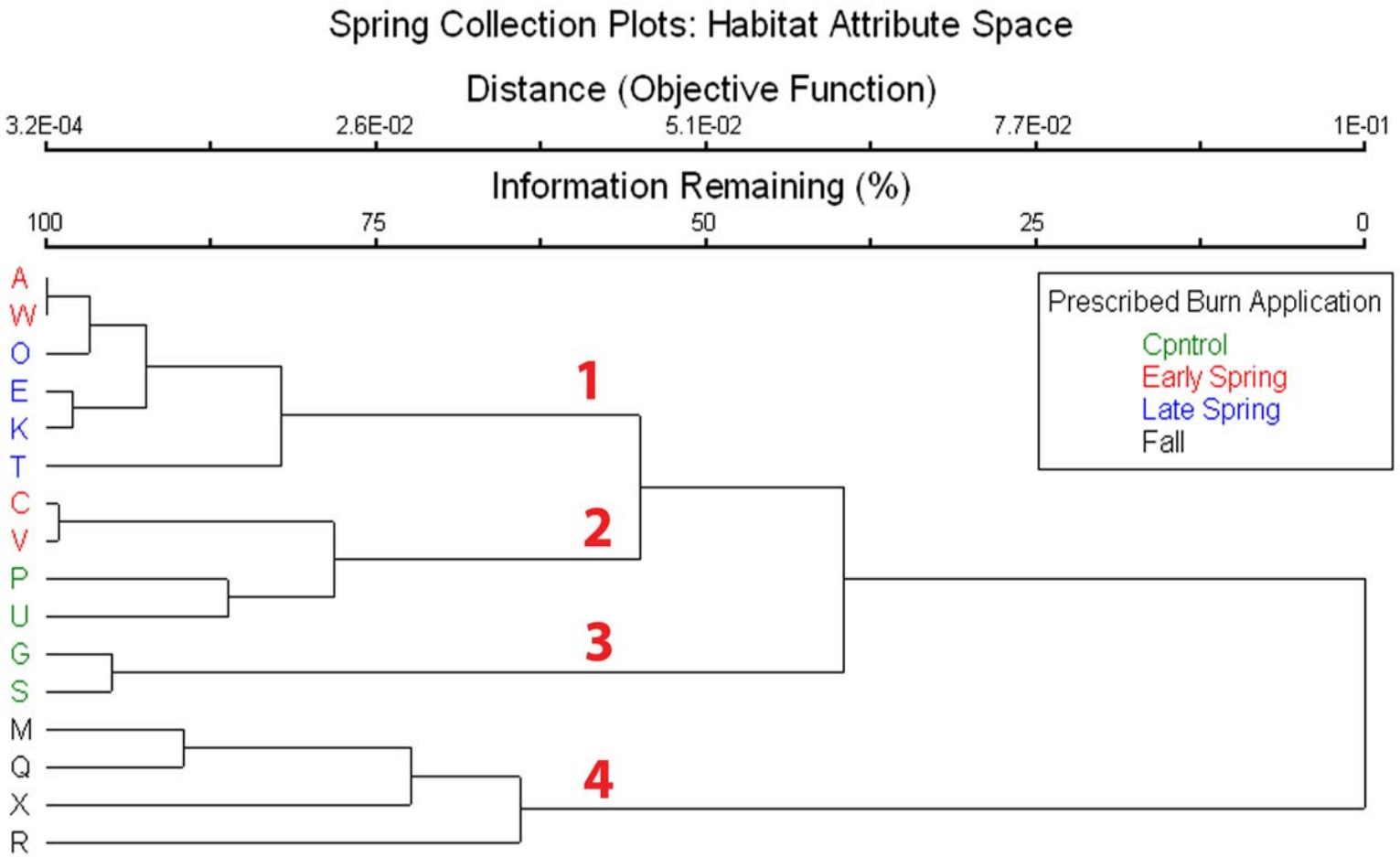


Figure 1.6. Ordination of spring collection units by fungal species assemblage.

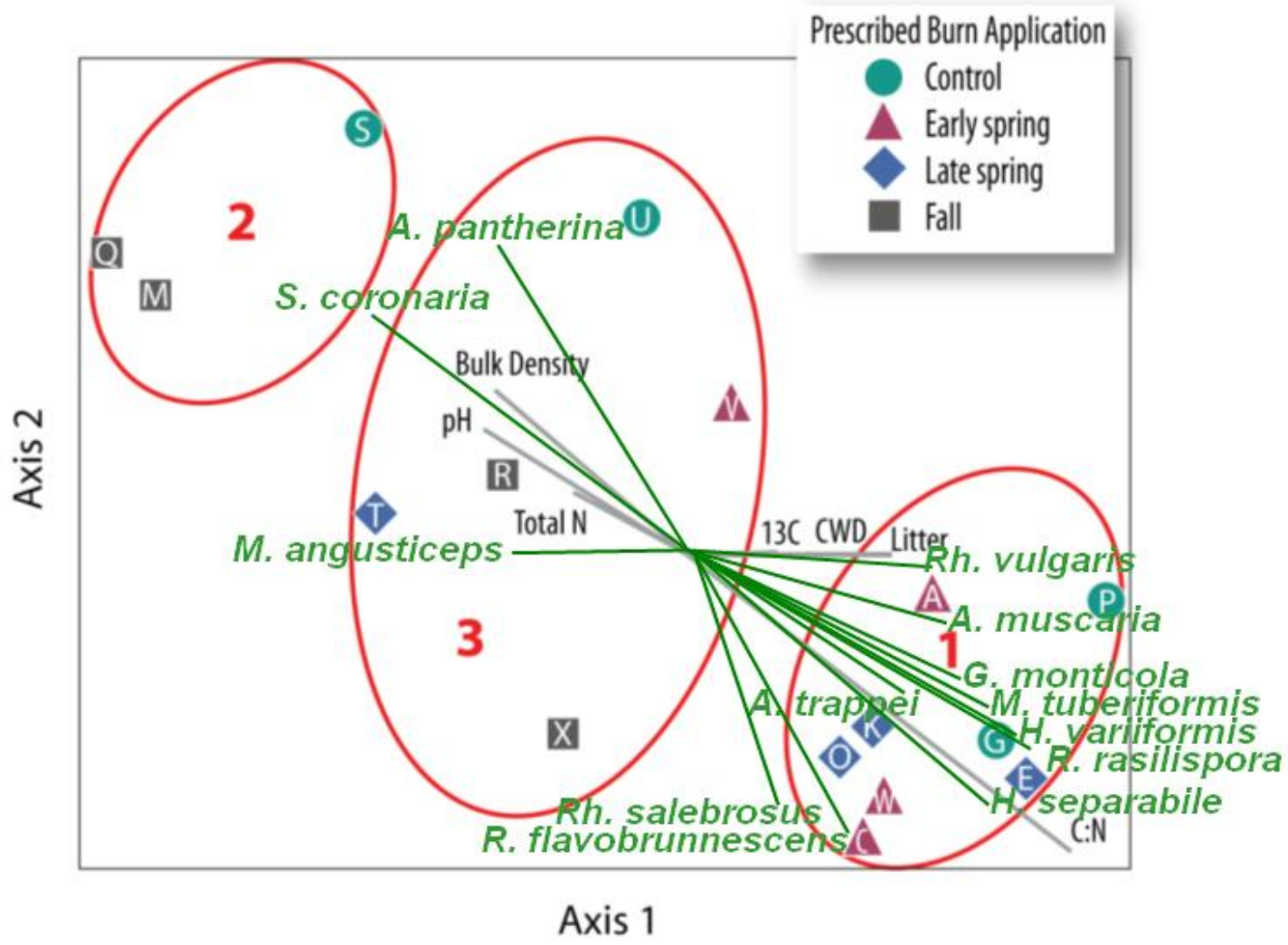


Figure 1.7. Dendrogram for the ordination of spring collection units by fungal species assemblage.

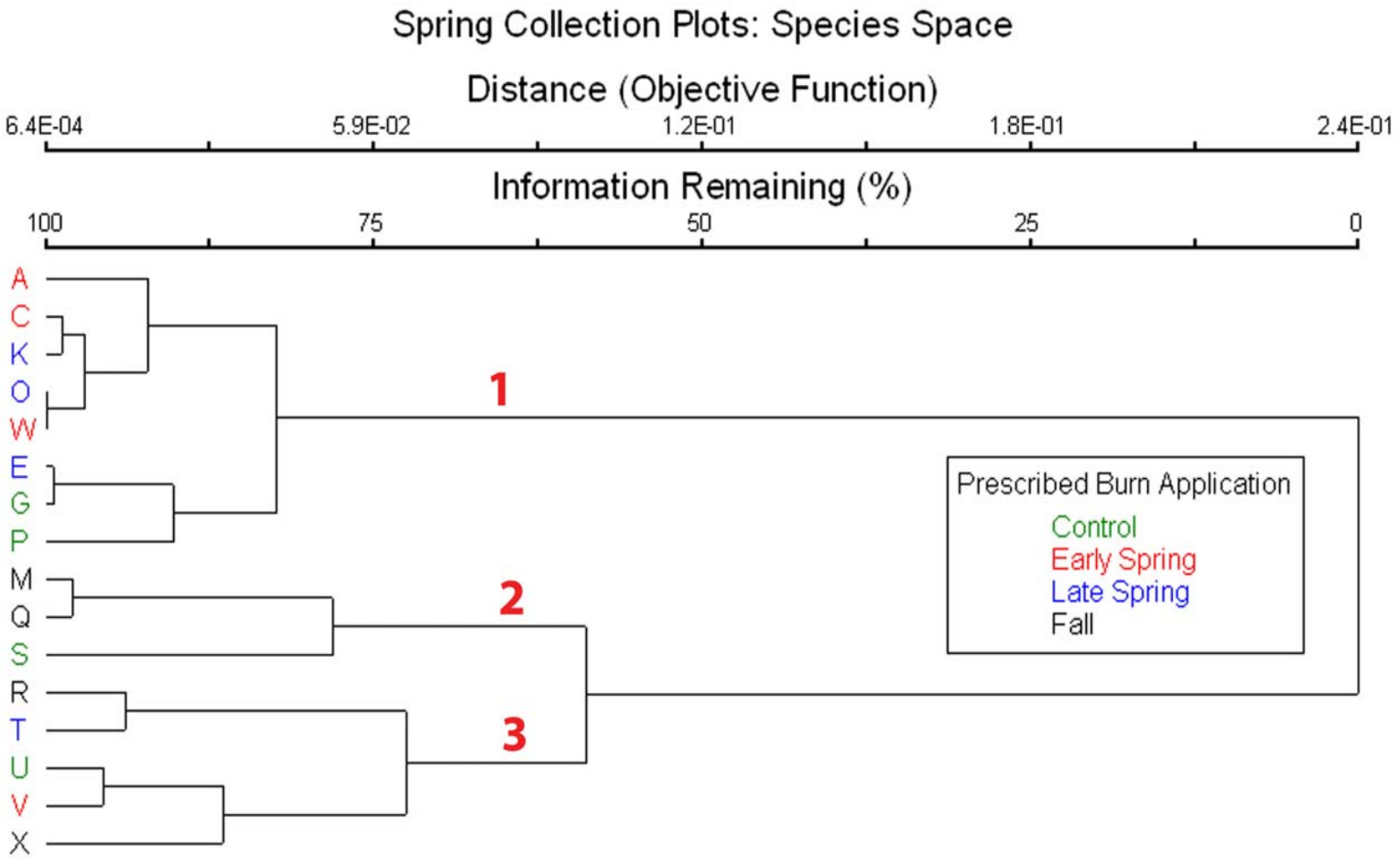


Figure 1.8. Ordination of fall collection units by habitat attributes.

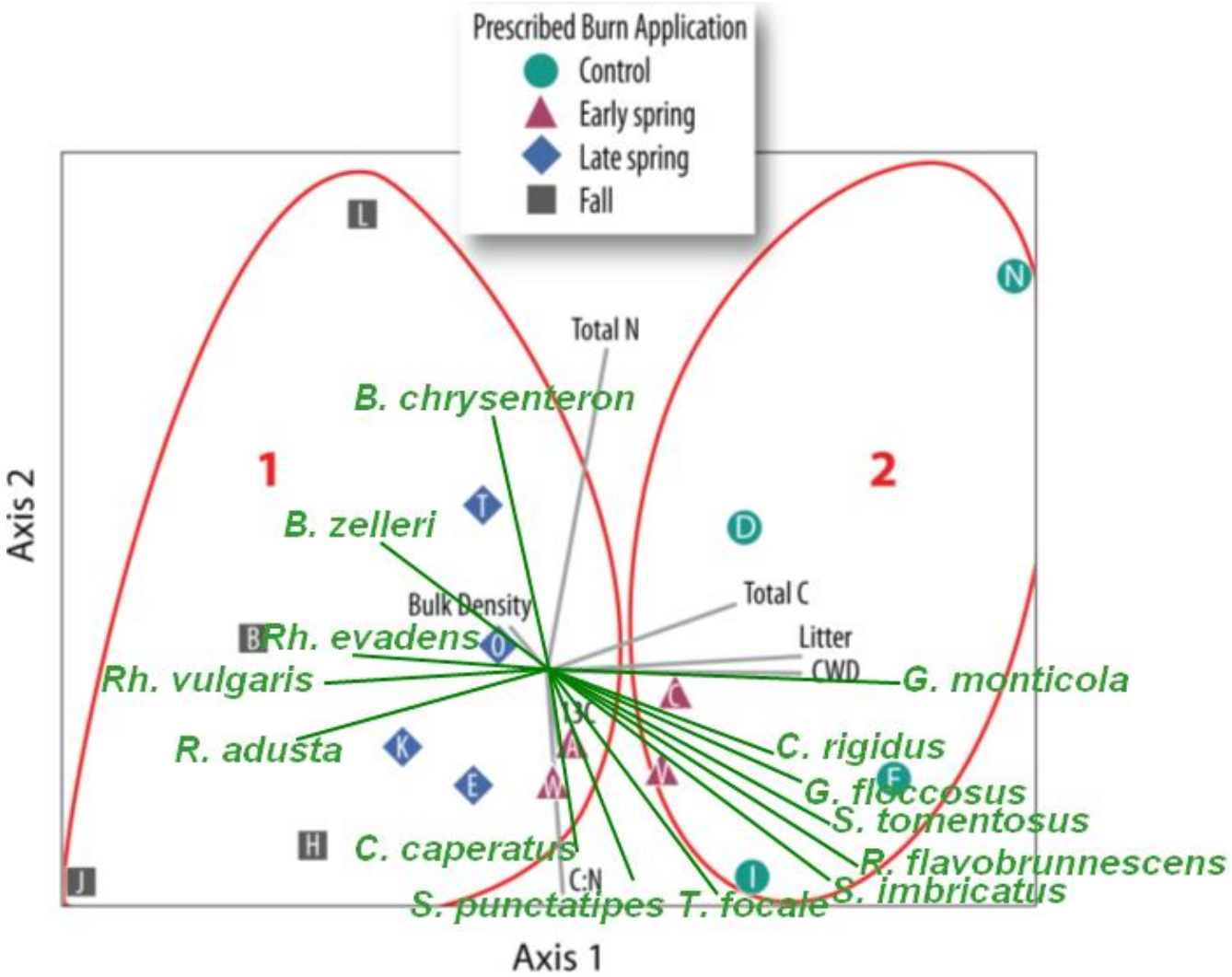


Figure 1.9. Dendrogram for the ordination of fall collection units by habitat attributes.

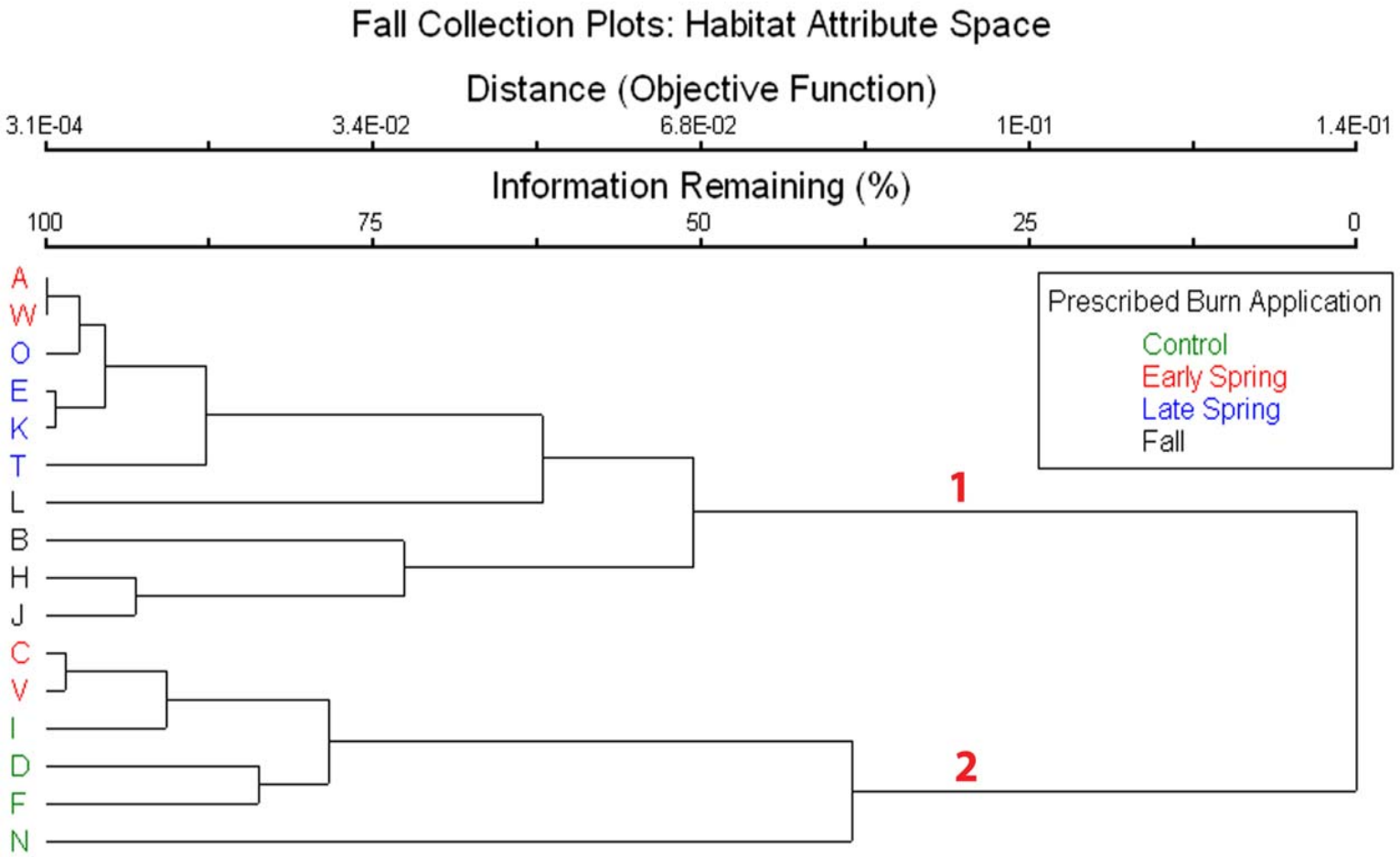


Figure 1.10. Ordination of fall collection units by fungal species assemblage.

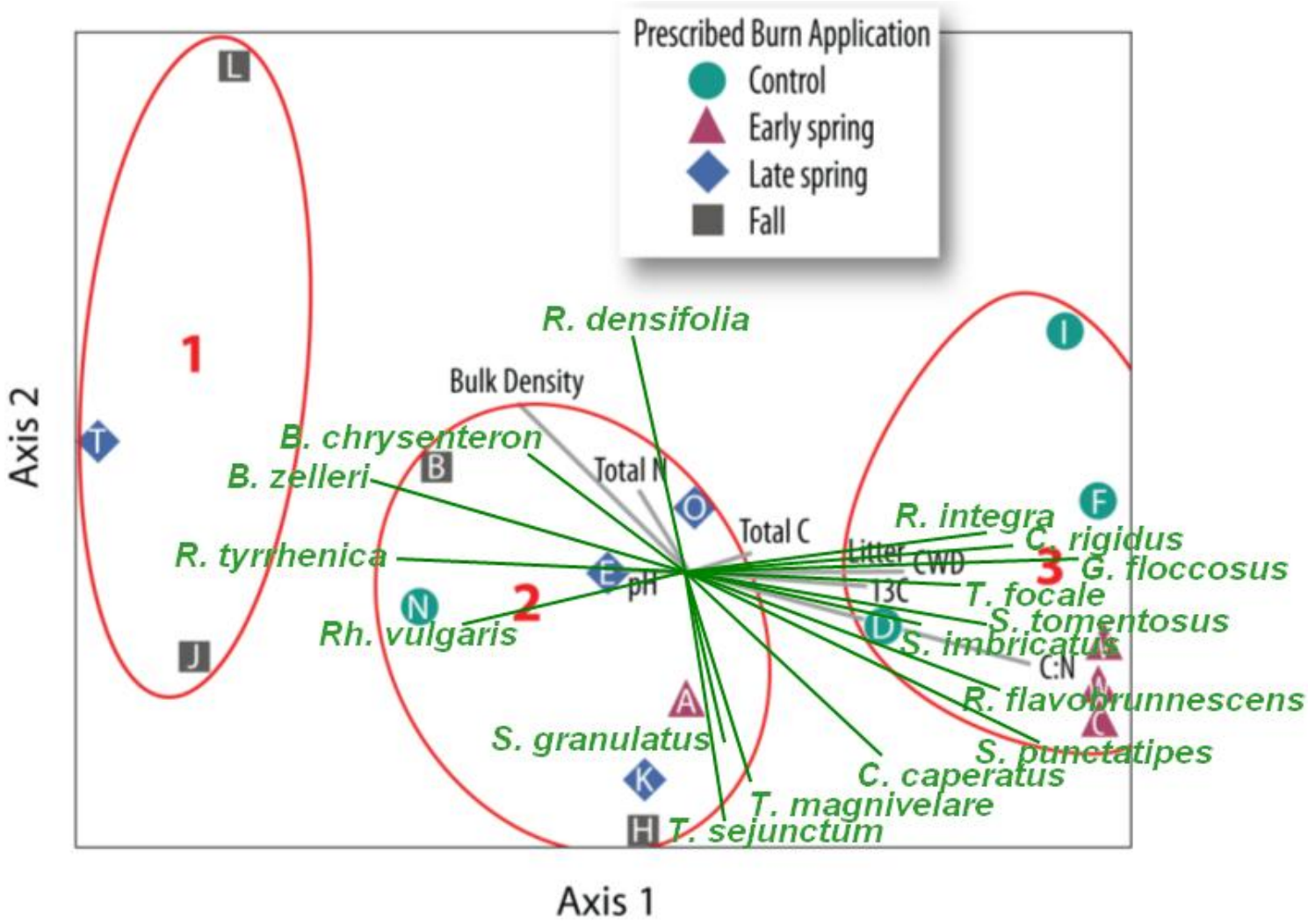


Figure 1.11. Dendrogram for the ordination of fall collection units by fungal species assemblage.

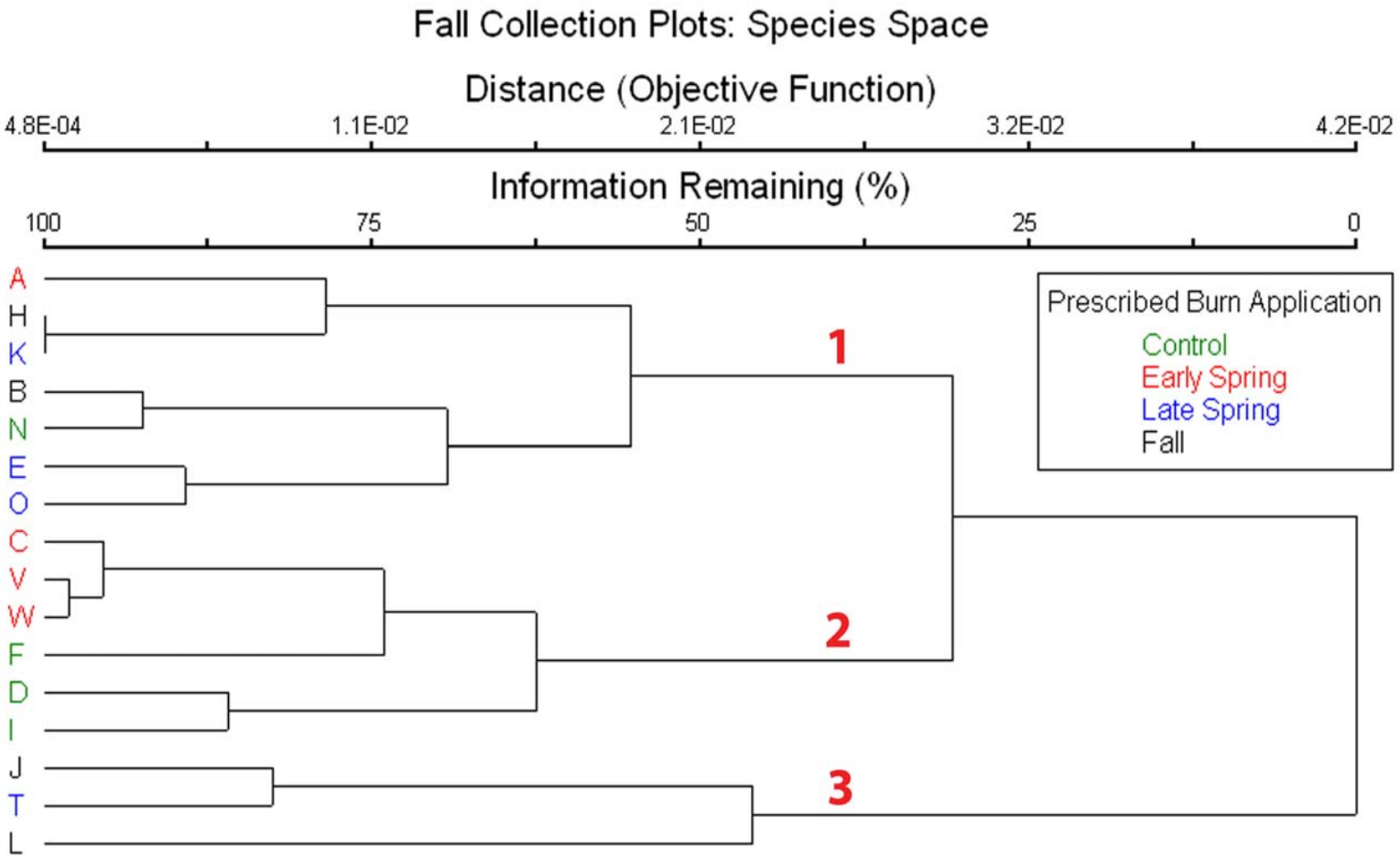


Figure 1.12. Map of mineral soil bulk density.

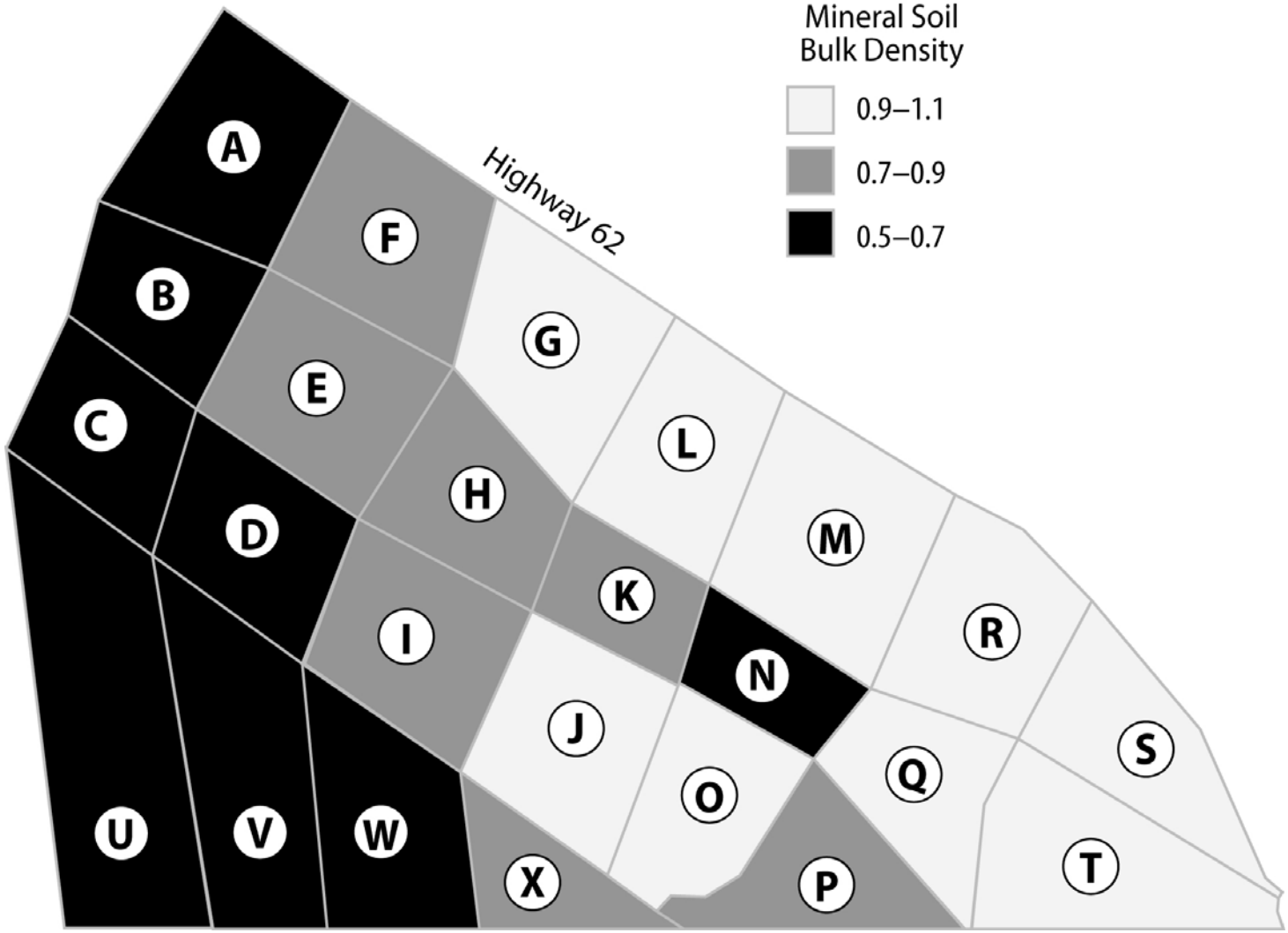


Figure 1.13. Map of $\delta^{13}C$ depletion.

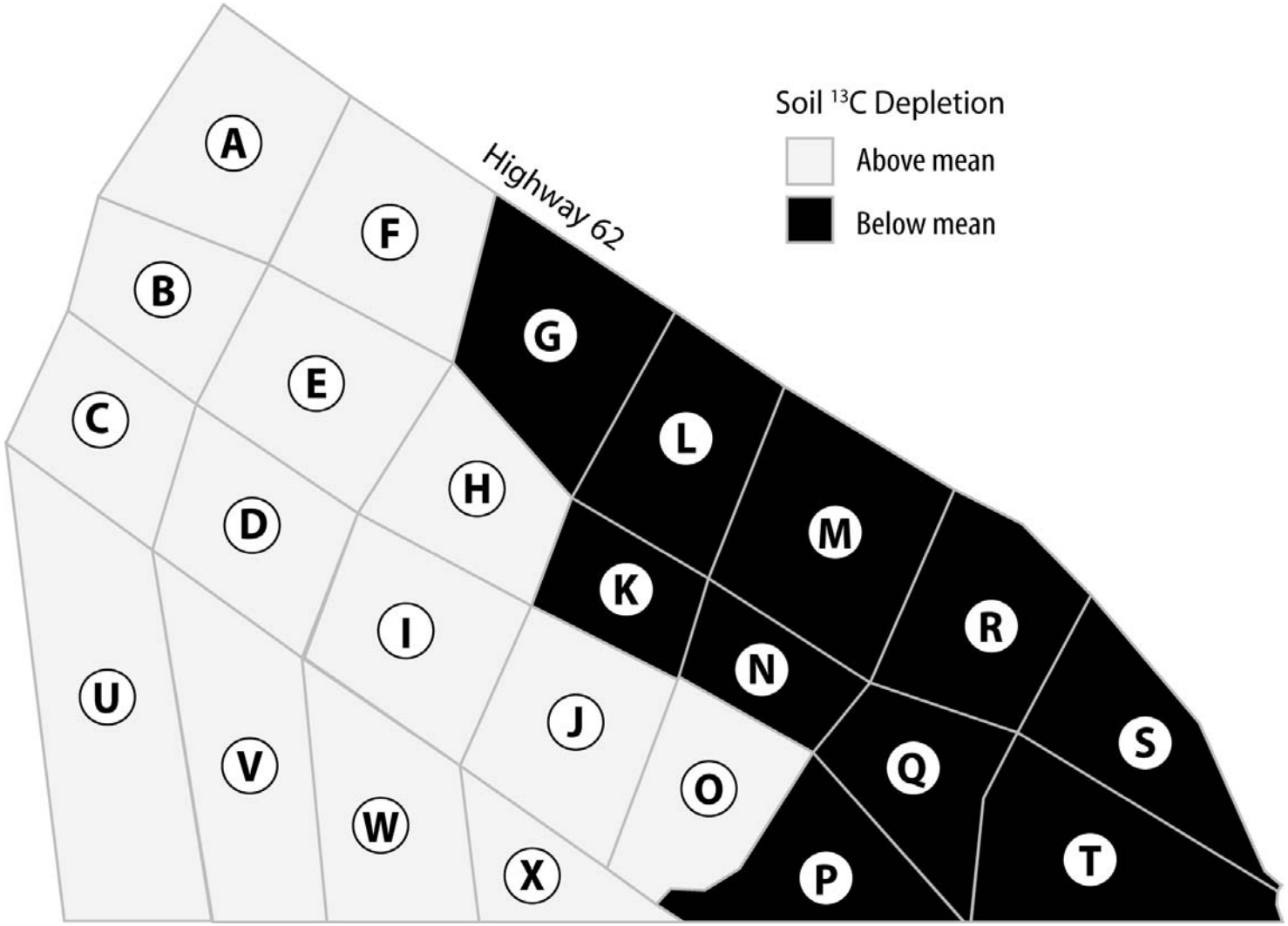


Figure 1.14. Map of soil N distribution.

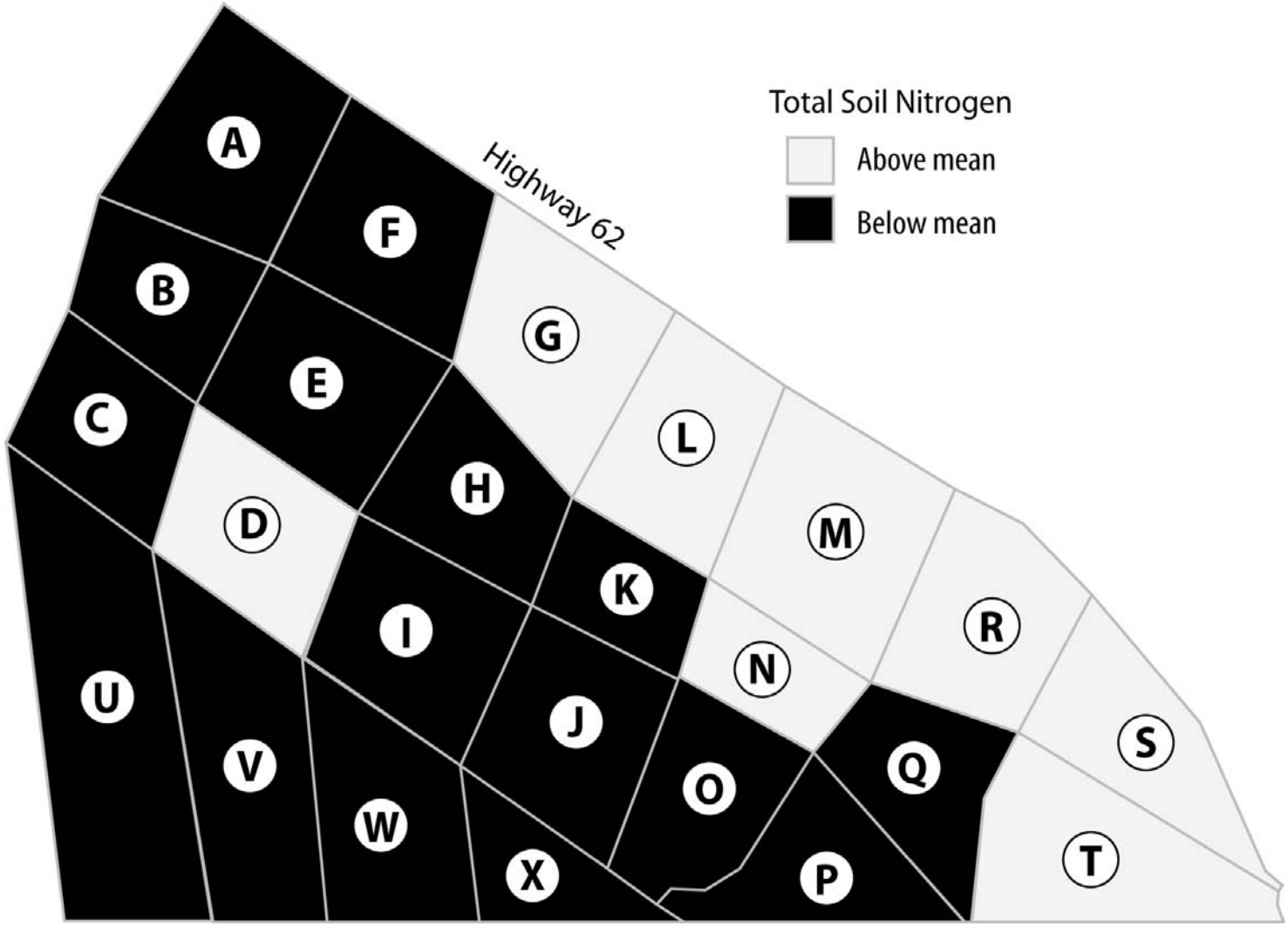


Figure 1.15. Map of C:N ratios.

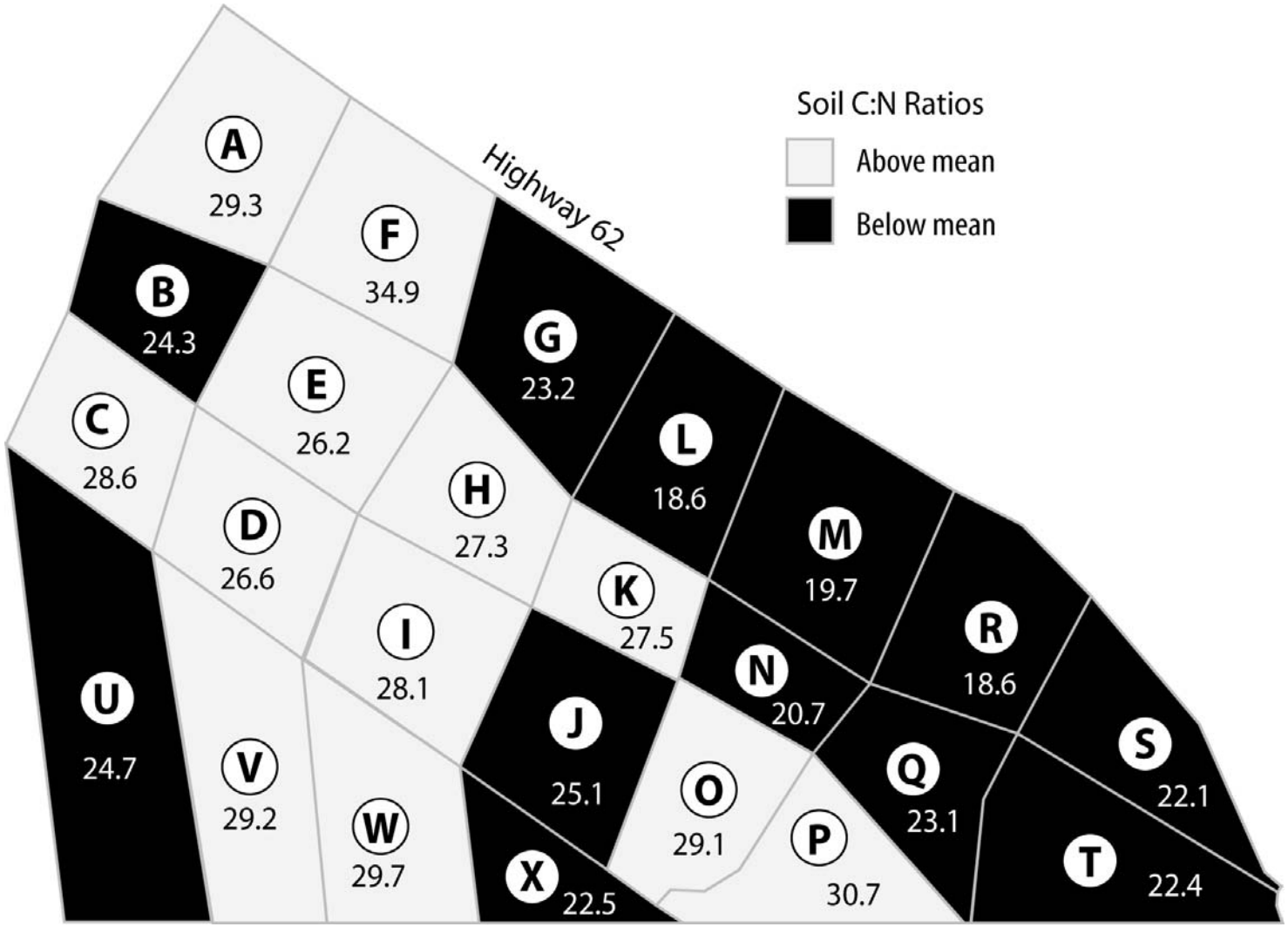
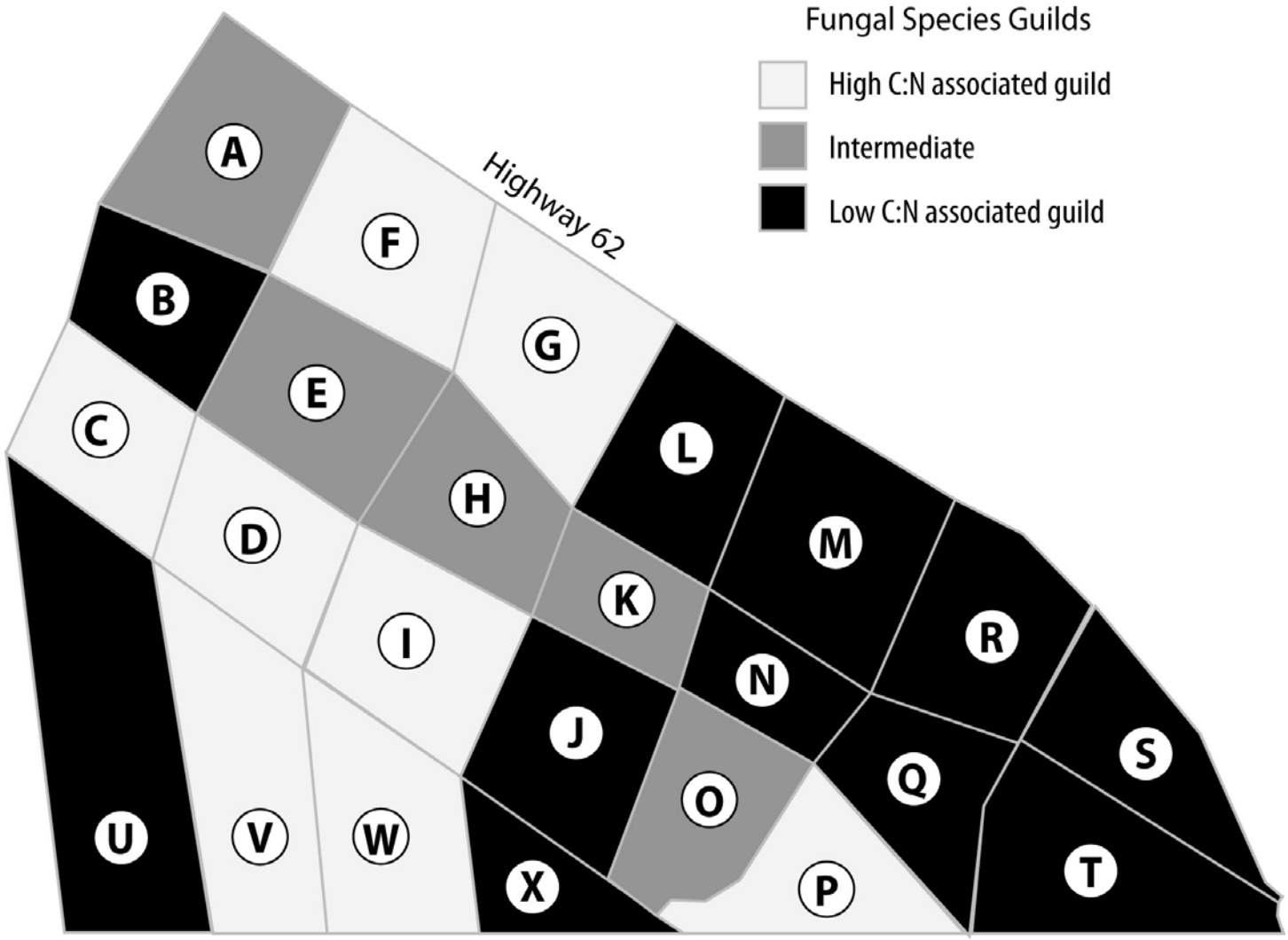


Figure 1.16. Map of mycorrhizal fungi guild indicator species fruiting patterns.



RELATIONSHIPS OF CURRENT AND PAST ANTHROPOGENIC DISTURBANCE TO MYCORRHIZAL SPOROCARP FRUITING PATTERNS AT CRATER LAKE NATIONAL PARK

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Relationships of current and past anthropogenic disturbance to mycorrhizal sporocarp fruiting patterns at Crater Lake National Park

Abstract

Intensive recreational use of alpine areas can create localized areas of concentrated disturbance where vegetation is altered, soils compacted, and surface fuels depleted. Many aspects of this disturbance type have been studied, but no research has focused on the effects of recreational use on mycorrhizal fungus sporocarp production. We measured the effects of recreational land or site use on soil properties and fuel levels, and related these attributes to mycorrhizal fungal sporocarp production at abandoned and in-use recreational sites at Crater Lake National Park over a three-year period. Significant differences were found between control and disturbed sites in soil bulk density, ^{15}N enrichment, and fuel levels, but not in total fungal collections or species diversity at the macrosite scale. Our sampling methodology was not designed to quantify the effects of anthropogenic disturbance on fungal fruiting patterns at the microsite scale, but there were clearly profound detrimental effects on fungal productivity in the most disturbed microsites. Within the disturbed units, the paucity of fungi collected in highly disturbed microsites was offset by the abundance and diversity of mycorrhizal fungi collected in protected microsites. Many fungi in this study did not demonstrate significantly different fruiting patterns or preferences between sites or treatments at the macrosite scale, but several indicator taxa were identified.

Introduction

Crater Lake National Park (CLNP) has been the site of concentrated recreational activities for over 100 years. Well before it was designated a National Park in

1902, areas near roads with flat ground and access to water were popular resting stops for wayfarers in the Crater Lake area. For example, the Cold Springs area was on the military road from Ft. Klamath to Medford and had been used for this purpose since approximately 1865. It was developed into a formal campground for park visitors in the early 20th century and decommissioned in the 1950's. Evidence of this history is apparent in the plant community (Wilson 2007) and soil properties to this day.

The response of mycorrhizal fungus fruiting patterns to disturbance is important because fungal sporocarps are a significant food source for wildlife (North et al., 1997; Cazares et al., 1999; Claridge et al., 1999; Mattson et al., 2002; Claridge and Trappe, 2004; Ashkannejhad and Horton, 2006; Jones et al., 2006) and hence are an important response variable to evaluate the effects of disturbance on wildlife carrying capacity. Another management consideration is that several mycorrhizal fungi in southwestern Oregon produce valuable edible mushrooms, such as matsutake (*Tricholoma magnivelare* Peck [Redhead]), chanterelles (*Cantharellus* and *Craterellus* spp.), king boletes (*Boletus edulis* Bull.), and morels (*Morchella spp.*) (Molina et al., 1993; Pilz and Molina, 2002).

Several researchers have examined the effects of recreational use on forested sites. Brown et al. 1977) found that soil compaction increased penetration resistance to water and slowed the growth of adjacent trees, with implications for C and N cycling. Kuss (1986) found that coarse-grained, highly porous, and sandy loam soils like those encountered at CLNP are more susceptible to compaction damage than silty clays. Parish (1971) reported loss of macropore space in compacted soils, resulting in an increase in soil moisture at the expense of soil air. Schumacher and Smucker (1984) observed root damage possibly resulting from hypoxic conditions in compacted soils, and Cole (1986) measured

reduced water potential in highly impacted sites. These conditions can persist for many years, and may explain the significant differences in vegetative cover between long-abandoned sites and undisturbed controls (Wilson 2007).

Soil compaction affects the ability of plants to propagate fine roots throughout the soil (Alessa and Earnhart 2000), and alters soil microbial communities in surface horizons (Zabinski and Gannon 1997). Waltert et al. (2002) found that mycorrhizas of mature trees in a Swiss beech (*Fagus sylvatica* L.) forest were not adversely affected by trampling, but those of seedlings were.

No studies to date have addressed the impacts of recreational use or soil compaction on mycorrhizal fungus fruiting patterns. We characterized soil properties and fuels levels, and surveyed mycorrhizal sporocarp fruiting patterns over a three year period at sites representing both past and current use paired with relatively undisturbed controls.

Our first hypothesis was that a history of intense anthropogenic disturbance influences belowground habitat, 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 coarse woody debris (CWD), fine woody debris (FWD) and litter mass. Our second hypothesis was that intense anthropogenic disturbance influences mycorrhizal fungus fruiting patterns, as measured by sporocarp inventories conducted over multiple years.

We combined the fuels data of Wilson (2007) with our soil attribute measurements to quantify many of the physical changes brought about by the current and past site use and related these to mycorrhizal fungus fruiting patterns.

Methods

Six sites with current or historic anthropogenic disturbance were paired with six relatively undisturbed control sites. The disturbed sites consisted of three active campsites (Mazama Village early seral, Mazama Village late seral, and Mason's Camp), two abandoned campsites (Annie Springs and Cold Springs), and one abandoned maintenance site (Anderson Bluffs). Control sites were of similar structure and age as the disturbed sites and, in all but one case, located near their disturbed counterpart.

We collected and identified both epigeous and hypogeous mycorrhizal fungal sporocarps on 1000 m^2 plots at each site in the spring and fall over three years. Site data including mineral soil bulk density, total mineral soil N, total mineral soil C, C:N ratio, $\delta^{15}N$ enrichment, $\delta^{13}C$ depletion, mineral soil pH, CWD mass, FWD mass, litter mass, stand age, and elevation were measured. We analyzed these data in several different ways to determine effects of past and current use on habitat attributes and fungal fruiting patterns and to seek relationships within and between the habitat attributes and fungal fruiting patterns.

Study sites

All of the study sites were in CLNP in southern Oregon, and all but one were in the southern half of CLNP (Fig. 1). Most sites were dominated by noble fir (*Abies procera* Rehder) and mountain hemlock [*Tsuga mertensiana* {Bong.} Carr.], and many had white pine (*Pinus monticola* Dougl.), or lodgepole pine (*Pinus contorta* Dougl. ex Loud.). Elevations ranged from 1750 to 1950 m and usually were snow-free from July to November. Throughout this discussion the plots will be abbreviated by their initials followed by the letter "C" for control and "D" for disturbed, eg. the Anderson Bluffs control plot is designated ABC and the

disturbed plot ABD. Soil types were identified from the Soil Survey of Crater Lake National Park, Oregon (Natural Resources Conservation Service, 2001) and site histories are from Unrau (1988), Kritzer (2001), and Wilson (2007).

Anderson Bluffs (ABC and ABD)

The Anderson Bluffs plots lie to the east of Pinnacles Road, 1 mile south of Rim Drive. This area was in regular use as a maintenance yard from the 1890s to 1980 and is still occasionally employed as a place to store gravel and road maintenance equipment. The disturbed plots are large areas south of the entry road with few trees, and had been used historically for heavy equipment parking and turnaround.

The control plots are located north of the entry road in an area of forest that has never been subjected to regular vehicular traffic. Both disturbed and undisturbed plots have noble fir, mountain hemlock, white pine, and lodgepole pine. Understory is minimal and mainly composed of *Arctostaphylos* and *Chimaphila*; soils are of the Union Peak-Sun Notch-Castlecrest series.

Annie Springs (ASC and ASD)

The Annie Springs disturbed site lies just west of Annie Springs. It was the site of the original CLNP headquarters complex, a Civilian Conservation Corps camp in the 1930s, and a campground until the 1950s. The site is at the foot of a steep escarpment and has large noble fir and mountain hemlock trees throughout. Several old roads through the area are regenerating with dense mountain hemlock and lodgepole pine saplings. Remnant asphalt chunks are scattered under the litter layer, as well as ceramic electrical insulators, old cans, and other archeological debris. Due to the lack of undisturbed forest in this area, the control

site was located at the northwest corner of CLNP. Although spatially disjunct, the control site shares the same plant community, stand structure, and soil type (Castlecrest gravelly ashy loam) as the Annie Springs disturbed site.

Cold Springs (CSC and CSD)

The Cold Springs Campground area lies on the east side of Highway 62 just north of the Lodgepole Picnic Area. The road network and camping pads are only detectable by careful observation today, but were extensive when in use. The stand is mostly larger noble fir and mountain hemlock, with scattered lodgepole pine. Former camping pads and roadways are more sparsely treed and mostly support moderately sized (~10-15 cm DBH) lodgepole pine. The control plots are across Highway 62 in a thickly vegetated forest of noble fir and mountain hemlock with a dense understory of lodgepole pine. This stand has significant ground and ladder fuels. Soils are Castlecrest gravelly ashy loam.

Mason's Camp (MCC and MCD)

The Mason's Camp group camp area is located west of Pinnacles Road just north of Lost Creek Campground. It was established in 1955 as a group camp but is closed to the public except for events by reservation, and has been used by the Masons for annual ceremonies since about 1980. The site has a large cleared area around a fire pit and the surrounding area has been used for parking. The site has large noble fir and mountain hemlock scattered about and occasional smaller lodgepole pine in the understory. The control plots lie about 0.5 km south of the campsite, near the water collection facility for the Lost Creek Campground. These plots contain mature noble fir and mountain hemlock and are at the base of a steep talus slope. Soils are of the Union Peak-Sun Notch-Castlecrest series.

Mazama Village (MVEC, MVED, MVLC, and MVLD)

The Mazama Village Campground sites were established between 1957 and 1962 and has been the largest camping area in CLNP ever since. They are located to the east of Highway 62 just north of the CLNP entrance station on the west rim of Annie Canyon. There were two ecotypes at Mazama Village: one with a late seral forest structure (MVLC and MVLD) and one an early seral structure (MVEC and MVED). The MVLD site is dominated by mature noble fir and mountain hemlock > 300 years of age: survey plots are located in campground loops C and D. Disturbed plots encompassed several campsites in current use, and most of the soil surface lacked any litter layer and was highly compacted, except for microsites within the driplines under smaller trees between camping pads. The control site lies to the east, across Annie Canyon from the disturbed plots.

The early seral sites are dominated by lodgepole pine, with some younger noble fir and mountain hemlock ca. 100 years of age. The disturbed plots are in campground loops B and E, and the control plots were located to the south of the campground in a stand of almost pure young lodgepole pine. Soils are Castlecrest gravelly ashy loam.

Fungal sporocarp sampling

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 the most likely microhabitats and maximize data collection. The method has been successfully used to quantify fungal diversity and habitat associations over broad ecotypes in southeastern Australia (Claridge et al. 2000). Field trials of time-constraint

sampling conducted at CLNP 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).

At each sampling iteration, one survey plot was established in each site. Sampling was performed each spring and fall for three years. Survey plots were moved within sites from season to season to eliminate effects of previous sampling efforts.

Fungal species identification

Fungal collections were identified by standard morphological methods augmented by restriction fragment length polymorphism (RFLP) analysis and sequencing of immature, degraded, or cryptic specimens. The internal transcribed spacer (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 species collected at CLNP originally were described 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 (pers comms., J. Ammirati, G. Bonito, and M. Castellano). Thus, many taxa given European names in this study are probably closely related to, but not the same as their European counterparts. Additionally, several genera (most notably *Cortinarius* and *Russula*) are taxonomically unresolved in North America, so in some cases, the names used may represent morphologically as yet indistinguishable species complexes. All collections were accessioned in the Oregon State University Mycological Herbarium (OSC).

Several researchers have attempted to link belowground mycorrhizal communities with aboveground sporocarps (Gardes and Bruns 1996; Dahlberg et al. 1997;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. Since 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. Certainly, a significant part of the mycorrhizal community in this ecosystem produced few or no sporocarps during our sampling, but an inventory system based on sampling root tip associated mycorrhizae was beyond the scope of this project. Due to tremendous variability in biomass between taxa and between seasons we chose to focus on fungal communities, rather than on standing crop biomass as indicative of a site's effect on the food web.

A relatively small number of saprobic species also were collected on the plots but were not included in data analysis. These were *Caloscypha fulgens* (Pers.) Boud., *Gastropila fumosa* (Zeller) P. Ponce de León, *Gastropila subcretacea* (Zeller) P. Ponce de León, *Collybia oregonensis* A.H. Sm., *Hypholoma capnoides* (Fr.) P. Kumm., *Lepiota magnispora* Murrill, *Lepista subconnexa* (Murrill) Harmaja, *Nivatogastrium nubigenum* (Harkn.) Singer & A.H. Sm., *Pholiota spp*, *Pluteus cervinus* P. Kumm., *Spathularia flavida* Pers., *Stropharia hornemannii* (Fr.) S. Lundell & Nannf., and *Trappea darkeri* (Zeller) Castellano.

Soil cores and bulk density

Soil cores were taken at a 10 cm depth from the surface of the B horizon with a 196.4 cm^3 AMS hammer type corer. Eighteen cores were taken from each study site. In the disturbed study sites, 9 "high impact" cores were taken from the most heavily disturbed areas, e.g., in campground sites comprised of the bare, heavily

trafficked areas around tables and fire rings, and 9 "low impact" cores were taken from interstitial areas, under the driplines of smaller trees and otherwise away from the most intense disturbance. Cores were dried at 60° C for 12 h and weighed. The weight was divided by the core volume to determine bulk density.

Almost all fungi in disturbed sites were collected in the relatively undisturbed low impact, low bulk density interstitial areas. Consequently, for soil analyses, ordinations, and logistic regressions we used only the 9 "low impact" cores from the disturbed sites. For each control site, 9 of the 18 cores were selected randomly for soil chemistry analysis.

Soil chemistry analysis

Cores were screened and ground to a sand consistency. One gram of fine soil from each sample was mixed in 5 ml of deionized water and the pH measured after 1 h of equilibration. Another 10 g from each core was further ground to flour consistency and 50 - 70 mg subsamples were weighed carefully into 8 x 5 mm tin cups and sent to the UC Davis Stable Isotope Facility for total C content, total N content, and $\delta^{13}C/^{15}N$ isotopic analysis.

Fuels: litter mass, fine and coarse woody debris

Fuels data are from Wilson (2007). Coarse (> 7.6 cm diameter) and fine (0.6 – 7.6 cm diameter) woody fuels were measured along these transects by Brown's (1974) planar-intersect method. Litter mass was determined by measuring the organic horizon depth at 14 locations per survey plot and collecting 4-6 samples per plot for site specific bulk density determination in the laboratory. Mass then was calculated by multiplying the laboratory determined bulk density by the field measured average forest floor depth.

Stand age and elevation

Stand age was determined by increment coring of 3 to 6 trees on each plot, augmented by counting rings on felled trees where available. In some cases, the boles were too large for the corer to reach the center; the age of these is presented as "greater than" the actual core ring count (e.g. >300 years). Topographic maps determined the elevation of each site.

Data analysis

Correlations among habitat attributes were identified with Pearson's analysis. Logistic regression identified correlations between species presence/absence and habitat attributes. Two-tailed Tukey-Kramer analysis tested for significant differences in habitat attributes, species diversity and abundance between disturbed and control sites. An (ln+1) transformation was applied to the variables of CWD, FWD, and litter mass. Correlations, regressions, and t-tests were performed with SAS statistical software (SAS 9.1, 2003).

Taxa collected on more than 9 plots or less than 4 plots were removed as they were uninformative to correlations (too few or too many to draw inferences), resulting in a dataset of 39 taxa. Sporocarp collection data were converted to presence-absence for ordination analysis and logistic regression.

Non-metric multidimensional scaling (NMS; Clark 1993), a form of ordination analysis (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 datasets, producing

a scattergram of the treatment sites that spatially orients them to minimize residuals between all variables. The solution with the lowest cumulative residuals (stress) may be in multidimensional space.

NMS ordination can be performed on the habitat attribute data, providing a scattergram graphically depicting relatedness of sites based on their soil and fuel properties. It also can be performed on species data, providing a scattergram depicting relatedness of sites based on their species assemblages. For each ordination, vector overlays of either habitat attributes or species assemblage can be applied, allowing visual interpretation of species associations with habitat attributes.

Cluster analysis (a companion procedure in PC-ORD) enables the objective identification of groups in the ordination whose members are closer to one another than they are to members of other groups. In species space, this can be used to identify biological guilds, and in habitat attribute space, it can be used to compare habitat attribute patterns with treatments.

Ordination mechanics

Numbers of collections and species diversity were excluded from habitat attribute ordination datasets. Row and column analysis was performed on the habitat attribute dataset; with unmodified data, the coefficient of variation (CV) of column totals was 279%, indicating 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 dataset indicated no outliers of > 2 s.d. Scree plot analysis within NMS indicated that a 2-dimensional solution was optimal, so final ordination was performed in 2-dimensional space with a random starting point by use of

Sorensen distance and without dimensional stepdown. This resulted in a plot CV of 14.9%, an R^2 of 0.876 with a final stress of 6.65 and instability of 0.00001 after 51 iterations.

Cluster analysis by use of Sorensen distance measure and flexible beta group linkage of -0.25 (McCune and Grace, 2002) was performed on the habitat attribute dataset, producing a dendrogram of plots grouped by similarity and a matrix of possible grouping combinations. To determine where on the branches to draw group boundaries, the dendrogram was objectively "pruned" by performing an Indicator Species Analysis on the matrix of all possible grouping combinations (Dufrene and Legendre 1997). The combination option with the lowest averaged *p*-value was selected as an optimal pruning level (number of groups in dendrogram). In the habitat attribute dataset, dendrogram pruning by ISA indicated that two groups provided the lowest cumulative *p*-value.

The collection dataset was binary (presence/absence), so Beals smoothing was applied. Beals smoothing is a transformation designed for datasets that contain a large number of zeros and replaces binary data with quantitative "favorability" values (Beals 1984, McCune 1994). Analysis of the smoothed dataset identified *Cortinarius magnivelatus* as a multivariate outlier (3.01 s.d.). It was removed, leaving 38 taxa in the dataset (indicated in Table 2 by their 4-letter abbreviations).

Scree plot analysis indicated that a 3-dimensional solution was optimal, so final ordination was performed in 3 dimensional space with a random starting point by use of Sorensen distance and without dimensional stepdown. This resulted in a

species CV of 41.2%, an R^2 of 0.958 with a final stress of 3.36 and instability of 0.00001 after 131 iterations. Dendrogram pruning by ISA indicated that two groups provided the lowest cumulative *p*-value.

For consistency and ease of comparisons, all ordinations were rotated so the C:N ratio vector points up. Vector lines for less significant associations ($R^2 < 0.400$) are suppressed in the scattergrams.

Results

Mycorrhizal fungus fruiting patterns were not correlated with site use or disturbance history at CLNP with this methodology. The primary factors in fungal fruiting patterns were geographic location and soil C and N levels, and these were significant in only a small number of taxa. Disturbed and control sites did not differ significantly in number of fungal collections or their diversity.

In all, 617 collections of mycorrhizal fungal sporocarps were identified, representing 166 species (Table 2). Because many taxa were collected either too frequently or infrequently to be informative, we analyzed just 38. Of these, ordination analysis identified 12 taxa correlated with levels of soil C and N, 7 of which also were significantly correlated by logistic regression with levels of soil C or N.

Levels of soil C and N were inversely correlated with C:N ratios, pH, and age (Table 3). We identified three sets of largely intracorrelated habitat attributes: 1) total C and total N, 2) C:N ratio, fuels, and ^{15}N enrichment, and 3) bulk density, stand age, and soil pH. Soil C:N ratios were correlated with bulk density, but not with pH or age.

The habitat attribute ordination is displayed with a habitat attribute vector overlay (Fig. 2) and with a species vector overlay (Fig. 3). In this ordination, the control sites tended toward the left side of the scattergram, most strongly influenced by low soil pH and bulk density and higher ^{15}N enrichment and litter levels (Fig. 2). The same factors also were the most influential in positioning the majority of the disturbed sites toward the right side of the scattergram.

The species vector overlay on the habitat attribute ordination (Fig. 3) indicates that fungal fruiting patterns tend to follow the vertical axis, either favoring high C:N ratios or high levels of total C and N, and relatively few taxa were associated with the horizontal axis that separated controls from disturbed sites. At a site scale, mycorrhizal fungus fruiting patterns were not significantly influenced by soil bulk density or pH.

Table 4 displays the taxa correlated with each axis of the ordinations, the R^2 of the ordination, the number of plots in each ordination group producing each taxon, and logistic regression *p*-values for each taxon correlated with habitat attributes at a significance of $\alpha < 0.10$. Group 1 are the sites in the upper half of the ordination scattergram, associated with lower levels of C and N. Group 2 are the sites in the lower half of the ordination scattergram, associated with higher levels of C and N. While the seven taxa in the upper third of the table are concentrated in the group 1 sites, and the five taxa in the bottom third of the table are concentrated in group 2 sites, the separation is not total. The 7 taxa in the middle of the table appeared as horizontal vectors in ordinations but had very few significant correlations with specific habitat attributes.

The R^2 values are reflections of the strength of the correlation of each taxon with ordination vectors. These often are paralleled by significant logistic regression correlations with specific habitat attributes. A taxon may have a high ordination vector R^2 value without significant logistic regression correlations if a number of factors all push it in the same ordination direction, even though none of those factors is individually significant.

Taxa appearing to favor sites with higher C:N ratios and lower levels of total C and N were *Cortinarius caperatus, Gastroboletus subalpinus, Gomphus floccosus, Ramaria cartilaginea, R. rubrievanescens*, and *Russula vinosa*. Taxa appearing to favor sites with lower C:N ratios and higher levels of total C and N were *Cortinarius depressus, C. gentilis, C. montanus*, and *Suillus brevipes*. No taxa were significantly correlated with bulk density, ^{13}C, pH, elevation, CWD, FWD, or litter, and only one was correlated with C:N ratio. No taxa were significantly correlated with site history.

The species ordination is displayed with a species vector overlay (Fig. 4) and a habitat attribute vector overlay (Fig. 5). This ordination is based entirely on similarity of species assemblage and is independent of any habitat attributes. There is little consistency in the horizontal orientation of the sites between this ordination and the habitat attribute ordination, but the vertical distributions are very similar: in both ordinations the same 6 sites are above the scattergram center and the other 6 are below.

In Fig. 4, most species vectors significant at $R^2 > 0.400$ point either up or down. The horizontal ones do not strongly associate with either group of sites and few significantly correlate with specific habitat attributes (Table 4). With the habitat

attribute overlay (Fig. 5) it is apparent that the primary dichotomy in species assemblages is between high C:N ratios (group 1) and levels of total C and N (group 2).

The fruiting pattern identified in the species ordination was consistent with that identified by the habitat attribute ordination. The taxa appearing to favor sites with higher C:N ratios and low levels of total C and N were the same, with the addition of *Rhizopogon evadens*. Taxa appearing to favor sites with low C:N ratios and high levels of total C and N also were consistent, with the addition of *Boletus zelleri*.

The species ordination (Fig. 4) further identified some taxa on horizontal vectors. *Hydnotrya variiformis* occurred on 8 sites, but not ASC or CSC. However, it otherwise demonstrated no strong habitat preferences. *Laccaria laccata* and *Ramaria longispora* had weak negative correlations with pH (p = 0.123 and 0.118, respectively) and weak positive correlations with fuels (p = 0.114 with litter, and 0.123 with CWD, respectively). They were collected in most sites on the left side of the ordination and few sites on the right. Three of the 4 sites on which *Cortinarius brunneus* and *C. cinnamomeoluteus* occurred were to the left of center, but these species showed no significant habitat preferences.

Table 5 presents the two-tailed Tukey-Kramer HSD p-values for differences in habitat attributes between the control and disturbed sites, between ordination groups, and between soil types. When grouped by site history, disturbed sites differed significantly in ^{15}N enrichment and fuel levels, and differed in bulk density only with data from the high impact soil cores. When compared by ordination groups, there were significant differences in total C, total N, ^{15}N, C:N

ratio, CWD, and age. Differences between ordination groups were suggestive but non-significant for FWD and litter mass. When grouped by soil types, only total C and N were significantly different.

Discussion

The most obvious forms of disturbance in recreational sites are changes to vegetation patterns, fuel levels, and soil compaction. None of these factors appear to influence significantly fungal fruiting patterns at CLNP at the macrosite scale. However, at the microsite scale the differences were profound: virtually no fungal sporocarps were collected in the most severely disturbed areas in the recreational sites; e.g. the bare and trampled soils around firepits and picnic tables. Practically all collections from these sites came from microhabitats that were less disturbed, interstitial, or peripheral to the areas of most severe disturbance. Because of their size, our survey plots included both highly disturbed and relatively undisturbed subsites. For this reason we did not detect the microsite differences in fungal fruiting patterns that existed between the disturbed and control units.

Since our sampling occurred in the snow-free months it was concurrent with recreational use, so recreationists may have removed sporocarps. However, the two sites with more severe disturbance not regularly used by the public (ABD and MCD) had a similar microsite fruiting pattern, suggesting habitat influence. At sites that had been abandoned for some time (ASD and CSD), intensely disturbed microsites were less apparent and fungal fruiting was more evenly distributed.

The sites segregated into the same two groups in both habitat attribute and species ordinations (Figs. 2-5). The sites at the lower part of both ordinations (higher C and N, lower C:N ratios) are located along Highway 62 west of Annie Canyon, and the soils at all sites are Castlecrest gravelly ashy loam.

The sites at the upper part of both ordinations (lower C and N, higher C:N ratios) were located east of Annie Canyon, except the disjunct ASC site in the northwest corner of the Park. The AB and MC sites had a Union Peak-Sun Notch-Castlecrest soil series, but ASC and MVLC were Castlecrest gravelly ashy loam.

A number of taxa were correlated (either positively or negatively) with total C and/or total N. However, several other habitat attributes were negatively correlated with total C and N: C:N ratios, soil pH, and stand age (Table 3). No taxa correlated with soil pH and one with C:N ratio, but 3 correlated with stand age (Table 4). It is likely that no single habitat attribute was responsible for fruiting patterns, as habitat attributes occurred in suites and the influence of individual attributes is difficult to isolate.

Gastroboletus subalpinus and *Russula vinicolor* were positively correlated with stand age, and *Boletus zelleri* was negatively so. The first two also were negatively correlated with total C and N. *Suillus brevipes* correlated significantly with C:N ratios at $\alpha < 0.10$, although C:N associations by several other taxa were suggestive; *Boletus zelleri, Cortinarius caperatus, C. depressus, C. gentilis*, and *Ramaria cartilaginea* all correlated at $p < 0.15$.

ABC was the only site in ordination group 1 to produce *Cortinarius depressus* or *C. gentilis*. It also was the only site in group 1 to have above-mean levels of C and N and a below-mean C:N ratio. Only one site in ordination group 2 (CSD) produced neither *Cortinarius depressus* nor *C. gentilis*.

When grouped by site history, disturbed sites differed significantly in ^{15}N enrichment and fuel levels, and differed in bulk density only with data from the high impact soil cores. When compared by ordination groups, there were

significant differences in total C, total N, ^{15}N enrichment, C:N ratio, CWD, and age. Differences between ordination groups were suggestive, but non-significant for FWD and litter mass.

The sites in current seasonal use (MVED and MVLD) had significantly less FWD than the other disturbed sites (ANOVA $p = 0.011$), and significantly less CWD ($p = 0.0664$) from the occasional use sites (ABD and MCD). These differences are likely the result of use patterns, such as firewood collection and traffic. ^{15}N was significantly more enriched in the abandoned sites (ASD and CSD) than in the Mazama Village sites, but not significantly different from the occasional use sites. Patterns of ^{15}N enrichment may be a function of site history, but the significance of differences between ordination groups (independent of site use) suggest that ^{15}N enrichment may be a function of wider geographic patterns, possibly related to soil types.

Table 5 indicates that the sites with Union Peak-Sun Notch-Castlecrest soil had significantly more total C and N than those with Castlecrest gravelly ashy loam. Overall, age was negatively correlated with total C and N, and the 4 sites in the Union Peak-Sun Notch-Castlecrest soil series were all in the 300+ year-old sere as well. No taxa were correlated with soil type.

Paradoxically, the two sites within the high C:N ordination group that had Castlecrest gravelly ashy loam (ASC and MVLC) had the highest levels of ^{15}N enrichment, contrasting with the other Castlecrest gravelly ashy loam sites which tended to have less ^{15}N enrichment.

The taxa that were positively correlated with ^{15}N enrichment also were positively correlated with stand age, and negatively correlated with total C and N (Table 4).

Suillus brevipes, the only taxon negatively correlated with ^{15}N was positively correlated with total C and N, and negatively correlated with C:N ratio. CWD was correlated with C:N ratios, and both age and C:N ratios are negatively correlated with total C and total N.

It is apparent that, although total C and N may be the strongest habitat attributes influencing fruiting patterns, they are negatively correlated with a suite of factors including C:N ratio, pH, and stand age. Several taxa favoring low C, low N, and high C:N sites also were correlated with ^{15}N enrichment. The nature of these correlations renders it difficult to deconvolve any one dominant factor.

It is interesting that levels of ^{15}N enrichment were correlated with the presence of several taxa, but were not correlated with the other factors influential on fruiting patterns (total C and N, C:N ratio, and stand age). ^{15}N enrichment also was correlated with fungal species diversity, and was one of two attributes correlated with site groupings by both treatment and by ordination, but it was not correlated with soil type.

In this study ^{15}N enrichment was not correlated with total N or stand age, but rather with fuels (Table 3). It was the only habitat attribute directly correlated with increased diversity of mycorrhizal sporocarps. Litter mass was not correlated with the likelihood of any species' occurrence, but it and ^{15}N enrichment were the only attributes correlated with increased diversity of mycorrhizal sporocarps.

Levels of ^{15}N enrichment in the soil are a function of the isotopic signatures of inputs and outputs, fractionation occurring during N transformation, and allocation of N forms within an ecosystem (Högberg 1997). The majority of N

in forest soils results from biological fixation and atmospheric deposition (dryfall). The products of biological N fixation are within ± 2‰ of atmosphere, and mineralization reactions are not isotopically discriminatory. Both nitrification and denitrification discriminate against the ^{15}N isotope, and because the products of these processes are mobile (either by leaching or volatilizing) ^{15}N depleted compounds are more likely to leave the system, resulting in the soil becoming ^{15}N enriched over time. Mycorrhizal fungi also discriminate against ^{15}N when transferring N to host plants, further enriching soil ^{15}N and depleting plant tissue concentrations (Hobbie et al 1999).

These processes explain why forest soils often become increasingly enriched with ^{15}N with stand age and in older (deeper) soils: Compton et al (2007) report ^{15}N enrichment rates of 1.1 - 2.1‰ per century in A and O horizons, concurrent with a reduction in available total soil N as forest stands age ("tightening" of the N pool). Here, we found no correlation with stand age and ^{15}N enrichment.

Conclusions

Our first hypothesis was that intense recreational site use influences above- and belowground habitat by affecting soil properties and surface fuels. We found significant differences between site histories in soil bulk density only when comparing the most disturbed subsites with controls. Bulk density was not significantly different between the less-disturbed interstitial areas of the recreation sites and control sites. There were significant differences in the levels of ^{15}N enrichment and surface fuels between recreation and control sites at the macrosite scale. Our sampling methodology was not designed to quantify the effects of anthropogenic disturbance on fungal fruiting patterns at the microsite scale.

Our second hypothesis was that intense recreational site use influences mycorrhizal fungus fruiting patterns. The fruiting patterns of most fungi were not significantly influenced by site use or history. Several taxa demonstrated significant associations with soil C and N, C:N ratios, and ^{15}N enrichment. Although site history and fungal fruiting patterns both were correlated with ^{15}N enrichment, this did not translate to correlations between site history and fungal fruiting patterns at the macrosite scale.

Intensive recreational use does not adversely impact the fruiting productivity or diversity of mycorrhizal fungi at the macrosite scale. Intensively disturbed microsites within recreational areas produce very few sporocarps, but the productivity and diversity of less impacted microsites is sufficient that at larger scales, recreational sites are not significantly different from undisturbed control sites in numbers of collections or numbers of species. The factors most influential upon fungal fruiting patterns were geographic location, soil C and N content, and the corresponding C:N ratio. These factors may be related by soil type, or by barriers to dispersal for some taxa. No patterns were observed in the fruiting of most fungal species, but a few were identified as possible indicators.

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Table 2.1. Mean habitat attribute values for all units, by ordination groups; values significantly different at $p < 0.10$ are bolded. Soil types: CC = Castlecrest gravelly ashy loam, UP = Union Peak – Sun Notch series

Ordination Group 1	Soil type	Low bulk density	High bulk density	Total % C	‰ $\delta^{13}C$ depletion	Total %N	‰ $\delta^{15}N$ enrichments	Soil C:N ratio
ABC	UP	0.649	0.649	3.526	-24.196	0.116	3.499	31.243
ABD	UP	0.766	0.984	1.531	-24.177	0.047	2.238	32.972
ASC	CC	0.694	0.694	2.452	-25.481	0.060	4.017	41.360
MCC	UP	0.868	0.868	2.031	-25.029	0.049	3.109	42.063
MCD	UP	0.980	1.06	1.917	-25.086	0.050	1.555	38.813
MVLC	CC	0.612	0.612	3.364	-25.134	0.104	4.232	32.123
Group mean		0.762	0.811	**2.470**	-24.851	**0.071**	3.108	**36.429**

Ordination Group 2	Soil type	Low bulk density	High bulk density	Total % C	‰ $\delta^{13}C$ depletion	Total %N	‰ $\delta^{15}N$ enrichments	Soil C:N ratio
ASD	CC	0.659	0.915	3.972	-24.887	0.140	1.800	28.509
CSC	CC	0.619	0.619	4.939	-25.275	0.166	3.150	30.484
CSD	CC	0.678	0.783	3.316	-25.268	0.117	2.941	28.692
MVEC	CC	0.606	0.606	4.973	-25.630	0.174	1.606	28.938
MVED	CC	0.630	0.84	4.731	-25.262	0.211	1.514	25.222
MVLD	CC	0.810	0.940	2.702	-25.065	0.104	1.627	25.821
Group mean		0.667	0.784	**4.105**	-25.231	**0.152**	2.106	**27.944**
Grand mean		0.714	0.798	3.225	-25.026	0.108	2.646	32.513

Table 2.1 (Continued). Mean habitat attribute values for all units, by ordination groups; values significantly different at $p < 0.10$ are bolded. Soil types: CC = Castlecrest gravelly ashy loam, UP = Union Peak – Sun Notch series.

Ordination Group 1	Soil pH	Elevation (m)	CWD (Mg ha^{-1})	FWD (Mg ha^{-1})	Litter (Mg ha^{-1})	Stand age	Collections	Species
ABC	4.73	1950	68.1	8.9	107.0	300	46	37
ABD	5.10	1950	43.5	3.8	42.1	300	44	32
ASC	4.83	1750	54.5	6.5	109.8	225	43	36
MCC	5.13	1890	25.4	8.3	111.0	300	55	40
MCD	5.37	1890	10.3	4.8	64.0	300	38	28
MVLC	4.73	1850	20.5	10.0	157.0	300	91	64
Group mean	4.983	1880.0	**37.1**	7.1	98.5	**287.5**	52.8	39.5
Ordination Group 2	**Soil pH**	**Elevation (m)**	**CWD (Mg ha^{-1})**	**FWD (Mg ha^{-1})**	**Litter (Mg ha^{-1})**	**Stand age**	**Collections**	**Species**
ASD	4.97	1850	18.9	5.8	62.4	300	49	39
CSC	4.67	1770	22.8	8.2	88.8	135	49	41
CSD	4.93	1770	14.4	4.9	72.6	135	52	42
MVEC	4.83	1890	18.1	5.1	74.0	100	54	43
MVED	4.67	1830	2.0	0.3	38.0	100	36	25
MVLD	5.13	1830	3.9	0.9	55.0	300	60	45
Group mean	4.867	1823.3	**13.4**	4.2	65.1	**178.3**	50.0	39.2
Grand mean	4.93	1853.8	26.1	5.7	83.1	237.1	51.5	39.3

Table 2.2. List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
Bosu	*Boletopsis subsquamosa*	(Fr.) Kotl. & Pouzar					1	1	1	1	1				5	5
Boze	*Boletus zelleri*	Murrill					2	2			1			1	6	4
Coal	*Cortinarius albobrunnoides*	M.M. Moser & McKnight	2	3		2		1	1		1		1	1	12	8
Cobr	*Cortinarius brunneus*	(Pers.) Fr.		1	2		1							1	5	4
Coca	*Cortinarius caperatus*	(Pers.:Fr.) Fr.	2	1	1			1	1	1	1		2		10	8
Coci	*Cortinarius cinnamomeoluteus*	P.D. Orton	1	1			1				1				4	4
Coclan	*Cortinarius clandestinus*	Kauffman		1							2	1	1		5	4

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations

were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
Coclar	*Cortinarius claricolor*	(Fr.) Fr.		2			1		1		2		1	1	8	6
Code	*Cortinarius depressus*	Fr.	1			1	1				1	2		2	8	6
Coge	*Cortinarius gentilis*	(Fr.) Fr.	1			1	1					1		1	5	5
Coma	*Cortinarius magnivelatus*	Morse ex Thiers & A.H. Sm.				1			1	1		2			5	4
Como	*Cortinarius montanus*	Kauffman					1		1		1	1		1	5	5
Cova	*Cortinarius variosimilis*	M.M. Moser & Ammirati		2		1	3		1				3	1	11	6
Gasu	*Gastroboletus subalpinus*	Trappe & Thiers	1	1	1				1	2			1		7	6

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
Gofl	*Gomphus floccosus*	(Schwein.) Singer	2		1				3					2	8	4
Hybr	*Hygrophorus brunneus*	Largent	2			1		1			1			2	7	5
Hygo	*Hygrophorus goetzii*	Hesler & A.H. Sm.		2		1	1	1	1				2	1	9	7
Hyhy	*Hygrophorus hypothejus*	(Fr.) Fr.	1					1			1	1			4	4
Hyse	*Hysterangium separabile*	Zeller		1		1						3	2	1	8	5
Hyva	*Hydnotrya variiformis var. pallida*	Gilkey	1	1		1		2	2		2	3	2		14	8
Lala	*Laccaria laccata var. pallidifolia*	(Scop.) Cooke	1		1		1	1			1		1	1	7	7
Leru	*Leucogaster rubescens*	Zeller & C.W. Dodge		1		1							1	1	4	4

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
Raca	*Ramaria cartilaginea*	Marr & D.E. Stuntz		2	1				3	3	1		2	2	14	7
Racy	*Ramaria cyaneigranosa var. cyaneigranosa*	Marr & D.E. Stuntz					1	1			1		1		4	4
Rafl	*Ramaria flavobrunnescens var. aromatica*	Marr & D.E. Stuntz		1	1	2	1		1		1		2	1	10	8
Ralo	*Ramaria longispora*	Marr & D.E. Stuntz	2		1		1				1				5	4
Raru	*Ramaria rubrievanescens*	Marr & D.E. Stuntz	2	1						1			1		5	4
Rhev	*Rhizopogon evadens*	A.H. Sm.	1						2	2	1		3		9	5
Rhvu	*Rhizopogon vulgaris*	A.H. Sm.				1			1		1		3	1	7	5
Ruae	*Russula aeruginea*	Fr.			2	1	1				1				5	4

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
Ruca	*Russula cascadensis*	Shaffer	1					1	1	1					4	4
Ruin	*Russula integra*	(L.) Fr.	1	1	1				2		1	1	1	1	9	8
Ruty	*Russula tyrrhenica*	Sarnari	1	1	1	1							1	1	6	6
Ruvi	*Russula vinosa*	Lindblad	1	1	1				1				2	2	8	6
Subr	*Suillus brevipes*	(Peck) Kuntze				3	1	2		1	1	1		1	10	7
Supu	*Suillus punctatipes*	(Snell & E.A. Dick) Singer	2	3		2		1	2	2	1	1	3	2	19	10
Trca	*Tricholoma caligatum*	(Viv.) Ricken					1	1	1				1		4	4
Trfl	*Tricholoma equestre*	(L.) P. Kumm.	1	3	1	1	3	2		2	2		3	1	19	10

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
Trfo	*Tricholoma focale*	(Fr.) Ricken		1			2	2	3	2		1		1	12	7
Trpo	*Tricholoma portentosum*	(Fr.) Quél.	1				1	1		1			1	1	6	6
Trsa	*Tricholoma saponaceum*	(Fr.) P. Kumm.	1		2	1	1	1			2	1	2		11	8
	Albatrellus ovinus	(Schaeff.) Kotl. & Pouzar					1	1				1			3	3
	Amanita gemmata var. gemmata	(Fr.) Bertill.			2										2	1
	Amanita muscaria var. formosa	(Pers.) Gonn. & Rabenh.												2	2	1
	Amanita velosa	(Peck) Lloyd										1	1		2	2
	Amanita silvicola	Kauffman							1	1		1			3	3

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Bankera fuligineoalba	(J.C. Schmidt) Coker & Beers						1							1	1
	Boletus abieticola	Thiers				1							2		3	2
	Boletus chrysenteron	Bull.				1								1	2	2
	Boletus coniferarum	Lebedeva				1									1	1
	Boletus edulis	Bull.												1	1	1
	Boletus fragrans	Vitt.											1		1	1
	Cantharellus formosus	Corner							1						1	1
	Cantharellus subalbidus	A.H. Sm. & Morse							1						1	1

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Chroogomphus pseudovinicolor	O.K. Mill.				2		1					2		5	3
	Chroogomphus vinicolor	(Peck) O.K. Mill.	1												1	1
	Cortinarius biformis	Fr.									1		1	1	3	3
	Cortinarius boulderensis	A.H. Sm.	1												1	1
	Cortinarius cylindripes	Kauffman					1								1	1
	Cortinarius delibutus	Fr.	2												2	1
	Cortinarius diosmus	Kühner											2		2	1
	Cortinarius elegantior	(Fr.) Fr.									1		1		2	2

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Cortinarius fulvo-ochrascens	Rob. Henry			2								2		4	2
	Cortinarius impolitus	Kauffman		1											1	1
	Cortinarius infractus	Berk.	1		1										2	2
	Cortinarius malachius	(Fr.) Fr.					1							1	2	2
	Cortinarius muscigenus	Peck	1					1							2	2
	Cortinarius mutabilis	A.H. Sm.		1					1			1			3	3
	Cortinarius papulosus	Fr.					1				1	2			4	3
	Cortinarius pinguis	(Zeller) Peintner & M.M. Moser		2	1	1	2	2	1	1	4	3	2	2	21	11

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Cortinarius rigidus	(Scop.) Fr.											1		1	1
	Cortinarius semisanguineus	(Fr.) Gillet					1								1	1
	Cortinarius subfoetidus	A.H. Sm.	1										1		2	2
	Cortinarius vibratilis	(Fr.) Fr.						1							1	1
	Cortinarius sp nov #1						1								1	1
	Cortinarius sp nov #2							1							1	1
	Cortinarius sp nov #3												1		1	1
	Cortinarius sp nov #4						1								1	1

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Dermocybe phoenicea var. occidentalis	(A.H. Sm.) Ammirati									1				1	1
	Elaphomyces granulatus	Fr.			1		1								2	2
	Elaphomyces muricatus	Fr.						2					1		3	2
	Gastroboletus ruber	(Zeller) Cázares & Trappe											1		1	1
	Gastroboletus turbinatus	(Snell) A.H. Sm. & Singer				1									1	1
	Gastroboletus vividus	Trappe & Castellano			1						1		1		3	3
	Gautieria monticola	Harkn.	1	2	1	1		1	4	2	2	1	1	4	20	11
	Gautieria pterosperma	Stewart nom prov.		1	1					1					3	3

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Geopora cooperi var. gilkeyae	Harkn.								1					1	1
	Gomphidius glutinosus	(Schaeff.) Fr.							1						1	1
	Gomphus kauffmanii	(A.H. Sm.) Corner	1		1										2	2
	Hebeloma mesophaeum	(Pers.) Quél.				1									1	1
	Hebeloma subsaponaceum	P. Karst.							1						1	1
	Hydnellum ferrugineum	(Fr.) P. Karst.						1							1	1
	Hydnellum peckii	Banker									1				1	1
	Hydnellum scrobiculatum	(Fr.) P. Karst.						1							1	1

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Hydnotrya cerebriformis	(Tul. & C. Tul.) Harkn.											1		1	1
	Hydnotrya inordinata	Trappe & Castellano					1								1	1
	Hygrophorus bakerensis	A.H. Sm. & Hesler				1				1	1				3	3
	Hygrophorus camarophyllus	(Alb. & Schwein.) Dumée, Grandjean & Maire					1								1	1
	Hygrophorus marzuolus	(Fr.) Bres.						1							1	1
	Hygrophorus pudorinus	(Fr.) Fr.												1	1	1
	Hygrophorus purpurascens	Gonn. & Rabenh.	1						1						2	2

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Hygrophorus pustulatus	(Pers.) Fr.				1									1	1
	Hygrophorus secretanii	Henning			1		1	1							3	3
	Hygrophorus subalpinus	A.H. Sm.					1	1					1		3	3
	Inocybe assimilata	Britzelm.				1							1		2	2
	Inocybe lanatodisca	Kauffman				1									1	1
	Inocybe leptophylla	G.F. Atk.							1						1	1
	Inocybe lilacina	(Peck) Kauffman			1								1		2	2
	Inocybe maculata	Boud.									1				1	1

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Inocybe olivaceobrunnea	J. Favre												1	1	1
	Inocybe rimosa	Britzelm.				1	1								2	2
	Laccaria bicolor	(Maire) P.D. Orton			1		1						1		3	3
	Laccaria nobilis	A.H. Sm.						1					1		2	2
	Lactarius caespitosus	Hesler & A.H. Sm.	1												1	1
	Lactarius kauffmanii	Hesler & A.H. Sm.	1												1	1
	Lactarius pallescens var. pallescens	Hesler & A.H. Sm.											1		1	1
	Lactarius pseudomucidus	Hesler & A.H. Sm.				1							1	1	3	3

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Lactarius riparius	Methven									1				1	1
	Lactarius rufus	(Scop.) Fr.					2	2					1		5	3
	Lactarius scrobiculatus var. montanus	(Scop.) Fr.			1					1					2	2
	Lactarius subflammeus	Hesler & A.H. Sm.											1		1	1
	Melanogaster tuberiformis	Corda									2				2	1
	Ramaria araiospora var. araiospora	Marr & D.E. Stuntz						1							1	1
	Ramaria flavigelatinosa var. carnisalmonea	Marr & D.E. Stuntz											1		1	1
	Ramaria flavigelatinosa var. flavigelatinosa	Marr & D.E. Stuntz			1	1									2	2

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Ramaria formosa var. formosa	(Pers.) Quél.											1		1	1
	Ramaria magnipes	Marr & D.E. Stuntz		1					1	1					3	3
	Ramaria rasilispora	Marr & D.E. Stuntz							1				1		2	2
	Ramaria rubripermanens	Marr & D.E. Stuntz									1		1		2	2
	Ramaria tsugina var. prasina	Marr & D.E. Stuntz							1						1	1
	Ramaria sp nov						1								1	1
	Rhizopogon albidus	A.H. Sm.				1					1				2	2
	Rhizopogon atroviolaceous	A.H. Sm.		1					1						2	2

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Rhizopogon ellenae	A.H. Sm.												1	1	1
	Rhizopogon hysterangiodes	A.H. Sm.								1					1	1
	Rhizopogon milleri	A.H. Sm.	2							1					3	2
	Rhizopogon ochraceorubens	A.H. Sm.				1		1							2	2
	Rhizopogon salebrosus	A.H. Sm.											1		1	1
	Rhizopogon subsalmonius	A.H. Sm.				1							1		2	2
	Rhizopogon truncatus	Linder		1					1	1					3	3
	Rhizopogon sp nov													1	1	1

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Russula adusta	(Pers.) Fr.									1		1		2	2
	Russula albonigra	(Krombh.) Fr.												1	1	1
	Russula azurea	Bres.	1	1	2	2		1	1	1	2	2	2	3	18	11
	Russula brevipes var. brevipes	Peck						1				1			2	2
	Russula claroflava	Grove			2									2	4	2
	Russula exalbicans	(Pers.) Melzer & Zvára							2			1		2	5	3
	Russula fragrantissima	Romagn.				2									2	1
	Russula gracillima	Jul. Schäff.			1										1	1

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Russula helodes	Melzer			1									1	2	2
	Russula nigricans	(Bull.) Fr.			1									1	2	2
	Russula occidentalis	Bon											2	1	3	2
	Sarcodon imbricatus	(L.) P. Karst.						1		1	1				3	3
	Sarcodon rimosus	(K.A. Harrison)			1										1	1
	Suillus granulatus	(L.) Roussel	1					2			1				4	3
	Suillus monticola	Thiers											1		1	1
	Suillus tomentosus	(Kauffman) Singer						2							2	1

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Suillus sp nov #1											1			1	1
	Suillus sp nov #2								1						1	1
	Tricholoma imbricatum	(Fr.) P. Kumm.											1		1	1
	Tricholoma magnivelare	(Peck) Redhead		1						2					3	2
	Tricholoma moseri	Singer					1								1	1
	Tricholoma pessundatum	(Fr.) Quél.											1		1	1
	Tricholoma sejunctum	(Sowerby) Quél.	1	1	1	3	1	1	2	2		2	3	1	18	11
	Tricholoma ustale	(Fr.) P. Kumm.					1								1	1

Table 2.2 (Continued). List of all fungal collections from study. Those with four-letter abbreviations were used in ordination analysis.

Abbr.	Species	Authority	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	Colls	Sites
	Tricholoma vaccinum	(Schaeff.) P. Kumm.			1										1	1
	Total Collections		46	44	43	49	49	52	55	38	54	36	91	60	617	
	Total Species		37	32	36	39	41	42	40	28	43	25	64	45	166	

Table 2.3. Pearson's correlations between habitat attributes. Estimates are above *p* – value. A negative sign preceding the *p* - value indicates an inverse correlation; values significant at $\alpha < 0.10$ are bolded.

	Bulk density	Total C %	δ^{13}C depletion	Total N %	δ^{15}N enrichment	C:N ratio	Mineral soil pH	Elevation	CWD mass	FWD mass	Litter mass	Stand age	Collections *
Total C %	-0.709												
	-0.004												
δ^{13}C depletion	0.227	-0.384											
	0.592	-0.173											
Total N %	-0.685	0.977	-0.338										
	-0.008	**0.000**	-0.255										
δ^{15}N enrichment	-0.325	-0.179	0.072	-0.300									
	-0.350	-0.604	0.879	-0.345									
C:N ratio	0.537	-0.647	0.009	-0.770	0.426								
	0.067	**-0.021**	-0.991	**-0.003**	0.153								
Mineral soil pH	0.927	-0.724	0.223	-0.675	-0.448	0.397							
	0.000	**-0.004**	0.564	**-0.012**	-0.162	0.204							
Elevation	0.218	0.010	0.629	0.017	-0.387	-0.146	0.307						
	0.787	-0.885	**0.036**	0.999	-0.249	-0.517	0.437						

* Based on data from all collections, not just the 38 taxa used in ordinations

Table 2.3 (Continued). Pearson's correlations between habitat attributes. Estimates are above *p* – values. A negative sign preceding the *p* - value indicates an inverse correlation; values significant at $\alpha < 0.10$ are bolded.

	Bulk density	Total C %	$\delta^{13}C$ depletion	Total N %	$\delta^{15}N$ enrichment	C:N ratio	Mineral soil pH	Elevation	CWD mass	FWD mass	Litter mass	Stand age	Collections*
CWD mass	-0.105	-0.336	0.374	-0.472	0.635	0.543	-0.089	0.069					
	-0.709	-0.278	0.228	-0.119	**0.022**	**0.069**	-0.760	0.863					
FWD mass	-0.054	-0.169	0.134	-0.353	0.655	0.556	-0.071	0.155	0.831				
	-0.756	-0.564	0.758	-0.247	**0.012**	**0.061**	-0.749	0.794	**0.001**				
Litter mass	-0.119	-0.110	-0.112	-0.282	0.807	0.495	-0.217	-0.097	0.596	0.835			
	-0.648	-0.715	-0.670	-0.368	**0.001**	0.103	-0.457	-0.595	**0.041**	**0.001**			
Stand age	0.562	-0.703	0.644	-0.706	0.131	0.401	0.565	0.509	0.320	0.296	0.264		
	0.072	**-0.006**	**0.030**	**-0.007**	0.593	0.198	**0.066**	0.115	0.313	0.391	0.427		
Collections*	-0.332	-0.046	-0.211	-0.065	0.492	-0.091	-0.243	-0.147	0.047	0.252	0.530	0.145	
	-0.420	-0.968	-0.690	-0.857	0.121	-0.809	-0.557	0.794	0.835	0.277	**0.035**	0.429	
Species*	-0.420	0.012	-0.271	-0.026	0.548	-0.100	-0.312	-0.230	0.146	0.334	0.590	0.066	0.974
	-0.262	0.868	-0.552	-0.962	0.073	-0.786	-0.410	-0.991	0.578	0.150	0.013	0.590	**0.000**

* Based on data from all collections, not just the 38 taxa used in ordinations

Table 2.4. Number of sites within each group that taxon is present, R^2 strength of ordination vector correlation, and logistic regression correlations between individual taxa and habitat attributes.

Taxon	# sites in group 1	# sites in group 2	Habitat attributes R^2	Species R^2	Logistic regression correlations C	N	^{15}N	C:N ratio	Age
Coca	6	2	0.529	0.895	-0.0973	-0.09			
Gasu	6	0	0.761	0.919	-0.0749		0.0991		0.0769
Gofl	3	1	0.537	0.391					
Raca	5	2	0.603	0.566	-0.0752	-0.0796			
Raru	4	0	0.483	0.735					
Rhev	4	1		0.628					
Ruvi	5	1	0.684	0.484	-0.0787	-0.0794	0.093		0.0769
Cobr	2	2		0.602					
Coci	2	2		0.607					
Hyva	1	3		-0.448					
Lala	3	4		0.76					
Ralo	2	2		0.759					
Ruae	1	3		0.589					
Trsa	3	5	-0.497			0.0622			
Boze	0	4		-0.405					-0.0844
Code	1	5	-0.59	-0.778	0.839				
Coge	1	5	-0.459	-0.731	0.0939	0.0877			
Como	1	4	-0.572	-0.698					
Subr	1	6	-0.79	-0.721	0.099	0.0811	-0.0539	-0.0932	

Table 2.5. Tukey-Kramer two-tailed HSD differences between site groupings. Bolded figures are significant at $\alpha < 0.05$.

	Compacted vs. control	Ordination group 1 vs. group 2	Union Peak vs. Castlecrest soil type
High bulk density	0.0603	0.5327	0.4865
Low bulk density	0.2647	0.1766	0.3532
C	0.5876	**0.0094**	**0.0188**
C^{13}	0.5436	0.1468	0.2936
N	0.9801	**0.0027**	**0.0054**
N^{15}	**0.0136**	0.083	0.9872
CN	0.1964	**0.0028**	0.1514
pH	0.1046	0.3936	0.1548
Elevation	0.481	0.7887	0.3274
CWD	**0.0500**	**0.0466**	0.4634
FWD	**0.0157**	0.1057	0.9006
Litter	**0.0014**	0.1358	0.9793
Age	0.9882	**0.0237**	0.1164
Collections*	0.2408	0.7335	0.6926
Species*	0.1406	0.9347	0.4248

* Based on data from all collections, not just the 38 taxa used in ordinations

Figure 2.1. Map of sites.

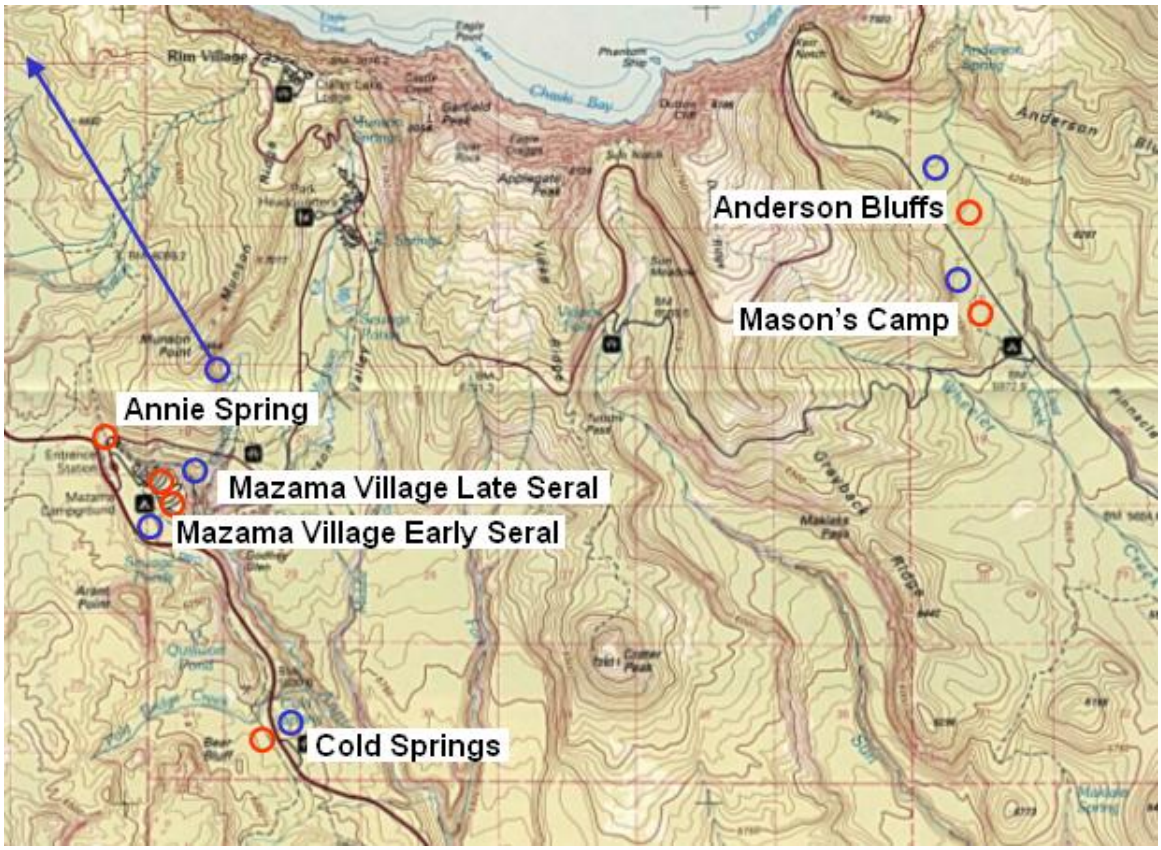


Figure 2.2. Habitat attribute ordination with habitat attribute overlay.

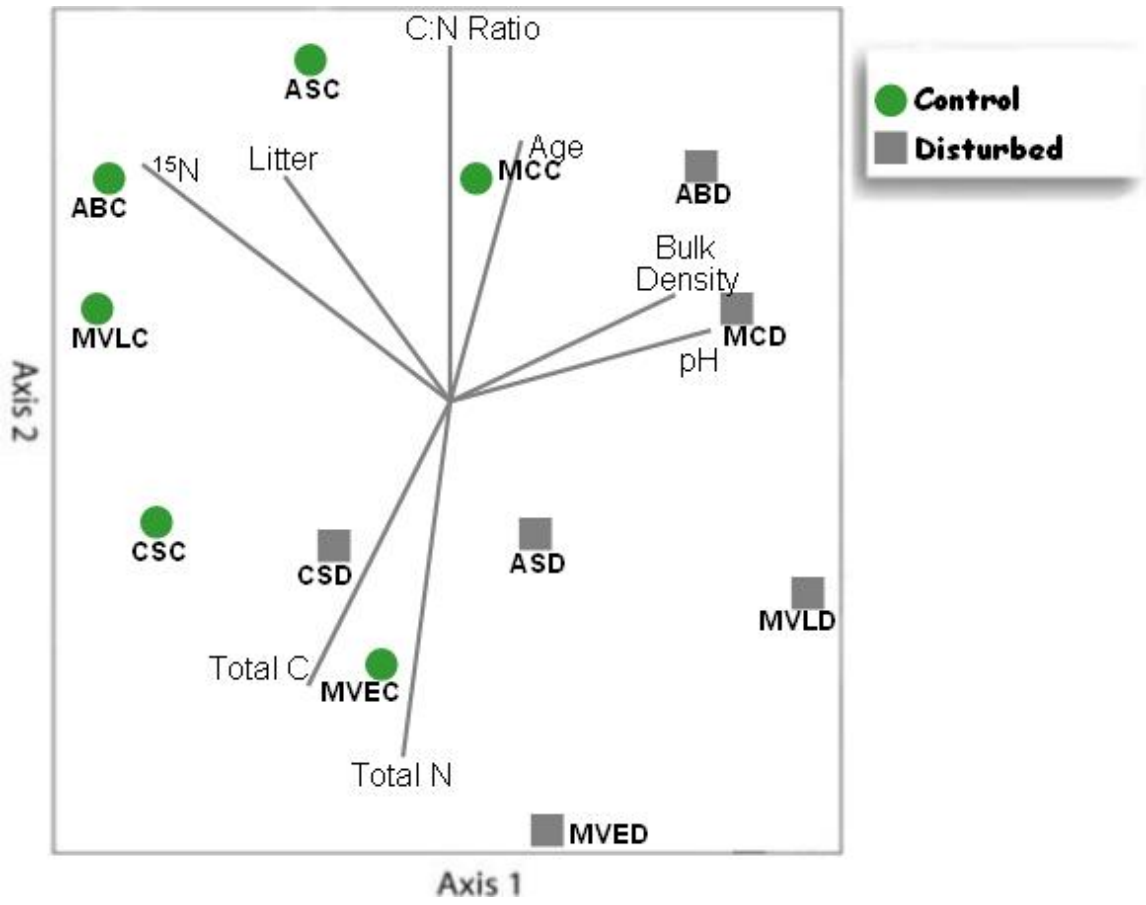


Figure 2.3. Habitat attribute ordination with species overlay.

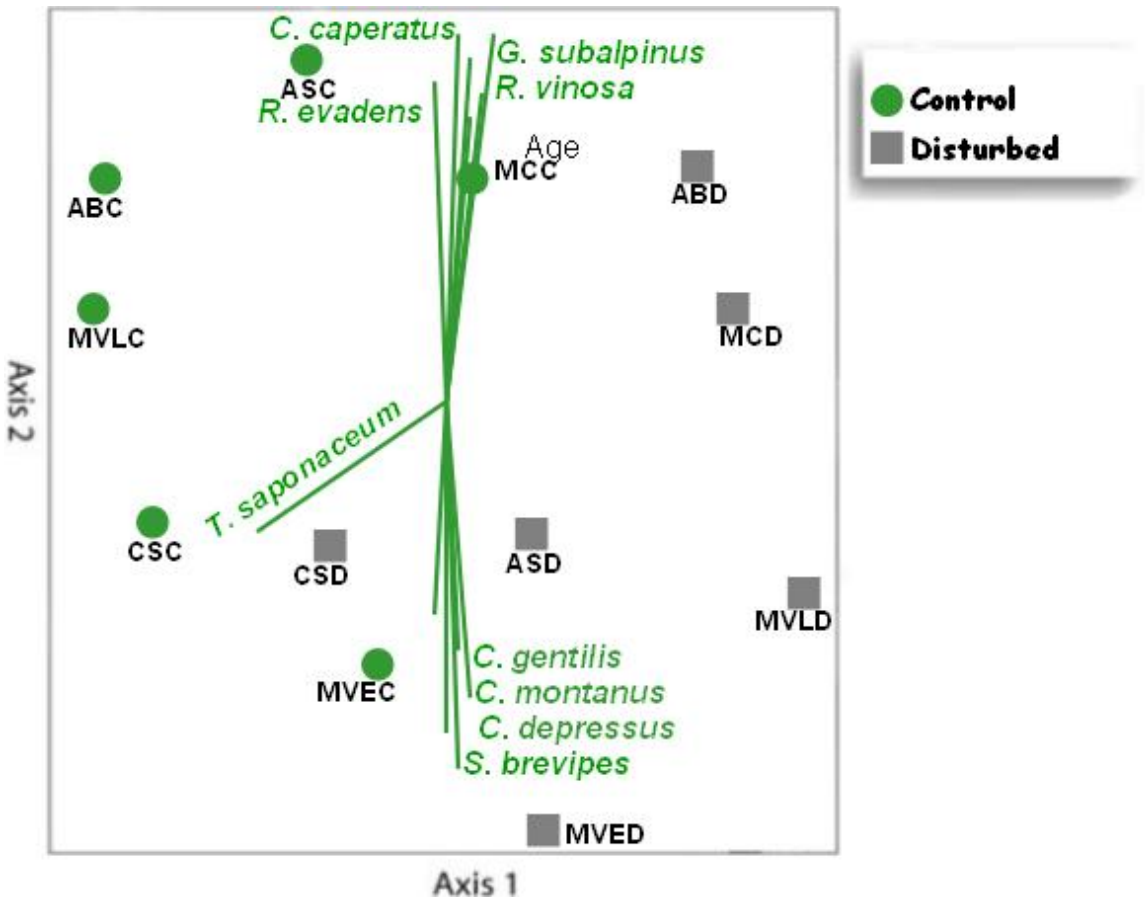


Figure 2.4. Species ordination with species overlay.

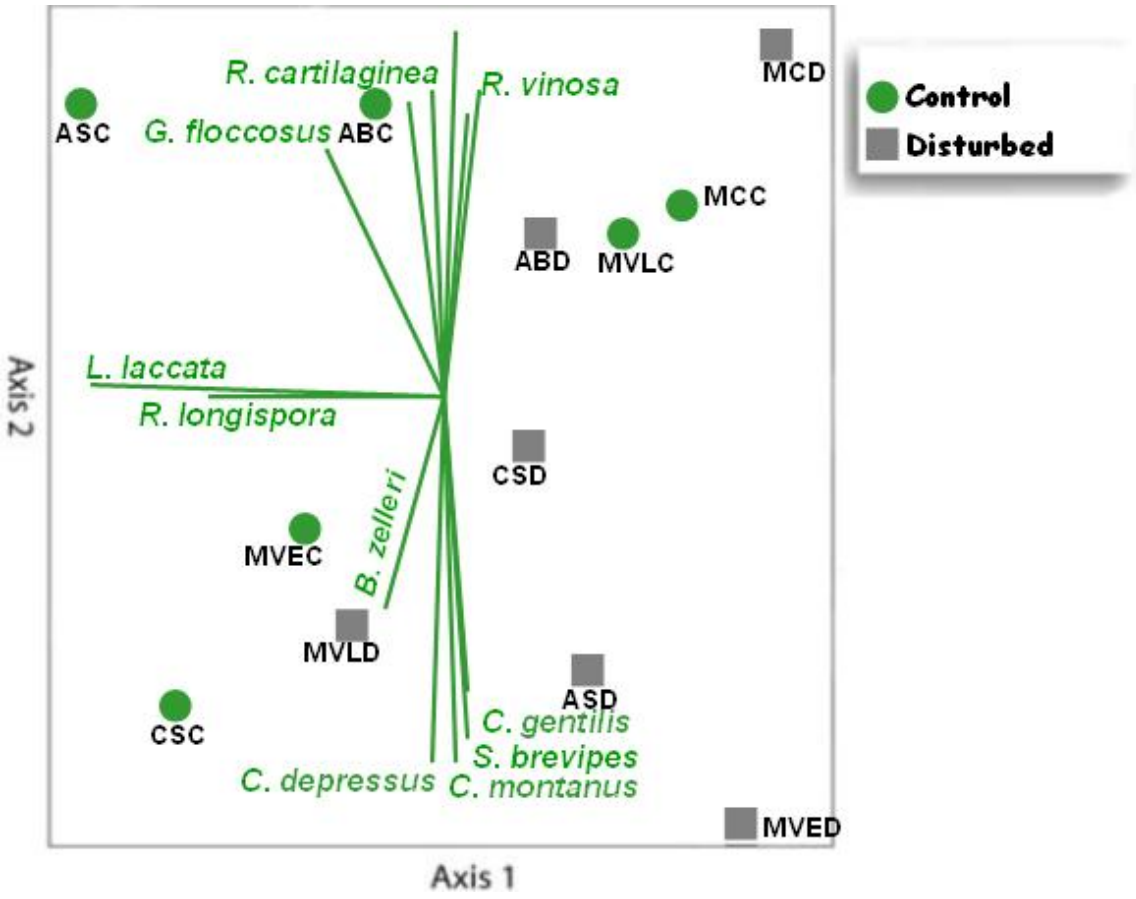
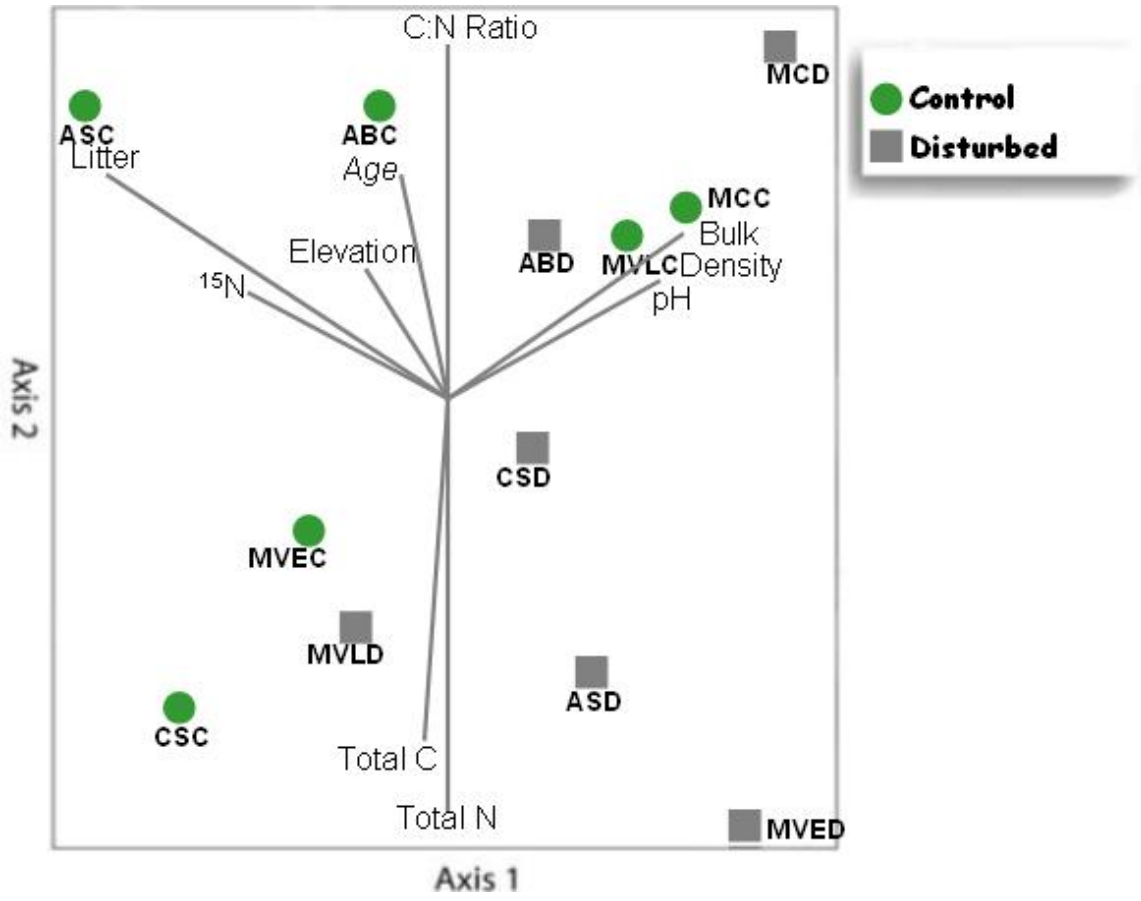


Figure 2.5. Species ordination with habitat attribute overlay.



DIVERSITY OF MAT-FORMING FUNGI IN RELATION TO SOIL PROPERTIES AND FOREST TYPE AT CRATER LAKE NATIONAL PARK

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Diversity of mat-forming fungi in relation to soil properties and forest type at Crater Lake National Park, Oregon

Abstract

We sampled ponderosa pine/white fir and mountain hemlock/noble fir communities at Crater Lake National Park (CLNP) for mat-forming soil fungi. Soil fungi collections were identified by DNA sequencing. Thirty-eight mat-forming genotypes were identified; members of the five most common genera (*Gautieria*, *Lepiota, Piloderma, Ramaria,* and *Rhizopogon*) comprised 67% of all collections. Abundance of fungal mats was correlated with high soil carbon to nitrogen (C:N) ratios, fine woody debris and needle litter mass in both forest community types. The mycorrhizal genera *Alpova* and *Lactarius* are newly identified as mat-forming taxa, as are the saprobic genera *Clitocybe*, *Flavoscypha, Gastropila*, *Lepiota* and *Xenasmatella*. Difficulties in defining what comprises a fungal 'mat' are discussed.

Introduction

The importance of fungi in forest ecosystems is well established (Smith and Read 1997). Mycorrhizal fungi form symbiotic relationships through the roots of trees that are critical to the ability of trees to obtain the nutrients they need for growth. The role of saprobic fungi in biomass decomposition and nutrient cycling in a forest also is a vital function (Dighton 2003). Most fungal biomass exists as hyphae that permeate the soil. Often these are too fine to see, but sometimes they form rhizomorphs or aggregations of mycelial strands that are visible to the naked eye. Some taxa create discrete zones in the soil, where they appear to dominate soil biota, forming structures referred to as "fungal mats" (Cromack et al. 1979).

Our aim was to sample mat-forming fungi at CLNP in the southern Oregon Cascade Mountains. We collected soil fungal samples and identified them by DNA sequencing. We also collected a suite of soil chemistry and surface fuels data and sought correlations

between these factors and the abundance of soil fungi, and when possible, habitat preferences for specific taxa.

The definition of exactly what qualifies as a 'fungal mat' has differed among researchers over the years. Must a mat be mycorrhizal? Must it be perennial, or extend into mineral soil? Must it be hydrophobic? Does size matter? In some of the first published references to fungal mats, Ramsbottom (1953) noted "irregular masses of soil held together by mycelial threads" under *Lepiota* and "compact masses of mycelium" under *Collybia*, and Hawker (1954) described *Hysterangium* species forming a "mass of flocculent pure white mycelium, which aggregates to form rhizomorphs which bear the fruit-bodies." Meyer (1963) referred to "hyphenfladen" (hyphal cakes) under *Laccaria amythestina*. Fisher (1972) described fungal mats as "up to 1 m in diameter…white, felt-like and 1-2 cm thick." Cromack et al. (1988) used the definition of "a sufficiently dense colonization of litter or soil horizons to create characteristic fungal-mat zones which are readily visible."

Griffiths et al. (1990) observed "…extensive mats within forest soils and litter layers that are characterized by a dense profusion of rhizomorphs…form(ing) distinct morphological entities that are easily differentiated from adjacent noncolonized soil." Unestam and Sun (1995) defined a fungal mat as "…a limited and rather homogenous mycelium of densely interwoven rhizomorphs, strands of hyphae, all belonging to the same species, perhaps the same clone… and apparently excluding most other mycorrhizal fungi…(having) a visible border with the surrounding soil, be it mycorrhizal or not." Nouhra et al. (2005) described "a compact hydrophobic aggregation of fungal strands, mycorrhizal roots, and substrate" under *Ramaria*, and Agerer (2006) described the mat subtype of mycorrhizae as a morphology that "…occupies rather large areas in the soil, where ectomycorrhizae (ECM) with their emanating hyphae and rhizomorphs are so densely aggregated that there is apparently no space for other ECM species." Dunham et al. (2007) defined mats for the purpose of their research as "…dense profusions of rhizomorphs associated with

obvious ectomycorrhizal root tips that aggregate soil and alter its appearance and were uniform in appearance for at least 0.5 m in diameter."

For many years, research on mat-forming fungi in the Pacific Northwestern United States focused on *Gautieria monticola* and *Hysterangium* spp., and a substantial body of literature exists on the properties of these fungi. Cromack et al. (1979) documented lower pH and higher levels of oxalic acid in mat tissue of *H. setchellii* (cited as *H. crassum*) and made the connection between fungal mats and accelerated mineral weathering as a source of primary mineral nutrition. Griffiths et al. (1990) reported higher acetylene reduction and lower denitrification rates in *H. setchellii* mat soils, and consequently, a concentration of mineralizable N. *Hysterangium setchellii* mat soils also tend to concentrate available N and P (Entry et al. 1991a), increase C and C:N ratios (Aguilera et al. 1993), and increase soil Al, DOC, Fe, H, Mn, PO_4, SO_4, and Zn (Griffiths et al. 1994).

Unestam (1991) measured increased hydrophobicity in *G. monticola*, *H. setchellii*, and *Rhizopogon* spp. mat soils as compared to non-mat soils, and Entry et al. (1992) hypothesized a connection between reduced leaching and nutrient concentrations in *H. setchellii* mats. This nutrient-rich microhabitat provides an environment conducive to the increased seedling regeneration rates in *G. monticola* and *H. setchellii* mat soils observed by Griffiths et al. (1991a). Increased lignin and cellulose decomposition rates measured by Entry et al. (1991b) in *H. setchellii* mats accelerate nutrient turnover and may be a function of the altered cellulase, laminarinase, peroxidase, and phosphatase activities observed by Griffiths and Caldwell (1992) and fatty acid esterases (Caldwell et al. 1991) found in mat tissue cultures. Increased concentrations of microbial (Griffiths et al. 1991b) and microarthropod (Cromack et al. 1988) activities in *H. setchellii* mats further contribute to accelerated nutrient turnover.

Other fungal genera reported as having mat-forming species include *Arcangeliella* (Caldwell et al. 1991), *Austrogautieria* (Caldwell et al. 1991), *Bankera* (Agerer and Otto 1997), *Boletopsis* (Agerer 1992a), *Chondrogaster* (Caldwell et al. 1991), *Cortinarius* (Bougher and Malajczuk 1986), *Geastrum* (Agerer and Beenken 1998a), *Gomphus* (Agerer et al. 1998b), *Hebeloma* (Hintikka 1974), *Hydnellum* (Hintikka and Naykki 1967), *Mycoamaranthus* (Caldwell et al. 1991), *Phellodon* (Agerer 1992b), *Piloderma* (Mikola 1962), *Ramaria* (Marr and Stuntz 1973), *Rhizopogon* (Unestam and Sun 1995), *Sarcodon* (Agerer 1991), *Sistotrema* (Dunham et al. 2007), *Suillus* (Unestam and Sun 1995), *Trechispora* (Dunham et al. 2007) and *Tricholoma* (Ogawa and Hamada 1965).

Methods

Study area

CLNP is in the Cascade Mountains of southern Oregon. At elevations up to ca. 1600 m a ponderosa pine (*Pinus ponderosa* Dougl ex Laws.)/white fir (*Abies concolor* Gord. & Glend. [Lindl.]) community is dominant (mixed conifer - *Abies concolor* zone sensu Franklin and Dyrness, 1973), and at higher elevations mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.)/noble fir (*Abies procera* Rehd.) community is dominant (*Tsuga mertensiana* zones sensu Franklin and Dyrness, 1973). Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) occurs throughout the park.

In a *Abies concolor* zone, 24 prescribed burn units of ca 2.8 ha were established by Perrakis and Agee (2006). Eight of these units were non-burned controls, 8 had prescribed burns applied in the spring of 2002, and 8 had prescribed burns applied in the autumn of 2002.

These units were at the south border of CLNP in southern Oregon (lat. 42° 48'N, long. 122° 50'W) and the fire history and plant community were characterized by McNeil and Zobel (1980). The elevation varied little across the site, with a gradient of 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 up to 20 cm thick, consists of of ponderosa pine and white fir needles and ranges in dry mass from about 3 to 6 kg m^{-2}. The humus layer (A horizon) is varies considerably in thickness and has diffuse interfaces with the litter above and mineral soil below.

The forest overstory is dominated by ponderosa pine with subdominant white fir. The midstory is primarily composed of white fir and lodgepole pine, and the minimal understory includes *Pyrola sp.*, *Carex sp.*, and a number of forbs. *Ceanothus velutinus* and *Arctostaphylos spp.* 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 fires were effective suppressed from 1902 through 1978. Prior to 1902, the overall fire return interval ranged from 12.8 to 40 yrs, with a mean of 21.1 yrs.

In the mountain hemlock/noble fir community, 8 units were undisturbed controls, 4 were recreational sites in current use, 3 were abandoned recreational sites, and 3 were wildfire sites that burned in 1976, 1996, and 2001, respectively. The sites all were in the southern half of CLNP, except one wildfire site (Border Fire) at the northwest corner of the park. Soil parent material is pyroclastic tephra deposited in the Mazama eruption ca. 7000 yrs ago. Mountain hemlock/noble fir communities have a highly variable fire return interval (15-157 yrs), with the majority of fires being low severity underburns (Chappell and Agee 1996). Stand replacing fires do occur, and all 3 wildfire sites we sampled had experienced almost total overstory mortality.

The control units were dominated by large, widely spaced overstory trees over 300 yrs of age. Understories were typified by *Arctostaphylos nevadensis*, *Carex rossii, Chimaphila*

umbellata, Corallorhiza maculata, Goodyera oblongifolia, Listeria caurina, Lupinus latifolius, *Luzula hitchcockii, Orthilla secunda,* and *Vaccinium scoparium* (Wilson 2007). Litter layers were deep (to 20 cm) and woody debris was abundant. The control units were sited nearby disturbed units; though one control unit was shared with the Annie Springs and Mazama Village late-seral disturbed units, and another control unit was shared with the Flying Dutchman and Goodbye Fire disturbed units.

Overstory trees at the recreational sites in current use ranged in age from 175 to over 300 yrs. These sites had been in consistent use since the 1870's (Picnic Hill), 1955 (Mason's Camp), and ca. 1960 (Mazama Village mid-seral and Mazama Village late-seral) (Green 1984). The understory composition is similar to the control units, with the addition of *Carex halliana, Carex multicostata, Elymus elymoides, Stipa occidentalis*, and *Juncus parryi.* They lacked the *Corallorhiza maculata, Goodyera oblongifolia,* and *Listeria caurina* found in the control units, had reduced canopy coverage, woody debris, and needle litter, and greater soil compaction.

Regular use of the abandoned recreational sites ended in the 1950's (Annie Springs), 1972 (Cold Springs), and 1980 (Anderson Bluffs). Overstory age ranged from 167 to over 300 yrs. Abandoned sites had higher mineral soil bulk density and lower fuel levels than proximate control units. Overstory composition was the same in abandoned sites and controls, but the abandoned sites had higher levels of graminoids and trees < 30 cm diameter at breast height (DBH), and lower levels of trees > 30 cm DBH than controls (Wilson (2007). Abandoned sites had higher proportions of lodgepole pine, and lower proportions of mountain hemlock and noble fir than controls.

The three wildfire sites formed a short chronosequence: The Goodbye Fire burned in 1976, the Flying Dutchman fire burned in 1996, and the Border Fire burned in 2001. The Goodbye Fire site had some conifer regeneration to 3 or 4 m in height, with a dense understory of *Arctostaphylos spp, Ceanothus velutinus*, and *Ribes spp*. The Flying

Dutchman fire had isolated patches of regenerating conifers to 1 m in height, a sparse understory of *Lupinus spp*, and almost no litter layer. The Border Fire site had no regeneration or understory plants, a very sparse litter layer with only a few small surviving trees (mostly < 3 m in height). All wildfire sites had substantial coarse woody debris (CWD) recruitment.

Soil cores and mineral soil bulk density

Six soil cores were taken with a hammer-type corer from random locations (by tossing a marker) throughout each treatment unit, labeled, and refrigerated in sealed plastic bags. Before coring, the litter layer was removed to the surface of the mineral soil. Cores were dried in an oven 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. Since 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 (335 cm^3) to obtain a "rock-free" volume. This volume was divided by the post-screening weight to reach a rock-free bulk density.

Fungal mat sampling

We collected and sequenced soil fungi that formed aggregations of hyphae or rhizomorphs sufficiently dense to aggregate their substrate to a depth of at least 2 cm, and usually at least 0.5 m^2 in area. However, a number of mats (such as those of the *Piloderma* morphotype) were rarely that large, and samples were collected from some mats that were as small as 200 cm^2. We did not attempt to distinguish between mycorrhizal and saprobic taxa in the field.

Each of the 42 units was sampled for a person-hour in July 2005, and again in September 2006. Sampling focused on microhabitats within each unit likely to support soil fungi, such as low areas, underneath fungal sporocarps and animal digs, and adjacent to decayed logs. To reveal mats, the litter surface was gently raked back to the upper layers of the A horizon. When fungal mats were observed, a tissue sample was collected and notes were taken on the appearance of fungi *in situ*.

Fungal mat identification

Samples were stored in a -20 °C freezer until ready for processing. Prior to DNA analysis, samples were rinsed with dH_20, and a small subsample of fungal tissue was carefully removed using tweezers and a stereo microscope. DNA was extracted from the samples following Gardes and Bruns (1996), 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 95% similarity were discarded from the dataset. A BLAST search provides a list of taxa most closely matching the search sequence, but often species within a genus are too similar to distinguish with confidence. Thus, names were assigned at the genus level, with probable species or species group identities suggested (Table 3.1). For ease of reading, in the discussion we use the species names with the caveat that there is uncertainty about the specific identifications.

Carbon, nitrogen, and isotopic analysis

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

Fuels: litter mass, fine and coarse woody debris

In each unit, ten 20 m long, fuel inventory transects were established for a total of 200 m. Coarse (>7.6 cm diameter) and fine (0.6 – 7.6 cm diameter) woody fuels were measured along these transects by Brown's (1974) planar intersect method, with the addition of litter depth measurements at three points along each transect. Woody debris mass was calculated by using the values for Pacific Northwest mixed-conifer forests derived by van Wagtendonk et al. (1996), and litter mass was calculated from 10-14 samples of litter depth and density at each unit (Perrakis and Agee 2006; Wilson 2007).

Soil pH

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

Data analysis

Correlations between the number of mat-forming fungi collected on each unit and the habitat attributes of the units were analyzed with linear regression. The habitat preferences of mat-forming fungi collected on at least 3 units within an ecotype were analyzed with logistic regression. Fungal mat associations with stand age were analyzed with chi-square. All statistical analyses were done using SAS 9.1 (SAS 2003).

Results

DNA was successfully amplified and sequenced from 169 mycelia collections, representing 38 taxonomic units (Tables 3.1 and 3.2). Members of the 5 most common genera (*Gautieria*, *Lepiota, Piloderma, Ramaria,* and *Rhizopogon*) comprised 67% of all collections. Ten taxa were collected only once. Three distinct genotypes of the mycorrhizal genus *Piloderma* and three distinct genotypes of the saprobic *Ramaria stricta* species complex were detected.

Habitat associations in the *Abies concolor* zone

Fifty (identified and unidentified) collections of soil fungi were made in the 8 control units, 54 in the 8 spring burn units, and 5 in the 8 fall burn units. The habitat attributes that correlated most strongly with the most abundant soil fungi were C:N ratio, coarse woody debris (CWD), fine woody debris (FWD), and litter mass. These attributes were largely intercorrelated and showed a significant response to burn treatment (Trappe et al. 2008).

Linear regressions indicated that the number of mat-forming taxa in the *Abies concolor* zone was positively correlated with soil C:N ratios, FWD mass, and needle litter mass, and negatively correlated with soil pH (Table 3.2). Significant interactions were detected between all of the significant variables; those between soil C:N ratios, FWD mass, and litter mass had the highest adjusted R^2 values. The overstory in this ecotype was of uniform age, and thus, stand age was not included in data analysis.

Ten taxa were collected on at least three units in the *Abies concolor* zone; logistic regression correlations with habitat attributes are displayed in Table 3.3. *Gautieria monticola* mats were positively correlated with total C and C:N ratios. *Lepiota magnispora* was positively correlated with FWD and litter mass. *Piloderma fallax* was positively correlated with C:N ratio, CWD levels, FWD levels, and litter levels, and negatively correlated with mineral soil bulk density and $\delta^{13}C$ depletion. *Piloderma* sp. also was positively correlated with C:N ratio and negatively correlated with $\delta^{13}C$ depletion. When all *Piloderma* were combined, the correlations were identical to those of *P. fallax*. *Ramaria stricta s.s.* was positively correlated with C:N ratio and negatively with soil pH.

Habitat associations in the mountain hemlock/noble fir community

Fifty-seven soil fungi collections were made in the 8 control units ($\bar{x}$= 7.1), 10 collections in the 4 in-use recreational units ($\bar{x}$= 2.5), 8 collections in the 3 abandoned

recreational units ($\bar{x}$ = 2.7), and 3 collections in the 3 wildfire units (= 1). All 3 collections from wildfire units came from the Goodbye Fire site (31 yrs post-fire). No soil fungi were observed at the other two wildfire sites (Flying Dutchman Fire sampled 11 yrs post-fire and the Border Fire sampled 2 yrs post-fire). This suggests that it may take 15+ yrs for mats to re-establish following wildfires.

Linear regressions indicated that the abundance of mat-forming taxa in the mountain hemlock ecotype also was positively correlated with stand age, soil C:N ratios and the mass of FWD and needle litter (Table 3.3). Significant interactions were detected between all of the significant variables; the interaction between stand age and litter mass had the highest adjusted R^2 value.

Five taxa were collected on at least three units; logistic regression correlations with habitat attributes are displayed in Table 3.4. All were mat-forming fungi. *Flavoscypha cantharella* mats were positively correlated with litter mass, and *Piloderma fallax* was positively correlated with $\delta^{15}N$ enrichment, C:N ratio, FWD, and litter mass, and negatively correlated with total N. *Ramaria stricta*/OSC 65995, *Gastropila subcretacea* and *Hydnellum peckii* did not have any significant correlations with measured habitat variables. No individual taxa correlated with stand age, but only one mat was detected in a stand less than 100 yrs old (*Hydnellum peckii*). Twenty-one of these 26 mats were collected in stands > 300 yrs old (χ^2= 0.004).

Newly identified mat-forming taxa

To the known ectomycorrhizal mat-forming genera we add *Alpova* and *Lactarius*. The saprobic genera *Clitocybe*, *Flavoscypha, Gastropila*, *Lepiota,* and *Xenasmatella* also formed distinct cohesive mats in the litter layer.

Discussion

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 were collected on a unit-level and did not account for microhabitat. For example, while many collections were in units with compacted soils and relatively sparse needle litter, the vast majority of such collections were made under the dripline of smaller trees or along slopes — microhabitats that retained a deeper litter layer and had less soil compaction. In burned sites, the same response was observed: mats were collected exclusively in areas where the fire had left patches of unburned litter. It was highly apparent in the field that where needle litter was sparse due either to anthropogenic disturbance or fire, the likelihood of finding mats decreased substantially. This is reflected in table 3.2, where interactions between litter mass and soil C:N ratios are shown to have a strong influence on the number of mat-forming fungi detected.

Mat-forming fungi were often observed directly below a sporocarp, and in only one case (*Rhizopogon truncatus*) was the fungal mat of the same taxon as the sporocarp. *Rhizopogon* sporocarps were collected from the very heart of *Gautieria* mats, *Rhizopogon* mats were observed directly beneath *Ramaria* sporocarps, and *Gautieria* sporocarps were collected from *Ramaria* mats. Notably absent from soil fungus collections were *Hysterangium* species, although a few sporocarps had been collected on the units. Often sporocarps of mat-forming taxa were collected with no associated visible mat, indicating that in some species, the formation of a mat is not consistent with the presence of the organism, or that the mat structure is not perennial.

Mycorrhizal taxa forming a "mat subtypes" of Agerer (2001) fell into 2 morphological subcategories at Crater Lake: a powdery morphotype and a mycelial morphotype. The powdery morphotype was produced by *Gautieria monticola* (Fig. 3.1a), *Hydnellum peckii* (Fig. 3.1b), and *Sistotrema albopallescens* (Fig. 3.1c). Soil within these mats was discolored (usually gray), and root tips often were abundant. The mycelia frequently

were too fine to detect with the unaided eye, but nevertheless, bound the substrate into a cohesive mass, often including mineral soil. The mats formed by these 3 taxa were indistinguishable from one another in the field.

The mycelial morphotype was characterized by fine but visible mycelia that bound the substrate together, and sometimes produced clumpy wefts or small fans (Figs. 3.1d-h). These mats were often at the interface between the A and O horizons and knit fine humus particles together into a solid mass (Fig.3.1i-k). In many cases, mycorrhizal mats were identified from the less-decomposed upper litter layer (Fig. 3.1l-m). Some, notably *Piloderma* spp, were closely associated with decayed CWD (Fig. 3.1n-o). Long-range foraging structures (sensu Agerer 2001), such as rhizomorphs or mycelial cords, were uncommon in mycorrhizal mats. The term "rhizomorph" refers specifically to a mycelial cord with differentiated hyphae; since we did not examine these microscopically we will use the more general term "mycelial cord", sensu Cairney et al. (1991).
A number of saprobic taxa also formed mats of fine mycelia that were indistinguishable from mycorrhizal mats (compare Fig. 3.1(h) and 3.1(k). Some saprobic mats were accompanied by profusions of mycelial fans and cords (Fig. 3.1(g) and Figs. 3.1(l)), features largely absent from mycorrhizal mats. Most were associated with the litter layer and did not obviously extend into the mineral soil layer.

That said, morphology and color are poor ways to identify the species of fungal mats: *Piloderma fallax* mats ranged in appearance from knits of bright yellow mycelial cords and wefts to dingy white hyphal sheets. The coarse white mycelial cord morphology was produced by many, but not all saprobic taxa, most commonly *Lepiota magnispora, Ramaria stricta s.l.*, and *Tyromyces chioneus*. The major groups of mat-forming fungi identified from CLNP are discussed below. Basidiomycetes are organized by major lineage, sensu Hibbett (2006).

Ascomycetes

None of the ascomycete taxa identified from Crater Lake soils were mycorrhizal. Only one unquestionably formed mats: *Flavoscypha cantharella*. All 6 collections of *F. cantharella* were from the *Tsuga mertensiana* zone. Five of the 6 collections were made in control units and one in an active-use campground (Mazama Village). The occurrence of *F. cantharella* was significantly correlated with litter mass (Table 3.4), and the collection from Mazama Village was in a protected microsite. *Flavoscypha cantharella* formed fragile, finely knit mats of pale yellow to whitish hyphae in the litter layer.

Members of the *Lecythophora/Phialophora* complex were identified from 2 collections of clumpy, pale yellow to whitish mats in organic soil. These taxa are common microfungal saprobes in needle litter (Sieber-Canavesi and Sieber 1993), but they probably were not the primary biomass component of the mats in which they were detected.

Atheliales

Piloderma spp. were the most common soil fungi collected in this survey, consistent with the findings of Dunham et al. (2007). We identified 3 distinct species of *Piloderma* at Crater Lake. The majority of *Piloderma* collections (45) matched *P. fallax* in GenBank. Two collections matched *P. byssinum*, and five matched a cryptic species, *Piloderma* spp.

Of the 31 collections of *Piloderma fallax* in the *Abies concolor* zone, 13 were made in control units, 16 in spring burn units, and 2 in fall burn units. In this ecotype, its presence was correlated with lower soil bulk densities, higher C:N ratios, and higher levels of CWD, FWD, and litter. In the *Tsuga mertensiana* zone, 11 collections were made in control units and 4 in disturbed units. Here too, it was correlated with higher C:N ratios, FWD, and litter, but not CWD. Smith et al. (2000) reported that *Piloderma fallax* have

yellow mycelia but white basidiomata. In the present study, most of the *P. fallax* mats were dark yellow, but 10 were white. The variations in mat color we observed may be a consequence of mode shift toward spore production, pleiomorphy, or some other factor.

Both collections of *P. byssinum* were from the *Abies concolor* zone — one in a spring burn unit and the other in a fall burn unit. *Piloderma byssinum* formed mats of finely knit, white hyphae permeating the A horizon and the mineral soil.

The cryptic *Piloderma* spp. was collected in one control unit and three spring burn units in the *Abies concolor* zone, and its presence was correlated with higher C:N ratios. In the *Tsuga mertensiana* zone, it was collected only in one control unit. It formed mats of white mycelial fans over substrate surfaces with thickened yellow areas (Fig. 3.1(n)), in contrast to the typically clumpy *P. fallax* morphology (Fig. 3.1(m)).

Boletales

All of the mat-forming fungi in the boletoid clade were in Rhizopogonaceae except one collection of *Suillus tomentosus*, present in the form of fine yellow hyphae binding the organic layer in a ponderosa pine/white fir unburned control unit. Dense hyphal aggregations have been observed under *Suillus* sporocarps at the H.J. Andrews Experimental Forest (R. Griffiths, pers. comm.), but it is unknown if these aggregations are perennial or ephemerally associated with sporocarp morphogenesis.

The *Rhizopogon salebrosus - R. subbadius* complex were not clearly distinguished by the results from BLAST searches. Mats formed by this complex bind organic soil and litter particles together with cobweb-like, white mycelia (Fig. 3.1(h)). They were identified from one control, one fall burn, and 5 spring burn units in the *Abies concolor* zone, and in one control unit in the *Tsuga mertensiana* zone.

Rhizopogon truncatus forms conspicuous, bright yellow-green mats that bind litter with a fine knit of hyphae and occasional, short mycelial cords (Fig. 3.1(e)). It was collected on one undisturbed and 2 disturbed sites in the *Tsuga mertensiana* zone, and a spring burn unit in the *Abies concolor* zone. It superficially resembles *Piloderma fallax* (Fig. 3.1(m)), but *R. truncatus* mats are of a brighter, less orangish chroma, and commonly are larger than *P. fallax* mats. In contrast to *Piloderma fallax*, the likelihood of *Rhizopogon truncatus'* occurrence was not correlated with higher CWD levels. It frequently occurred at the interface between the A and O horizons in needle litter (Fig. 3.1(e)) and, in the field, did not appear to require CWD substrates.

Rhizopogon vulgaris formed dense mats of fine, white hyphal knit detected several times under sporocarps of other taxa, most commonly *Ramaria flavobrunnescens* var. *aromatica*. Mats formed by *R. vulgaris* were collected in 4 controls and one spring burn unit in the *Abies concolor* zone.

Alpova trappei formed mats of finely knit, yellow-green mycelia in decaying needle litter at the interface between the A and O horizons (Fig. 3.1d). The mycelia did not visibly extend into the mineral soil. *Alpova trappei* was identified from mats in 2 spring burn units in the *Abies concolor* zone.

Cantharellales

Two ectomycorrhizal genera recently identified as mat-forming by Dunham et al.. (2007) were detected in mats at Crater Lake: *Sistotrema* and *Trechispora*. *Sistotrema albopallescens* (Fig. 3.1c) formed a grey, powdery mat closely resembling that of *Gautieria monticola* (Fig. 3.1a). *Sistotrema* most frequently is found as an apparent saprobe on humus, bark and wood (Jülich and Stalpers 1980), but Currah et al. (1992) identified *S. brinkmanni* as a mycorrhizal symbiont with the orchid, *Piperia unalascensis*. Mycorrhizal associations with achlorophyllous plants are well documented (Castellano and Trappe 1985, Kretzer et al. 2000), and Went (1973) noted dense conglomerations of

rhizomorphs in the immediate vicinity of *Corallorhiza maculata, Pterospora andromeda,* and *Sarcodes sanguinea*. Although all three of these taxa occur at Crater Lake, but knowledge of their mycota is lacking.

Two species of *Trechispora* formed mats at Crater Lake: *T. alnicola* (Fig. 3.1k) with a dense, fine white knit of hyphae binding needle litter together, and *T. subsphaerospora* with looser aggregations of white mycelial cords. The genus *Trechispora* is notable for its production of calcium oxalate (Larsson 1994), which has been associated with mineral weathering (Cromack et al. 1979; Griffiths et al. 1994) and enhanced nutrient uptake by host plants (Malaczuk and Cromack 1982).

Agaricales

Seven mat-forming species of *Cortinarius* species were detected; *C. boulderensis, C. brunneus*, *C. caperatus*, *C. montanus*, *C. pinguis*, *C. rigidus*, and *C. subfoetidus*. These mats were similarly composed of fine white hyphae with occasional clumps, binding organic material together (Fig. 3.1f).

Gastropila subcretacea, a saprobic taxon not previously identified as mat-forming, was collected on two control units in the *Abies concolor* zone, and in the *Tsuga mertensiana* zone on a control unit and an in-use campground. Mat morphology was of dingy white, fine mycelial cords, largely confined to the needle litter (Fig. 3.1j).

Lepiota magnispora was among the more common taxa detected in Crater Lake soils. Its morphology was usually long and thick, ropy white to pale yellow mycelial cords similar to those of *Ramaria stricta* (Fig. 3.1l), but it also produced finer hyphae that bound soil and litter particles together. In the *Abies concolor* zone, *L. magnispora*

was collected on control and spring burn units but not in fall burn units, and was correlated with levels of FWD and litter mass (Table 3.4). In the *Tsuga mertensiana* zone it was only collected on two control units.

Tricholoma magnivelare (matsutake) is among the better-known and intensively studied mat-forming fungi, due to their commercial value and habit of growing from "shiros" (Hosford et al. 1997). At Crater Lake, it formed dense mats of fine, white hyphae binding litter particles together and extending somewhat into the mineral soil horizon. Although *T. magnivelare* sporocarps were collected from spring burn units in the *Abies concolor* zone and anthropogenically disturbed sites in the *Tsuga mertensiana* zone, mats were detected only in 2 control units in the *Abies concolor* zone. Matsutake appears to withstand a degree of disturbance, but no sporocarps or mats were observed in the fall burn units.

Tricholoma saponaceum and *T. sejunctum* also formed dense, whitish to yellowish sheets and clumps of hyphae, primarily in the litter layer. Sporocarps of both *T. saponaceum* and *T. sejunctum* are very common throughout CLNP, but their mats were collected only from control and spring burn units in the *Abies concolor* zone. They are closely enough related that we could not distinguish between them base on the results from BLAST searches. *Tricholoma intermedium* and *T. equestre* were detected once each in control units in the *Abies concolor* zone; their mats were white and similar in morphology to those of *T. magnivelare.*

Gomphales

Gautieria monticola was collected in 4 control and 2 spring burn units in the *Abies concolor* zone, and adjacent control and current-use units in the *Tsuga mertensiana* zone. *Gautieria monticola* is one of the better known and well

studied mat-forming taxa (Griffiths et al. 1991a; Griffiths and Caldwell 1992), and the mats observed at Crater Lake were consistent with its well-documented powdery grayish morphology (Fig. 3.1a).

Ramaria flavobrunnescens var. *aromatica* sporocarps were the most commonly collected *Ramaria* species but only were twice detected forming mats. While sporocarps were collected on all prescribed burn treatments in the ponderosa pine ecotype, mats only were observed in control units. Mat morphology was dense, white hyphae binding organic litter and also forming sheets across substrate surfaces. *Ramaria rasilispora* was another common coral fungus at Crater Lake; mats of this taxon were detected under sporocarps of the same species in 2 spring burn units in the *Abies concolor* zone. Their mat morphology resembled that of *R. flavobrunnescens* var. *aromatica*.

The *Ramaria stricta* complex at Crater Lake appears to have 3 distinct genotypes. The first unequivocally matched *R. stricta* in GenBank; all but one of these were collected in the *Abies concolor* zone (3 in control, 1 in fall burn, and 3 in spring burn units). The second genotype group matched GenBank sequences of *R. stricta* or *R. pinicola* with comparable similarity; this group was collected exclusively in the *Abies concolor* zone. It was collected in 4 control and 6 spring burn units. The third group matched *R. stricta* and an unnamed collection OSC 65995 (OSC Herbarium, Oregon State University) with comparable similarity. It was collected in the *Abies concolor* zone on one control and 2 spring burn units, and in the *Tsuga mertensiana* zone on 4 control units and one in-use recreational site (Mazama Village Campground). The morphology of all 3 genotypes in the *R. stricta* complex was similar to that of *Lepiota magnispora*, having prominent mycelial cords, usually white, but sometimes with yellowish tints (Fig. 3.1l). The likelihood of occurrence correlated only with higher soil C:N ratios, but field observations indicated

they were restricted to microsites with a well-developed litter layer. This is intuitive, given *Ramaria stricta s.l.* is in the saprobic subgenus *Lentoramaria* (Humpert et al. 2001).

Polyporales

Xenasmatella vaga was detected in 2 spring burn units in the *Abies concolor* zone and in 2 control units in the *Tsuga mertensiana* zone. It formed dense, yellow aggregations of hyphae knitting woody debris and needle litter together, as well as sheets over organic substrates. Nakasone (1996) and Allmér et al. (2006) documented its occurrence on corticated CWD (as *Phlebiella vaga*). At Crater Lake, we found *X. vaga* extending from CWD pieces and forming cohesive mats in surrounding organic litter (Fig. 3.1i).

Tyromyces chioneus formed mats of loosely woven, white mycelial cords binding organic litter (Fig. 3.1g). It was collected in 2 disturbed units in the mountain hemlock ecotype. While this species did bind litter particles together, it did not coat nor dominate the substrate biomass, but rather, wove through the substrate as diffuse mycelial cords.

Russulales

Lactarius scrobiculatus was detected in two mats, one of yellow hyphae binding soil underneath *Cortinarius* sporocarps in the *Abies concolor* zone, and another of a dingy white color binding organic material in the *Tsuga mertensiana* zone. Both were collected in undisturbed control units. This is the first known account of mat formation in Russulaceae.

Thelephorales

The genus *Hydnellum* is one of the first fungal taxa to have been identified as mat-forming (Hintikka and Naykki 1967). *Hydnellum peckii* was detected in 7 units: 2 spring burn units in the *Abies concolor* zone, and 3 controls and 2 disturbed units in the *Tsuga*

mertensiana zone. It formed a gray, powdery mat (Fig. 3.1b), very similar to that of *Gautieria monticola*, and was one of the few mats detected in a wildfire burn site (Goodbye Fire).

Definitions of mats

The formation of the mat morphology by some fungi is thought to confer an evolutionary advantage due to the efficiency and effectiveness of site occupation by dense masses of tissue to concentrate enzymantic activity and exclude competitors. Many mats appear to be long-lived and may have limited mobility, in the sense of expanding in directions toward resources and not toward areas of depleted resources. The definition of what precisely constitutes a mat probably will always be a matter of opinion. Most will agree that a mat is a dense aggregation of fungal hyphae that has a distinct edge or border, and has an element of depth rather than being superficial. Further characterizations are subject to exceptions and problems with quantification. For example, if a mat is defined as cohesively binding its substrate, what constitutes "cohesive?" *Piloderma fallax* (Fig. 3.1m) is widely accepted as being mat-forming (Mikola 1962; Smith et al. 2000) but frequently binds its substrate only loosely and does not thoroughly permeate its environs any more than the saprobic *Tyromyces chioneus* (Fig. 3.1g). Some mat-forming fungi (such as *Piloderma fallax*) are associated with downed CWD (Smith et al. 2000; Elliott et al. 2007), and most discussions of fungal mats are restricted to those residing in the soil. There is, however, precedent for the term being used with reference to decomposition occurring in stumps and standing snags (*Fomitopsis officianalis* and *F. pinicola* in Arora, 1986; *Phellinus weirii* in McDougall and Blanchette, 1996).

Some researchers have restricted their collecting to ectomycorrhizal mats, but in our experience it is difficult to discern mycorrhizal from saprobic mats in the field. Mycorrhizal root tips are not always easily detectable, and confident identification of the mat-forming fungus usually is not possible without genetic typing. By the broad

morphological definitions above, many saprobic taxa clearly form mats. Saprobic mats often have an abundance of mycelial cord morphology (Fig. 3.1g and 3.1l), but not always (Fig. 3.1i).

One difference that might be expected in developmental patterns between mycorrhizal and saprobic mats is that saprobes may be restricted to surface organic material, while mycorrhizal fungi, with their carbon source secured, are more likely to extend into the B horizon foraging for mineral nutrients. However, many of the mycorrhizal mats we observed were visible only in the organic A and O horizons (Figs. 3.1h.e, k,f,j) and were quite similar in their substrate affinities to saprobic mats (Figs. l, i). Additionally, several mycorrhizal mat-forming taxa, such as *Hysterangium* (Amaranthus et al. 1994) and *Piloderma* (Smith et al. 2000; Elliott et al. 2007), are associated with coarse woody debris, and if their hyphae extend into mineral soil, it is not always apparent (Goodman and Trofymow 1998). Some *Piloderma* species have fungal mats in organic soil (Dunham et al. 2007), while other *Piloderma* species can colonize mineral soil horizons (Landweert et al. 2003).

Another criterion sometimes used is that a mat is monopolized by one fungal organism, or at least appears homogenous in its composition (Unestam and Sun 1995; Agerer 2006; Dunham et al. 2007). However, we frequently encountered situations where the sporocarp of one taxon was collected from the heart of a mat formed by a different one. Murata et al. (2005) reported genetic mosaics within matsutake shiros, and multiple mycorrhizal root tip morphotypes have been isolated from a single *Gautieria* mat (J. Eberhart, pers. comm.; van Breemen et al. 2000). Clearly hyphae of several origins can be in mats, whether or not they are visibly distinguishable. Mats commonly are mottled with tissues of various morphotypes and colors that are clearly different taxa, intraspecific variability notwithstanding.

Mats often are assumed to be perennial, a characteristic perhaps more likely to apply to ectomycorrhizal than saprobic mats, although little research has followed individual mats for more than a few seasons. *Hysterangium* mats observed and mapped in the summer were not visible in the winter in heavy rain, except where sheltered under logs (R. Griffiths, pers. comm.). These mats again appeared in the spring at their former locations, suggesting that moisture concentrations affect their opacity. This may be a function of the calcium oxalate crystals attached to the hyphae, and although these crystals are not easily water soluble, they may become translucent when wet or diminish in quantity when fungal metabolism slows. Hyphal aggregations are common at the base of sporocarps in many taxa, but it is unknown if they persist when the sporocarp is absent.

The issue of size also is difficult to quantify. Hyphal assemblages are ubiquitous in forest soils (Genney et al. 2006), and undoubtedly, the largest mat started out as a few hyphae. For research purposes, some criterion must necessarily be established to distinguish between 'mats' and a few mycelial cords in proximity to each other. The criteria used by each researcher necessarily are a function of the research question at hand, and thus a universal definition of minimum mat size is impractical. Extramatrical mycelium from ECM constitutes a major allocation of C resources into the soil ecosystem (Hogberg and Hogberg 2002), supporting the early work on substantially increased soil respiration in fungal mats as indicative of the increased C resource allocation to them (Hintikka and Naykki 1967; Griffiths et al. 1990). Recent experimental research on mycorrhizal hyphal production demonstrates that the mineral composition of the soil core can affect hyphal production by ectomycorrhizal fungi (Wallander et al. 2004; Hendricks et al. 2006). This type of research could include an integrated set of measures for evaluating microbial communities within and adjacent to fungal mats, as indicated in the overviews by Leckie (2005) and Allen et al. (2007).

Mycorrhizal networks provide multiple interconnections and pathways within fungal mats for mycorrhizal network functioning within both organic and mineral soil substrates, thus enhancing decomposition and mineral weathering, and the release of nutrient elements such as N, P and K through mycelial and hyphal penetration of soil substrates (Unestam and Sun 1995; Johnmans et al. 1997; Unestam and Finlay 1998a, b). Fungal nutrient cycling pathway functions first were indicated by extensive sampling of fungal rhizomorph tissues in both temperate and tropical forests (Stark 1972). Subsequent work demonstrated C and N transfers within fungal networks (Simard et al. 1997; He et al. 2006). Furthermore, there can be considerable interchange of nutrients, C resources, and water resources due to the presence of extensive mycorrhizal networks (Simard and Durall 2004; He et al. 2006; Allen et al. 2007; Querejeta et al. 2007).

Fungal mats formed by ECM enhance decomposition and release of nutrients (N, P, K, Ca, Mg) through increased weathering (Hintikka and Naykki 1967; Fisher 1972; Griffiths et al. 1990; Griffiths and Caldwell 1992; Griffiths et al. 1994). These mat structures can persist for long periods of time, perhaps years (Hintikka and Naykki 1967). Individual fungal rhizomorphs can persist for several months, surviving through a growing season in a pinyon/juniper woodland (Treseder et al. 2005). Fungal mats formed by *Hydnellum ferrugineum,* (Fr.) in a study by Hintikka and Naykki (1967), and *H. scleropodium,* in a study by Fisher (1972), measurably decreased the soil humus layer and mineral soil organic C and N, indicating the presence of a complex microbial community able to decompose resistant C substrates. Interestingly, mat-forming fungi, such as *H. ferrugineum* and *H. peckii,* once were widespread in Europe prior to increased pollution, and currently are on the red list in some countries (Gulden and Hanssen 1992). They may be sensitive to increased N deposition, such as the ECM fungi negatively impacted by a nitrogen-deposition gradient (Lilleskov et al. 2002). If fungal mats are mobilizing organic N resources in the soil, as indicated by recent research on N cycling (Schimel and Bennett 2004; Taylor et al. 2004), this would help to explain the classic ECM fungal mat

observations concerning soil N mobilization (Hintikka and Naykki 1967; Fisher 1972), as well as current confirmation of organic N uptake by ECM (Taylor et al. 2004).

CLNP represents a pristine forest environment within which to study mat-forming fungi. These fungi would be ideal for future research on mycorrhizal utilization of organic N sources, as indicated by previous ECM research (Griffiths and Caldwell 1992; Taylor et al. 2004). Natural abundance stable isotope data from ^{13}C and ^{15}N has been helpful in interpreting mycorrhizal vs. saprophytic trophic status from fungal sporocarps of species collected in forest ecosystems (Hobbie et al. 2001; Taylor et al. 2003). Basidiomycete ECM species can exhibit ^{13}C isotope natural abundance values that are similar to those for saprophytic fungi. Examples include two species of *Hydnellum*, *H. ferrugineum* and *H. peckii,* from the study by Taylor et al. (2003). The ECM species, *H. peckii*, occurs at CNP (Fig. 3.1b). The morphological colonization of fine roots of *Pinus sylvestris* by *H. ferrugineum*, with normal ECM formation at the leading edge of the fungal mat and the loss of outer cortex and carbonized appearance of colonized roots at the trailing edge of the fungal mat (Agerer 1993; Lefevre and Müller 1998), indicates a type of ECM formation that shows saprotrophic characteristics as the mat advances and leaves behind a zone of colonized soil. The ^{13}C isotopic signature observed in *H. ferrugineum* by Taylor et al. (2003) may be indicative of this fact. Similarly, *Tricholoma magnivelare* has been observed to leave some colonized conifer roots partially atrophied at the back edge of the fungal mat colony (Lefevre 2003).

Hydrophobicity has been documented in some mat types (Griffiths et al. 1991b; Unestam 1991; Nouhra et al. 2005), while others have been described as "becoming wet seasonally" (Griffiths et al. 1991b). For the majority of mat-forming taxa, no data on hydrophobicity exist. Accordingly it is premature to consider hydrophobicity an attribute common to all fungal mats or to require it as a prerequisite for 'mat' status.

A functional definition of mats also is difficult to apply. In the most intensively studied mats (*Gautieria* and *Hysterangium*), many unique physiological and chemical properties have been identified (Griffiths et al. 1991b; Entry et al. 1992; Aguilera 1993; and others). None of these properties can easily be measured in the field, and it is largely unknown if other mat-forming fungi (mycorrhizal or saprobic) share these properties.

Conclusions

The advent of DNA typing has vastly increased our ability to identify previously cryptic mat-forming species. At CLNP, we identified 36 mycorrhizal, mat-forming genotypes and 21 saprobic, mat-forming genotypes. Among the mycorrhizal genotypes, two genera had not been previously identified as mat-forming. The abundance of mats in an ecosystem is highly correlated with the mass of needle litter, and areas without needle litter coverage generally lacked mats. Mats are sensitive to severe disturbance, and may take over 15 years to re-colonize after a wildfire event. The fungus forming a particular mat is extremely difficult to identify confidently in the field, and a universal definition of exactly what does and does not constitute a fungal mat remains elusive. Researchers have historically defined mats in the context of their particular study design, and necessarily will continue to do so.

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Figure 3.1. Fungal mat morphologies: (a) *Gautieria monticola*. (b) *Hydnellum peckii*. (c) *Sistotrema albopallescens.* (d) *Alpova trappei.* (e) *Rhizopogon truncatus.* (f) *Cortinarius brunneus.* (g) *Tyromyces chioneus.* (h) *Rhizopogon salebrosus/subbadius.*

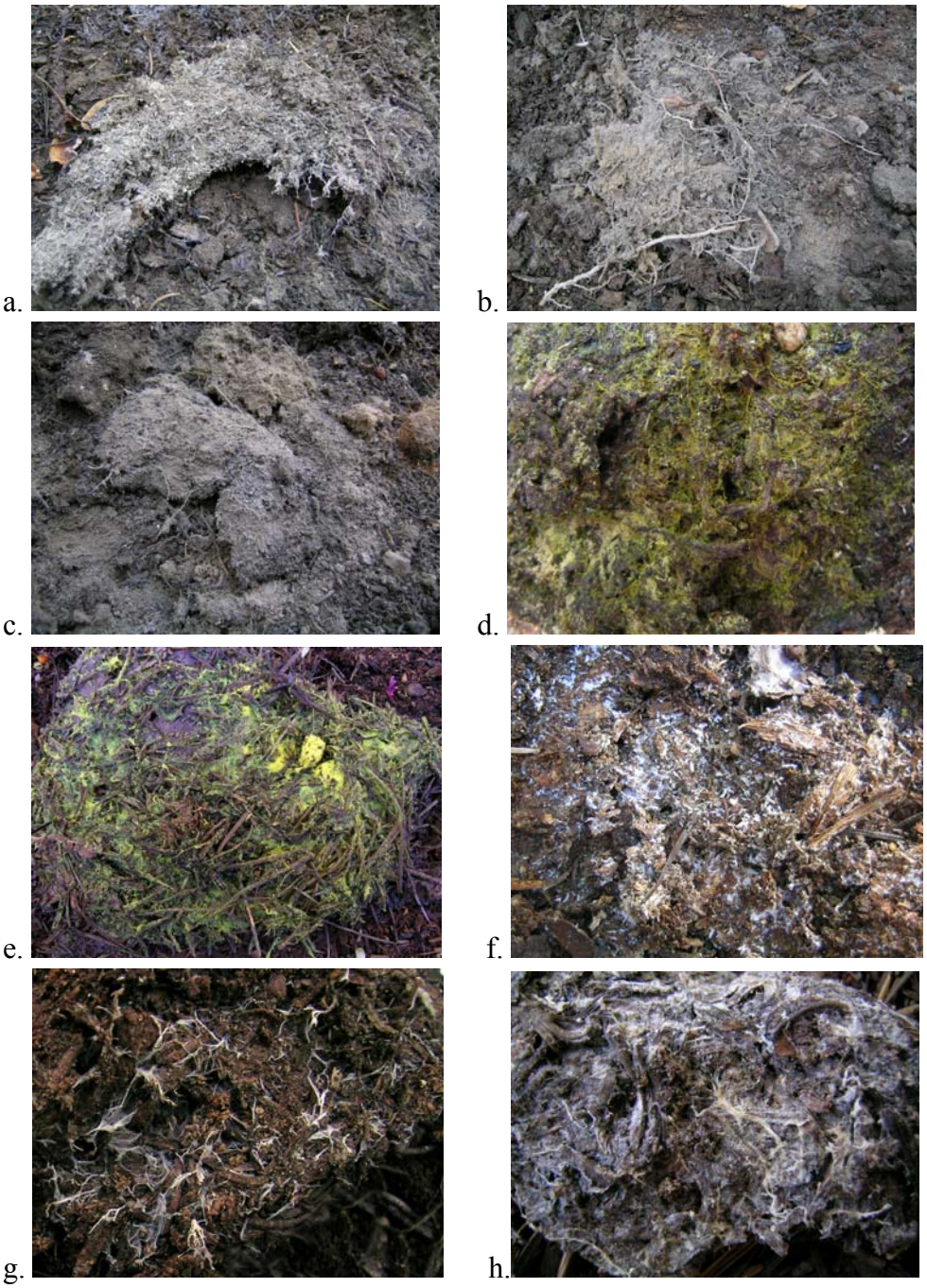
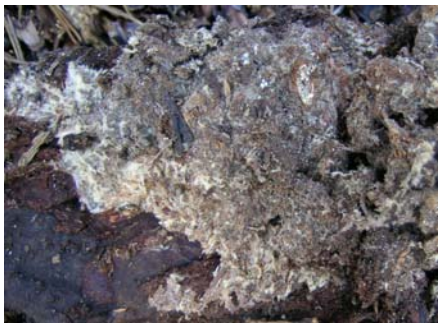


Figure 3.1 (Continued). Fungal mat morphologies: (i) *Xenasmatella vaga.* (j) *Gastropila utriformis*. (k) *Trechispora alnicola.* (l) *Ramaria stricta.* (m) *Piloderma fallax.* (n) *Piloderma* sp.

i. 

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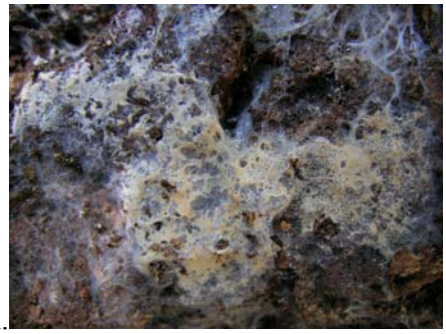
n. 

Table 3.1. List of mat-forming fungi from Crater Lake National Park. *A.c.* = *Abies concolor* zone, *T.m.* = *Tsuga mertensiana* zone. Trophism: M = mycorrhizal, S = saprobic.

Habitat	Number collected	Species	Trophism	GenBank Match	% match
A.c.	2	*Alpova sp.* (*trappei*)	M	AF074920	99-100
A.c.	1	*Cortinarius sp.* #1 (*caperatus*)	M	AY669575	100
T.m.	1	*Cortinarius sp.* #2 *(pinguis*)	M	DQ517414	95
T.m.	2	*Cortinarius sp.* #3 *(boulderensis*)	M	DQ499466	95-97
A.c.	1	*Cortinarius sp.* #4 (*brunneus/gentilis*)	M	AF430287 AF325589	95-96
T.m.	1	*Cortinarius sp.* #5 (*montanus*)	M	AF478578	96
A.c./T.m.	2	*Cortinarius sp.* #6 (*rigidus*)	M	AY669658	95-97
T.m.	2	*Cortinarius sp.* #7 (*subfoetidus*)	M	AF325609	96-97
T.m.	6	*Flavoscypha sp.* (*cantharella*)	S	AF072082	95-98
A.c./T.m.	5	*Gastropila sp.* (*subcretacea*)	S	DQ112598	96-99
A.c./T.m.	8	*Gautieria sp.* (*monticola*)	M	AF377105	95-99
A.c./T.m.	7	*Hydnellum sp.* (*peckii*)	M	AY569030	95-98
A.c./T.m.	2	*Lactarius sp.* (*scrobiculatus*)	M	EF530942	96-98
A.c./T.m.	7	*Lepiota sp.* (*magnispora*)	S	AF391023	96-100
A.c.	2	*Piloderma sp.* #1 (*byssinum*)	M	DQ365683	95-96
A.c./T.m.	45	*Piloderma sp.* #2 (*fallax*)	M	DQ371931	95-97
A.c./T.m.	5	*Piloderma sp.* #3	M	EF218793	95-98
A.c.	2	*Ramaria sp.* #1 (*flavobrunnescens var. aromatica*)	M	AY102864	95-97
A.c.	2	*Ramaria sp.* #2 (*rasilispora*)	M	DQ365602	95-96
A.c./T.m.	8	*Ramaria sp.* #3 (*stricta*)	S	DQ367910	95-99
A.c./T.m.	8	*Ramaria sp.* #4 (*stricta OSC65995*)	S	DQ365600	95-97

Table 3.1 (Continued). List of mat-forming fungi from Crater Lake National Park. AC = *Abies concolor* zone, TM = *Tsuga mertensiana* zone. Trophism: M = mycorrhizal, S = saprobic.

Habitat	No. collected	Species	Trophism	GenBank Match	% match
A.c./T.m.	10	*Ramaria sp.* #5 (*stricta/pinicola*)	S	DQ367910 DQ365649	95-97
A.c.	2	*Rhizopogon sp.* #1 (*rubescens/roseolus*)	M	AJ810045 AJ810043	98-99
A.c./T.m.	8	*Rhizopogon sp.* #2 (*salebrosus/subbadius*)	M	DQ822822 AF377152	95-98
A.c.	1	*Rhizopogon sp.* #3 (*subpurpurascens/milleri*)	M	AF377132 AF377135	95-96
T.m.	2	*Rhizopogon truncatus*	M	By RFLP	
A.c.	4	*Rhizopogon sp.* #4 (*vulgaris*)	M	AF062931	95-97
T.m.	1	*Sistotrema sp.* (*albopallescens*)	M	AM259210	98
A.c.	1	*Suillus sp.* (*tomentosus*)	M	STU74614	98
T.m.	2	*Trechispora sp.* #1 (*alnicola*)	M	DQ411529	95-96
A.c./T.m.	2	*Trechispora sp.* #2 (*subsphaerospora*)	M	AF347080	95-97
A.c.	1	*Tricholoma sp.* #1 (*equestre*)	M	AF458454	95
A.c.	1	*Tricholoma sp.* #2 (*intermedium*)	M	AF377202	96
A.c.	3	*Tricholoma sp.* #3 (*magnivelare*)	M	AF527370	96-99
A.c.	5	*Tricholoma sp.* #4 (*saponaceum*)	M	DQ370440	95-97
A.c.	1	*Tricholoma sp.* #5 (*sejunctum*)	M	AB036899	96
A.c.	2	*Tyromyces sp.* (*chioneus*)	S	AJ006676	95-97
T.m.	4	*Xenasmatella sp.* (*vaga*)	S	AY805620	95-98

Table 3.2. Collection numbers of mat-forming fungi.

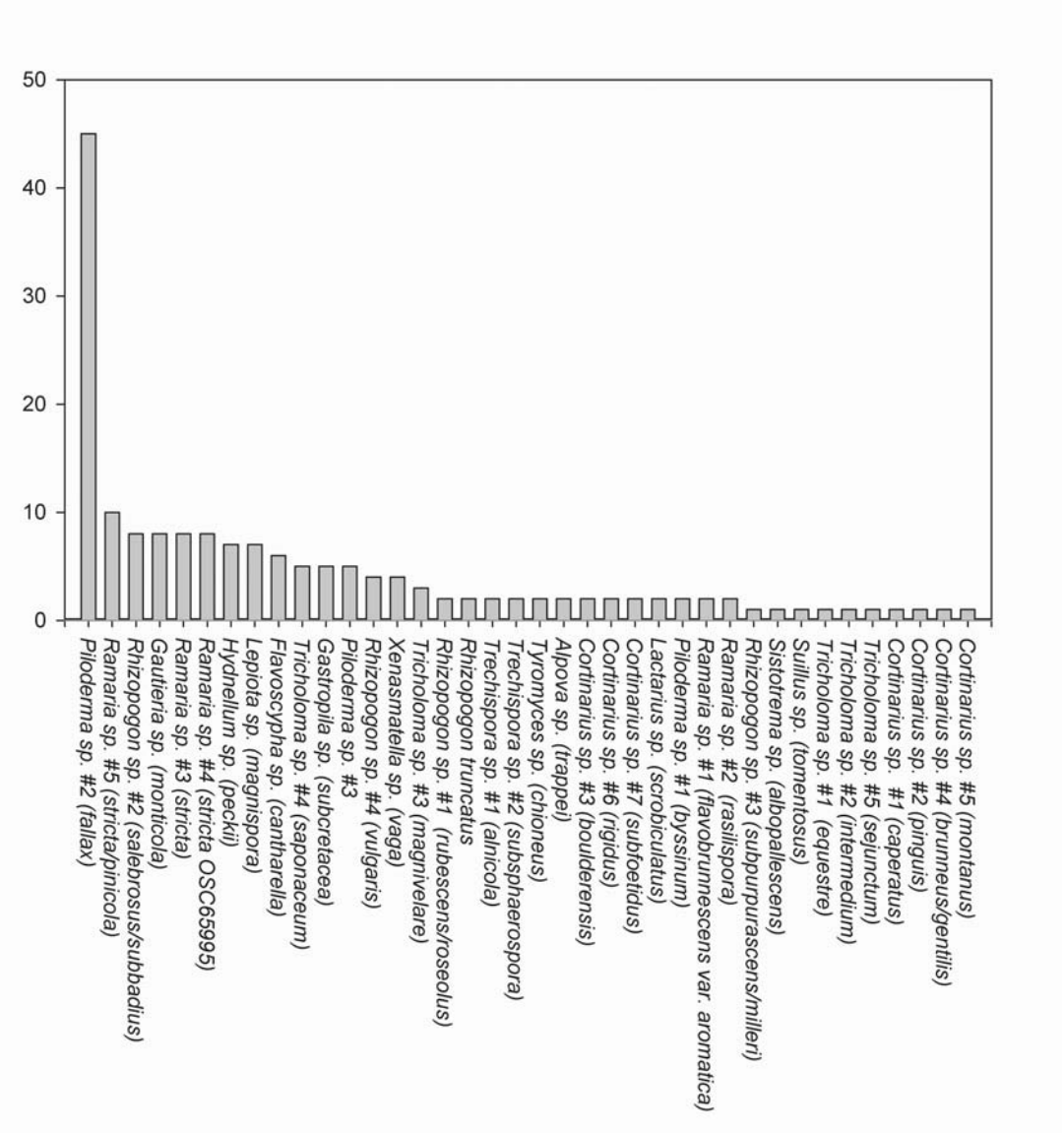


Table 3.3. Linear regression estimates of number of mats detected in each habitat type. A negative sign indicates a reverse correlation; values significant at $\alpha < 0.05$ are bolded. CWD = coarse woody debris, FWD = fine woody debris.

Abies concolor zone			*Tsuga mertensiana* zone		
Habitat variable	p-value	adj. R^2	Habitat variable	p-value	adj. R^2
Bulk density	-0.1706	0.042	Bulk density	-0.1391	0.0773
Total C	0.1196	0.0659	Total C	-0.5274	0
$\delta^{13}C$	-0.6788	0	^{13}C	-0.5632	0
Total N	-0.8899	0	Total N	-0.2747	0.0162
$\delta^{15}N$	0.2183	0.0257	^{15}N	0.112	0.0971
C:N ratio	**0.0308**	**0.1582**	C:N ratio	**0.0037**	**0.3815**
CWD	0.665	0.106	CWD	0.5932	0
FWD	**0.0129**	**0.2157**	FWD	**0.0424**	**0.1852**
Litter	**0.0223**	**0.1798**	Litter	**0.002**	**0.5775**
Soil pH	**-0.0173**	**0.1967**	Soil pH	-0.2082	0.0406
C:N x FWD	**0.0017**	**0.3383**	Stand age	**0.0236**	**0.2363**
C:N x Litter	**0.004**	**0.2889**	C:N x FWD	**0.0022**	**0.4189**
C:N x pH	0.1642	0.0445	C:N x Litter	**0.0001**	**0.646**
FWD x Litter	**0.0494**	**0.1263**	C:N x Stand age	**0.0021**	**0.4236**
FWD x pH	0.0608	0.1121	FWD x Litter	**0.001**	**0.4706**
Litter x pH	**0.0318**	**0.1561**	FWD x Stand age	**0.0014**	**0.4498**
			Litter x Age	**0.001**	**0.6117**

Table 3.4. *P* values of logistic regression of habitat associations on those taxa collected at least 3 times within a habitat type. A negative sign indicates a reverse correlation; values significant at $\alpha < 0.05$ are bolded. CWD = coarse woody debris, FWD = fine woody debris.

Abies concolor zone	n	Bulk density (g cm^{-3})	Total C (%)	$\delta^{13}C$ (‰)	Total N (%)	$\delta^{15}N$ (‰)
Gautieria monticola	6	-0.311	0.0731	-0.41	-0.677	0.155
Lepiota magnispora	4	0.776	0.348	0.201	0.13	0.986
Piloderma fallax	15	**-0.039**	0.637	-0.154	-0.214	-0.777
Piloderma sp.	4	0.63	0.178	-0.161	-0.353	0.314
Ramaria stricta	6	-0.375	0.812	-0.615	-0.126	0.281
Ramaria stricta/OSC65995	3	0.703	0.622	0.372	0.46	0.115
Ramaria stricta/pinicola	6	0.138	0.453	0.539	0.603	0.651
Rhizopogon salebrosus	5	-0.105	0.897	0.793	-0.448	0.625
Rhizopogon vulgaris	4	-0.159	0.099	-0.274	0.419	-0.999
Tricholoma saponaceum	5	0.966	0.532	0.936	0.592	0.256

Tsuga mertensiana zone	n	Bulk density (g cm^{-3})	Total C (%)	$\delta^{13}C$ (‰)	Total N (%)	$\delta^{15}N$ (‰)
Flavoscypha cantharella	6	0.505	0.599	0.542	0.591	-0.973
Gastropila subcretacea	3	0.484	-0.332	-0.875	-0.271	-0.822
Hydnellum peckii	4	0.877	-0.927	-0.142	-0.580	0.972
Piloderma fallax	15	-0.124	-0.149	-0.693	-0.115	0.136
Ramaria stricta/OSC65995	5	-0.586	0.561	0.142	0.540	-0.651
Rhizopogon truncatus	3	0.156	-0.517	0.275	-0.386	-0.585

Table 3.4 (Continued). *P* values of logistic regression of habitat associations on those taxa collected at least 3 times within a habitat type. A negative sign indicates a reverse correlation; values significant at $\alpha < 0.05$ are bolded. CWD = coarse woody debris, FWD = fine woody debris.

Abies concolor zone	C:N ratio	CWD (Mg ha^{-1})	FWD (Mg ha^{-1})	Litter mass (Mg ha^{-1})	Soil pH
Gautieria monticola	0.056	0.118	0.104	0.128	-0.124
Lepiota magnispora	-0.705	0.227	0.067	0.094	-0.462
Piloderma fallax	**0.017**	0.063	**0.031**	**0.048**	-0.19
Piloderma sp.	0.088	0.117	0.645	0.305	0.71
Ramaria stricta	**0.04**	0.138	0.641	0.682	-0.233
Ramaria stricta/OSC65995	0.8541	0.381	0.732	0.678	0.188
Ramaria stricta/pinicola	0.299	0.559	-0.905	0.497	-0.233
Rhizopogon salebrosus	0.299	-0.722	0.799	0.997	-0.194
Rhizopogon vulgaris	0.495	0.145	0.223	0.148	-0.122
Tricholoma saponaceum	-0.403	0.383	0.439	0.208	-0.243

Tsuga mertensiana zone	C:N ratio	CWD (Mg ha^{-1})	FWD (Mg ha^{-1})	Litter mass (Mg ha^{-1})	Soil pH
Flavoscypha cantharella	0.642	-0.486	0.52	0.096	-0.317
Gastropila subcretacea	0.252	-0.277	-0.985	0.419	0.756
Hydnellum peckii	0.336	0.575	0.568	0.578	0.620
Piloderma fallax	0.052	0.052	0.099	**0.042**	-0.226
Ramaria stricta/OSC65995	0.693	0.872	0.660	0.233	-0.317
Rhizopogon truncatus	0.701	0.637	0.806	-0.559	0.385

CONCLUSIONS

In the preceding chapters we learned that the fruiting of many fungi at Crater Lake National Park are sensitive to soil chemistry. There is a set of fungi that prefer to fruit where levels of total C and total N are relatively high and C:N ratios are relatively low, and another set that fruits where levels of total C and total N are relatively low and C:N ratios are relatively high. Prescribed burn treatments and anthropogenic perturbations can affect these soil properties and subsequently influence fungal fruiting patterns, however only stand-replacing wildfires had the potential to halt mycorrhizal fungal fruiting and mat formation entirely. Even after the most intense prescribed burn or years of human use, mycorrhizal fungi continued to fruit and form fungal mats.

In the first chapter, we collected and identified a total of 566 collections representing 133 species of mycorrhizal fungi over three years. The treatment units 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 unit G, all units with a C:N ratio below 26 produced a distinct guild of indicator fungal sporocarps, indicated by the presence of *Amanita pantherina, Boletus chrysenteron, Boletus zelleri*, and *Sarcosphaera coronaria*. Most units with a C:N ratio above 26 produced a distinctly different guild of indicator fungal sporocarps, indicated by the presence of *Cortinarius rigidus, Hydnotrya variiformis, Hysterangium separabile, Lactarius rufus, Russula integra, R. albonigra*, and *Suillus tomentosus*. Units spatially transitional between higher and lower C:N soils produced fungal fruiting patterns intermediate between the high- and low-C:N guilds.

Our first hypothesis was that prescribed burning at different seasons influences belowground habitat differently. The fall burns in particular had significant effects on soil C:N ratios, pH, and surface fuel levels. Our second hypothesis was that prescribed

burning at different seasons influences mycorrhizal fungus fruiting patterns differently. With the exception of *Morchella angusticeps*, which responded more to the treatment itself than the effects on soil properties, the timing and consequent intensity of prescribed burn treatments influenced fungal communities only indirectly, as a function of their effects on soil attributes. However, in this study the different treatments appeared to serve more as adjustments to the pre-existing soil attributes rather than as primary drivers. The fall burn treatments effectively promoted the fruiting of low C:N guild indicator species, but in no unit or treatment was mycorrhizal fungal fruiting suppressed entirely.

In chapter 2, we learned that mycorrhizal fungus fruiting patterns are not correlated with site use or disturbance history at Crater Lake National Park. The primary factors in fungal fruiting patterns were geographic location and soil C and N levels, and these were significant in only a small number of taxa. Disturbed and control sites did not differ significantly in number of fungal collections or their diversity.

617 collections of mycorrhizal fungal sporocarps representing 166 species were identified from the anthropogenic disturbance sites and their controls. Of these, ordination analysis identified 12 taxa correlated with levels of soil C and N, seven of which were also significantly correlated by logistic regression with levels of soil C or N.

Our first hypothesis was that intense recreational site use influences above- and belowground habitat by affecting soil properties and surface fuels. We found significant differences between site histories in soil bulk density only when comparing the most disturbed subsites with controls. Bulk density was not significantly different between the less-disturbed interstitial areas of the recreation sites and control sites. There were significant differences in the levels of ^{15}N enrichment and surface fuels between recreation and control sites.

Our second hypothesis was intense recreational site use influences mycorrhizal fungus fruiting patterns. The fruiting patterns of most fungi were not significantly influenced by site use or history. Several taxa demonstrated significant associations with soil C and N, C:N ratios, and ^{15}N enrichment. Although both site history and fungal fruiting patterns were both correlated with ^{15}N enrichment, this did not translate to correlations between site history and fungal fruiting patterns.

Intensive recreational use does not adversely impact the fruiting productivity or diversity of mycorrhizal fungi. Intensively disturbed microsites within recreational areas produce very few sporocarps, but the productivity and diversity of less impacted microsites is sufficient that at larger scales recreational sites are not significantly different from undisturbed control sites. The factors most influential of fungal fruiting patterns were geographic location, and soil C and N content and the corresponding C:N ratio. These factors may be related by soil type, or by barriers to dispersal for some taxa. No patterns were observed in the fruiting of most fungal species, but a few were identified as possible indicators.

In chapter 3 we successfully amplified and sequenced the DNA from 169 collections, representing 38 taxonomic units. Members of the 5 most common genera (*Gautieria*, *Lepiota, Piloderma, Ramaria,* and *Rhizopogon*) comprised 67% of all collections. Ten taxa were collected only once. Three distinct genotypes of the mycorrhizal genus *Piloderma* and 3 distinct genotypes of the saprobic *Ramaria stricta* species complex were detected.

In the ponderosa pine/white fir community 50 collections of mat-forming fungi were made in the 8 control units ($\bar{x}$= 8.4), 54 in the 8 spring burn units ($\bar{x}$= 6.8), and 5 in the 8 fall burn units ($\bar{x}$= 0.6). The habitat attributes that correlated most strongly with the

most abundant soil fungi were C:N ratio, coarse woody debris (CWD), fine woody debris (FWD), and litter mass. These attributes were largely intercorrelated and showed a significant response to burn treatment.

In the mountain hemlock/noble fir community, 57 collections of mat-forming fungi were made in the 8 control units ($\bar{x}$= 7.1), 10 collections in the 4 in-use recreational units ($\bar{x}$= 2.5), 8 collections in the 3 abandoned recreational units ($\bar{x}$= 2.7), and 3 collections in the 3 wildfire units (= 1). All 3 collections from wildfire units came from the Goodbye Fire site (31 yrs post-fire). No soil fungi were observed at the other two wildfire sites (Flying Dutchman Fire sampled 11 yrs post-fire and the Border Fire sampled 2 yrs post-fire). This suggests that it may take 15+ yrs for mats to re-establish following wildfires.

Linear regressions indicated that the abundance of mat-forming taxa in the mountain hemlock ecotype also was positively correlated with stand age, soil C:N ratios and the mass of FWD and needle litter (Table 3.3). Significant interactions were detected between all of the significant variables; the interaction between stand age and litter mass had the highest adjusted R2 value.

The advent of DNA typing has vastly increased our ability to identify previously cryptic mat-forming species. At Crater Lake National Park, we identified 36 mycorrhizal, mat-forming genotypes and 21 saprobic, mat-forming genotypes. Among the mycorrhizal genotypes, two genera had not been previously identified as mat-forming. The abundance of mats in an ecosystem is highly correlated with the mass of needle litter, and areas without needle litter coverage generally lacked mats. Mats are sensitive to severe disturbance, and may take over 15 years to re-colonize after a wildfire event. The fungus forming a particular mat is extremely difficult to identify confidently in the field, and a universal definition of exactly what does and does not constitute a fungal mat remains elusive.

We have provided only a snapshot of the responses of mycorrhizal fungal fruiting patterns to environmental conditions and disturbance modes at Crater Lake National Park. These research sites provide an opportunity to study relationships between above- and belowground interactions, fungal succession, and long-term community shifts. Having identified the species members of fungal guilds in each of these units and their relationship to soil attributes and disturbances, the logical follow-up is to continue monitoring these sites over the ensuing years. The fact that they are 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.

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