

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

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Abstract: Intensive recreational use of subalpine forests 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 Crater Lake National Park, Oregon. Control and disturbed sites differed significantly 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 methods were not designed to quantify the effects of anthropogenic disturbance on fungal fruiting patterns at the microsite scale, but fungal productivity was markedly reduced 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 fungal species did not differ significantly in fruiting patterns or in preferences between sites or treatments at the macrosite scale, but several indicator taxa were identified.

Résumé : L'usage récréatif intensif des forêts subalpines peut engendrer des zones localisées de perturbation concentrée où la végétation est modifiée, les sols sont compactés et la quantité de combustibles de surface est réduite. Plusieurs aspects de ce type de perturbations ont été étudiés mais aucun travail de recherche ne s'est attardé aux effets de l'usage récréatif sur la production de carpophores par les champignons mycorrhiziens. Nous avons mesuré les effets de l'usage récréatif des terres ou des sites sur les propriétés du sol et le niveau de combustibles et relié ces attributs à la production de carpophores par les champignons mycorrhiziens au parc national de Crater Lake. Il y avait des différences significatives entre les sites témoins et perturbés dans le cas de la densité apparente du sol, de l'enrichissement en ^{15}N et du niveau de combustibles mais pas dans le cas du nombre total de champignons collectés et de la diversité des espèces à l'échelle des macrosites. Nos méthodes d'échantillonnage n'étaient pas conçues pour quantifier les effets des perturbations anthropogéniques sur les patrons de fructification des champignons à l'échelle des microsites mais la productivité des champignons était réduite de façon marquée dans les microsites les plus perturbés. Dans les parcelles perturbées, la pénurie de champignons collectés dans les microsites fortement perturbés était compensée par l'abondance et la diversité des champignons mycorrhiziens collectés dans les microsites protégés. Les patrons de fructification ou les préférences de plusieurs espèces de champignons n'étaient pas significativement différents selon le site ou le traitement à l'échelle des macrosites mais plusieurs taxons indicateurs ont été identifiés.

[Traduit par la Rédaction]

Introduction

Crater Lake National Park (CLNP) has experienced concentrated recreational activities for more than a century. 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. For example, the Cold Springs area had been used as a military road from Fort Klamath to Medford since about 1865. It was developed into a

formal campground for park visitors in the early 20th century and used until the 1950s. Evidence of this history is apparent in the plant community (Wilson 2007) and soil properties to this day.

Several researchers have examined the effects of recreational use on forested sites. Brown et al. (1977) found that soil compaction decreased water infiltration and slowed the growth of adjacent trees, with implications for carbon (C) and nitrogen (N) cycling. Kuss (1986) found that coarse-

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grained, highly porous, sandy loam soils like those at CLNP are more susceptible to compaction than silty clays. Parish (1971) reported a loss of macropore space in compacted soils, resulting in an increase in soil moisture at the expense of soil air. Shierlaw and Alston (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 through 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.

Mycorrhizal fungi are critical to the 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). These fungi exist as perennial networks of mycelia in the soil and on the tips of roots, where they interface with plant cortical cells and nutrient exchange occurs. It has been estimated that 1 g of healthy forest soil can contain more than 200 m of fungal mycelia (Leake et al. 2004), representing a nutrient foraging capacity far beyond that of fine roots alone. The sporocarps (mushrooms and truffles) are the ephemeral reproductive structures, or fruiting bodies, of these perennial organisms.

Mycorrhizal fungi are susceptible to damage caused by soil compaction, potentially impacting the ability of plant communities to access nutrients and water (Amaranthus et al. 1996). Mycorrhizal fungus sporocarps are a significant food source for wildlife (North et al. 1997; Cazares et al. 1999; Ashkannejhad and Horton 2006) and, hence, are an important response variable to evaluate the effects of disturbance on food webs and wildlife carrying capacity.

No studies to date have addressed the impacts of recreational use or soil compaction on mycorrhizal fungus fruiting patterns. We characterized soil properties and levels of fuels and surveyed mycorrhizal sporocarp fruiting patterns over a 3 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 the belowground habitat, as measured by soil total C and N, mineral soil bulk density, C/N ratios, and $\delta^{13}\text{C}$ and ^{15}N isotopic signatures, and influences aboveground habitat, as measured by 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 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 national park maintenance site (Anderson Bluffs). The control sites were similar in structure and age to the disturbed sites and, except for one case, were located near their disturbed counterpart.

We collected and identified both epigeous and hypogeous mycorrhizal fungal sporocarps from 1000 m² plots at each site in the spring and fall over 3 years. Because we were interested in the differences between the disturbed and undisturbed sites, the plots were not randomly placed. Rather, the disturbed site plots were centered on the areas most visibly impacted by use, and the control site plots were placed as far from stand edges and other mitigating features as topography permitted. Site data, including mineral soil bulk density, total mineral soil N, total mineral soil C, C/N ratio, $\delta^{15}\text{N}$ enrichment, $\delta^{13}\text{C}$ depletion, mineral soil pH, CWD mass, FWD mass, litter mass, stand age, and elevation, were measured. We analyzed these data in several ways to determine the 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 study sites were in CLNP in southern Oregon, and all but one were in the southern half of CLNP. An overstory inventory was performed in 2003 by a total census of three 20 m \times 100 m macroplots per site (Wilson 2007). 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.) (Table 1). The elevations ranged from 1750 to 1950 m and usually were snow-free from July to November. Throughout this discussion the sites will be abbreviated by their initials followed by the letter "C" for control and "D" for disturbed, e.g., the Anderson Bluffs control site is designated ABC and the disturbed site, 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 (1.6 km) south of Rim Drive. This area was regularly used 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 (ABD) 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 (ABC) 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. The understory is minimal and

Table 1. Stand composition of research sites shown as trees per hectare (Wilson 2007).

	10–30 cm dbh		>30 cm dbh	
	Control	Disturbed	Control	Disturbed
Anderson Bluffs				
Shasta red fir	13 (7)	0	8 (4)	18 (2)
Mountain hemlock	153 (29)	73 (41)	190 (10)	125 (28)
Lodgepole pine	0	7 (7)	0	10 (5)
Subalpine fir	0	0	0	2 (2)
Western white pine	0	7 (7)	2 (2)	7 (7)
Annie Springs				
Shasta red fir	20 (20)	13 (7)	65 (28)	3 (2)
Mountain hemlock	127 (18)	420 (239)	265 (28)	130 (21)
Lodgepole pine	0	53 (35)	3 (2)	57 (15)
Subalpine fir	40 (23)	27 (18)	2 (2)	0
Western white pine	0	0	0	0
Cold Springs				
Shasta red fir	0	20 (12)	0	3 (2)
Mountain hemlock	120 (61)	120 (80)	7 (7)	2 (2)
Lodgepole pine	347 (24)	380 (50)	253 (27)	245 (8)
Subalpine fir	87 (7)	0	25 (12)	3 (2)
Western white pine	0	0	0	0
Mason's Camp				
Shasta red fir	213 (29)	80 (50)	155 (31)	118 (9.3)
Mountain hemlock	80 (42)	20 (12)	67 (22)	18.3 (11)
Lodgepole pine	0	53 (33)	7 (7)	5 (3)
Subalpine fir	0	0	0	0
Western white pine	27 (7)	13 (0.7)	10 (3)	8 (2)
Mazama Village early				
Shasta red fir	7 (7)	0	12 (12)	2 (2)
Mountain hemlock	460 (155)	67 (18)	105 (98)	10 (8)
Lodgepole pine	173 (88)	307 (66)	130 (7)	130 (18)
Subalpine fir	73 (41)	127 (75)	12 (3.3)	32 (19)
Western white pine	0	0	0	0
Mazama Village late				
Shasta red fir	20 (20)	47 (27)	65 (28)	30 (15)
Mountain hemlock	127 (18)	100 (40)	265 (28)	127 (6.0)
Lodgepole pine	0	140 (64)	3 (2)	35 (10)
Subalpine fir	40 (23)	0	2 (2)	7 (2)
Western white pine	0	0	0	0

Note: Values are means and standard errors are in parentheses.

composed mainly 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, ceramic electrical insulators, old cans, and other archeological debris are scattered under the litter layer. Because of the lack of undisturbed forest in this area, the control site (ASC) is 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 (ASD).

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. Today, the road network and camping pads are only detectable by careful observation but were extensive when in use. The stand is composed mostly of larger noble fir and mountain hemlock, with scattered lodgepole pine. Former camping pads and roadways are more sparsely treed and primarily 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 disturbed site (MCD) is west of Pinnacles Road just north of Lost Creek Campground. It was established in 1955 as a group camp but is now closed to the public except for events by reservation; it has been used by the Freemasons for annual ceremonies since about 1980. MCD 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 site (MCC) lies 1 km south of MCD near the water collection facility for the Lost Creek Campground. MCC contains mature noble fir and mountain hemlock and is at the base of a steep talus. 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 the campground has been the largest camping area in CLNP ever since. The campground is located to the east of Highway 62 just north of the CLNP entrance station on the west rim of Annie Canyon. There are two ecotypes at Mazama Village: one with a late seral forest structure (MVLC and MVLD) and one with 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. The disturbed plots encompass several campsites in current use, and most of the soil surface lacks any litter layer and is 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 ~100 years of age. The disturbed plots are in campground loops B and E, and the control plots are located to the south of the campground in a stand composed almost purely of young lodgepole pine. Soils are Castlecrest gravelly ashy loam.

Fungal sporocarp sampling

We collected mycorrhizal fungal fruiting data in the spring and fall by time-constraint sampling (Claridge et al. 2000). In time-constraint sampling, plots of a standard area are sampled (methodically searching for aboveground and belowground fungal sporocarps) 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 m² (20 m × 50 m) survey plots sampled for 100 person-minutes captured the asymptotes of detected fruiting body diversity (M. Trappe, unpublished data, 2001). While the survey plot size of 1000 m² was designed for effective fungal sporocarp sampling, it was too large to quantify the microsite variations within these highly heterogeneous sites.

At each sampling iteration, one survey plot was established in each site. Each site was sampled once in the spring

and once in the fall for 3 years. Although this strategy provides only a snapshot of fungal standing crop, the unpredictable and often brief window of appropriate weather combined with the number of plots needing survey limited the number of plot visits feasible in a season. As not every fungal species present will fruit every year (Luoma et al. 1991), we attempted to overcome these limitations by sampling over the course of 3 years. Additionally, we moved survey plots within sites from season to season to capture as representative a sampling as possible and to eliminate possible effects of previous sampling efforts.

The term “fungal collection” is defined as all of the fungal sporocarps of a given species collected on a plot in any one survey iteration, e.g., 20 sporocarps of *Suillus punctatipes* gathered at MCC in the fall of 2003 comprise one “fungal collection”. Because of the large magnitude of variability in fecundity and sporocarp mass among fungal taxa, we did not collect biomass data.

Fungal species identification

Fungal collections were identified by standard morphological methods augmented by restriction fragment length polymorphism (RFLP) analysis and by sequencing immature, degraded, or cryptic specimens. The internal transcribed spacer (ITS) region of the nrDNA was used for all molecular analyses; the RFLP patterns of cryptic collections were compared with those of known specimens identified by standard morphological methods (Gardes and Bruns 1996; Horton and Bruns 2001) 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 that have not yet been described and named (J. Ammirati, G. Bonito, and M. Castellano, personal communications, 2006). Thus, many taxa given European names in this study are probably closely related to but are 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.

Soil cores and bulk density

Soil cores were taken to a 10 cm depth from the surface of the A horizon with a 5.6 cm diameter hammer-type corer (AMS Corp., American Falls, Idaho, USA). Eighteen cores were taken from each study site. In the disturbed study sites, nine “high impact” cores were taken from the most heavily disturbed areas (e.g., the bare, heavily trafficked areas around tables and fire rings in campsites), and nine “low impact” cores were taken from interstitial areas, e.g., under the driplines of smaller trees, and 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 the disturbed sites were collected in the relatively undisturbed low impact, low bulk density interstitial areas. Accordingly, for soil analyses, ordinations,

and logistic regressions, we used only the nine low impact cores from the disturbed sites. For each control site, nine 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 were further ground to flour consistency, and 50–70 mg subsamples were weighed carefully into 8 mm × 5 mm tin cups and assayed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures relative to international standards (Hoefs 2008) by the University of California – Davis Stable Isotope Facility, using a Europa ANCA-GSL elemental analyzer interfaced to a PDZ 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

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 four to six samples per plot for site-specific bulk density determination in the laboratory. Then mass 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 three to six 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 or absence and habitat attributes. A 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 (version 9.1, SAS Institute Inc. 2003).

Nonmetric 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 (production of sporocarps) of mycorrhizal fungi. NMS provides closeness-of-fit relationships between all explanatory and dependent variables for complex multivariate data sets, 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.

Taxa collected from more than nine plots or from fewer than four plots were removed from the data set for both ordination and logistic regression analyses, as they were uninformative about correlations (too few or too many to draw inferences, e.g., a taxon found on every plot does not provide information about its habitat preferences between plots). PC-ORD identified *Cortinarius magnivelatus* as a multivariate outlier, so it too was removed from the data set, resulting in a final data set of 38 taxa. Sporocarp collection data were converted to presence–absence data or ordination analysis and logistic regression.

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 can also 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 using a Sørensen distance measure and flexible beta group linkage ($\beta = -0.25$ (McCune and Grace 2002)) was performed on the habitat attribute data set, 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 (ISA) 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 the dendrogram). In the habitat attribute data set, dendrogram pruning by ISA indicated that two groups provided the lowest cumulative p value.

The collection data set was binary (presence or absence), so Beals smoothing was applied. Beals smoothing is a transformation designed for data sets that contain a large number of zeros, and it replaces binary data with quantitative “favorability” values (Beals 1984; McCune 1994). 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

In all, 617 collections of mycorrhizal fungal sporocarps were identified, representing 166 species. Because many of the taxa were collected either too frequently (more than 9 of 12 plots) or infrequently (less than 4 of 12 plots) to be informative, our final data set consisted of 38 taxa (Table 2). Of these, ordination analysis identified 12 taxa correlated with levels of soil C and N, seven of which were also significantly correlated with concentrations of soil C or N by logistic regression.

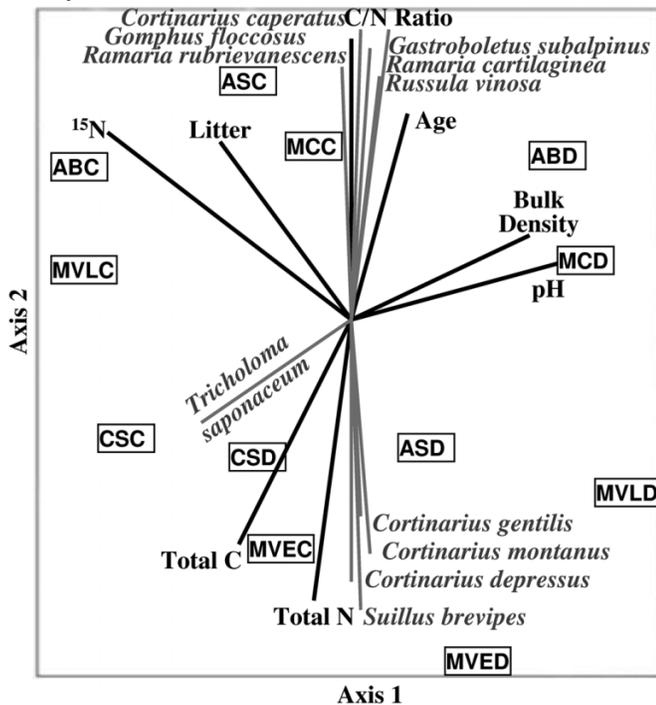
We identified three sets of largely intracorrelated habitat attributes: (i) total C and total N; (ii) C/N ratio, fuels, and

Table 2. Fungal sporocarp collections used in data analysis.

Species	ABC	ABD	ASC	ASD	CSC	CSD	MCC	MCD	MVEC	MVED	MVLC	MVLD	No. of collections	No. of sites
<i>Boletopsis subsquamosa</i>					1	1	1	1	1				5	5
<i>Boletus zelleri</i>					2	2			1			1	6	4
<i>Cortinarius albobrunnoides</i>	2	3		2			1	1	1		1	1	12	8
<i>Cortinarius brunneus</i>		1	2		1							1	5	4
<i>Cortinarius caperatus</i>	2	1	1			1	1	1	1			2	10	8
<i>Cortinarius cinnamomeoluteus</i>	1	1			1				1				4	4
<i>Cortinarius clandestinus</i>		1							2	1	1		5	4
<i>Cortinarius claricolor</i>		2			1		1		2		1	1	8	6
<i>Cortinarius depressus</i>	1			1	1				1	2		2	8	6
<i>Cortinarius gentilis</i>	1			1	1					1		1	5	5
<i>Cortinarius montanus</i>					1		1		1	1		1	5	5
<i>Cortinarius variosimilis</i>		2		1	3		1				3	1	11	6
<i>Gastroboletus subalpinus</i>	1	1	1				1	2				1	7	6
<i>Gomphus floccosus</i>	2		1				3					2	8	4
<i>Hygrophorus brunneus</i>	2			1		1			1			2	7	5
<i>Hygrophorus goetzii</i>		2		1	1	1	1					2	9	7
<i>Hygrophorus hypothejus</i>	1					1			1	1			4	4
<i>Hysterangium separabile</i>		1		1						3	2	1	8	5
<i>Hydnotrya variiformis</i> var. <i>pallida</i>	1	1		1			2	2	2	3	2		14	8
<i>Laccaria laccata</i> var. <i>pallidifolia</i>	1		1		1	1			1			1	7	7
<i>Leucogaster rubescens</i>		1		1								1	4	4
<i>Ramaria cartilaginea</i>		2	1				3	3	1			2	14	7
<i>Ramaria cyaneigranosa</i> var. <i>cyaneigranosa</i>					1	1			1			1	4	4
<i>Ramaria flavobrunnescens</i> var. <i>aromatica</i>		1	1	2	1		1		1			2	10	8
<i>Ramaria longispora</i>	2		1		1				1				5	4
<i>Ramaria rubrievanescens</i>	2	1						1				1	5	4
<i>Rhizopogon evadens</i>	1						2	2	1			3	9	5
<i>Rhizopogon vulgaris</i>				1			1		1			3	7	5
<i>Russula aeruginea</i>			2	1	1				1				5	4
<i>Russula cascadenis</i>	1					1	1	1					4	4
<i>Russula integra</i>	1	1	1				2		1	1	1	1	9	8
<i>Russula tyrrhenica</i>	1	1	1	1							1	1	6	6
<i>Russula vinosa</i>	1	1	1				1				2	2	8	6
<i>Suillus brevipes</i>				3	1	2		1	1	1		1	10	7
<i>Tricholoma caligatum</i>					1	1	1					1	4	4
<i>Tricholoma focale</i>		1			2	2	3	2		1		1	12	7
<i>Tricholoma portentosum</i>	1				1	1		1				1	6	6
<i>Tricholoma saponaceum</i>	1		2	1	1	1			2	1	2		11	8

Note: Site key: ABC, Anderson Bluffs control; ABD, Anderson Bluffs disturbed; ASC, Annie Springs control; ASD, Annie Springs disturbed; CSC, Cold Springs control; CSD, Cold Springs disturbed; MCC, Mason's Camp control; MCD, Mason's Camp disturbed; MVEC, Mazama Village early seral control; MVED, Mazama Village early seral disturbed; MVLC, Mazama Village late seral control; MVLD, Mazama Village late seral disturbed

Fig. 1. Ordination by habitat attributes with species assemblage overlay.



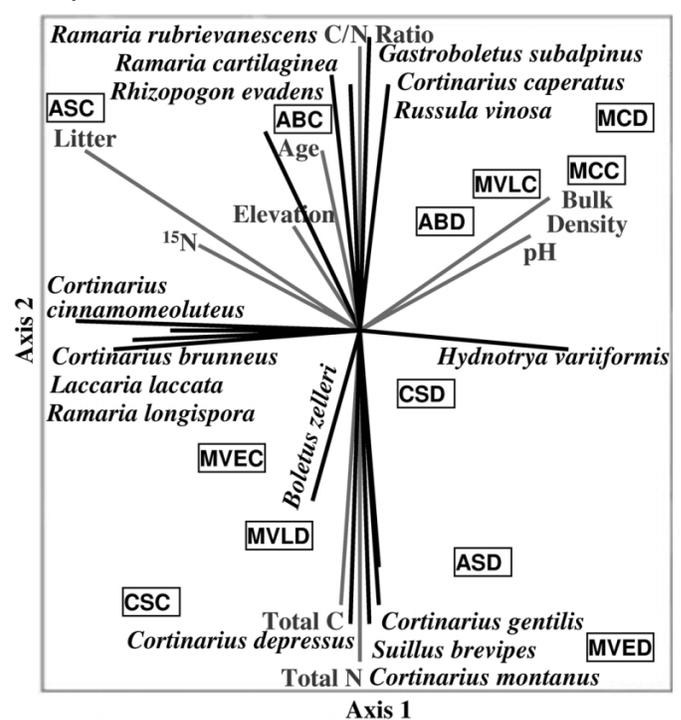
¹⁵N enrichment; and (iii) bulk density, stand age, and soil pH (Table 3). Soil C and N concentrations were correlated inversely with C/N ratios, pH, and age. Soil C/N ratios were correlated with bulk density but not with pH or age.

The ordination by habitat attribute is displayed in Fig. 1. In this ordination, the sites are plotted based on their similarity in soil properties and fuels; species vectors are overlaid but had no effect on the placement of the sites in the scattergram. The control sites tended toward the left side of the scattergram, i.e., most strongly influenced by low soil pH and bulk density and by higher ¹⁵N enrichment and litter levels. The same factors were also the most influential in positioning the majority of the disturbed sites toward the right side of the scattergram.

The fungal fruiting patterns tended to follow the vertical axis, favoring either high C/N ratios or high total C and N concentrations, and were largely independent of site history (control vs. disturbed). At a macrosite scale, mycorrhizal fungus fruiting patterns were not significantly influenced by soil bulk density or pH.

The taxa appearing to favor sites with higher C/N ratios and lower levels of total C and N were *Cortinarius caperatus* (Pers.:Fr.) Fr., *Gastroboletus subalpinus* Trappe and Thiers, *Gomphus floccosus* (Schwein.) Singer, *Ramaria cartilaginea* Marr and D.E. Stuntz, *Ramaria rubrievanescens* Marr and D.E. Stuntz, and *Russula vinosa* Lindblad. The taxa appearing to favor sites with lower C/N ratios and higher levels of total C and N were *Cortinarius depressus* Fr., *Cortinarius gentilis* (Fr.) Fr., *Cortinarius montanus* Kauffman, and *Suillus brevipes* (Peck) Kuntze. No taxa were significantly correlated with bulk density, ¹³C, pH, elevation, CWD, FWD, or litter, and only one was correlated with C/N ratio. No taxa were significantly correlated with site history. *Tricholoma saponaceum* (Viv.) Ricken was col-

Fig. 2. Ordination by species assemblage with habitat attributes overlay.



lected at every site with an above-mean level of N (including ABC; Table 4), but also at two sites with a below-mean N (ASC and MVLC).

The ordination by species assemblage is displayed in Fig. 2. In this ordination, the sites are plotted based on their similarity in fungal communities; habitat attribute vectors are overlaid but had no effect on the placement of the sites in the scattergram. There is little consistency in the horizontal orientation of the sites between this ordination and the habitat attribute ordination (Fig. 1), but the vertical distributions are very similar — in both ordinations the same six sites are above the scattergram center (group 1 sites) and the other six are below it (group 2 sites). Tables 2 and 3 summarize this dichotomy, with Table 4 presenting values for all units, by the two ordination groups. Table 5 presents a summary of the two ordination groups.

In Fig. 2, most species vectors significant at $R^2 > 0.400$ indicate either up or down. The horizontal species vectors do not strongly associate with either group of sites and few significantly correlate with specific habitat attributes. The primary dichotomy in species assemblages is between high C/N ratio sites (group 1) and high total C and N sites (group 2).

Table 6 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 $\alpha < 0.10$. While the seven taxa in the upper third of the table are concentrated in 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 seven taxa in the middle of the table appeared as horizontal vec-

Table 3. Pearson's correlations between habitat attributes.

	Bulk density	Total C (%)	$\delta^{13}\text{C}$ depletion	Total N (%)	$\delta^{15}\text{N}$ enrichment	C/N ratio	Mineral soil pH	Elevation	CWD mass	FWD mass	Litter mass	Stand age	Collections*
Total C (%)	-0.709 0.004												
$\delta^{13}\text{C}$ depletion	0.227 0.592	-0.384 0.173											
Total N (%)	-0.685 0.008	0.977 0.001	-0.338 0.255										
$\delta^{15}\text{N}$ enrichment	-0.325 0.350	-0.179 0.604	0.072 0.879	-0.300 0.345									
C/N ratio	0.537 0.067	-0.647 0.021	0.009 0.991	-0.770 0.003	0.426 0.153								
Mineral soil pH	0.927 0.001	-0.724 0.004	0.223 0.564	-0.675 0.012	-0.448 0.162	0.397 0.204							
Elevation	0.218 0.787	0.010 0.885	0.629 0.036	0.017 0.999	-0.387 0.249	-0.146 0.517	0.307 0.437						
CWD mass	-0.105 0.709	-0.336 0.278	0.374 0.228	-0.472 0.119	0.635 0.022	0.543 0.069	-0.089 0.760	0.069 0.863					
FWD mass	-0.054 0.756	-0.169 0.564	0.134 0.758	-0.353 0.247	0.655 0.012	0.556 0.061	-0.071 0.749	0.155 0.794	0.831 0.001				
Litter mass	-0.119 0.648	-0.110 0.715	-0.112 0.670	-0.282 0.368	0.807 0.001	0.495 0.103	-0.217 0.457	-0.097 0.595	0.596 0.041	0.835 0.001			
Stand age	0.562 0.072	-0.703 0.006	0.644 0.030	-0.706 0.007	0.131 0.593	0.401 0.198	0.565 0.066	0.509 0.115	0.320 0.313	0.296 0.391	0.264 0.427		
Collections*	-0.332 0.420	-0.046 0.968	-0.211 0.690	-0.065 0.857	0.492 0.121	-0.091 0.809	-0.243 0.557	-0.147 0.794	0.047 0.835	0.252 0.277	0.530 0.035	0.145 0.429	
Species*	-0.420 0.262	0.012 0.868	-0.271 0.552	-0.026 0.962	0.548 0.073	-0.100 0.786	-0.312 0.410	-0.230 0.991	0.146 0.578	0.334 0.150	0.590 0.013	0.066 0.590	0.974 0.001

Note: Pearson's correlation estimates are placed above p values. A negative sign preceding the estimate indicates an inverse correlation. P values significant at $\alpha < 0.10$ are in bold.

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

Table 4. Mean habitat attribute values for all units, by ordination groups.

Site*	Latitude (°N)	Longitude (°W)	Soil type [†]	Low bulk density [‡]	High bulk density [‡]	Total C (%) [‡]	δ ¹³ C depletion (‰) [‡]	Total N (%) [‡]
Ordination group 1								
ABC	42.900	122.052	UP	0.65 (0.06)	0.65 (0.06)	3.53 (0.66)	-24.20 (0.33)	0.116 (0.034)
ABD	42.899	122.049	UP	0.77 (0.08)	0.98 (0.09)	1.53 (0.39)	-24.18 (0.38)	0.047 (0.011)
ASC	43.065	122.257	CC	0.69 (0.08)	0.69 (0.08)	2.45 (0.45)	-25.48 (0.33)	0.060 (0.010)
MCC	42.886	122.048	UP	0.87 (0.12)	0.87 (0.12)	2.03 (0.50)	-25.02 (0.30)	0.049 (0.011)
MCD	42.884	122.047	UP	0.98 (0.09)	1.06 (0.12)	1.92 (0.59)	-25.08 (0.36)	0.050 (0.008)
MVLC	42.869	122.161	CC	0.61 (0.11)	0.61 (0.11)	3.36 (1.16)	-25.13 (0.45)	0.104 (0.033)
Group mean				0.762	0.811	2.47	-24.85	0.071
Ordination group 2								
ASD	42.871	122.171	CC	0.66 (0.11)	0.92 (0.16)	3.97 (1.06)	-24.89 (0.58)	0.140 (0.035)
CSC	42.841	122.148	CC	0.62 (0.08)	0.62 (0.08)	4.94 (1.23)	-25.28 (0.41)	0.166 (0.059)
CSD	42.841	122.145	CC	0.68 (0.08)	0.78 (0.10)	3.32 (0.57)	-25.27 (0.34)	0.117 (0.025)
MVEC	42.862	122.162	CC	0.61 (0.12)	0.61 (0.12)	4.97 (1.32)	-25.63 (0.50)	0.174 (0.064)
MVED	42.865	122.160	CC	0.63 (0.07)	0.84 (0.09)	4.73 (1.45)	-25.26 (0.22)	0.211 (0.066)
MVLD	42.868	122.164	CC	0.81 (0.09)	0.94 (0.10)	2.70 (0.98)	-25.07 (0.23)	0.104 (0.034)
Group mean				0.667	0.784	4.11	-25.23	0.152
Grand mean				0.714	0.798	3.29	-25.03	0.11

*Explanation of sites is provided in the Note of Table 1.

[†]UP, Union Peak – Sun Notch series; CC, Castlecrest gravelly ashy loam.

[‡]Values are means with standard errors in parentheses. Mean values significantly different at $p < 0.10$ are in bold.

tors in ordinations but had few significant correlations with specific habitat attributes.

The R^2 values in Table 6 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 ordination factors influence it in the same ordination direction, even though none of those factors is individually significant.

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 are the same, with the addition of *Rhizopogon evadens* A.H. Smith. Taxa appearing to favor sites with low C/N ratios and high levels of total C and N area also consistent, with the addition of *Boletus zelleri* Murrill.

The species ordination (Fig. 2) further identified some taxa on horizontal vectors. *Hydnotrya variiformis* Gilkey occurred on eight sites but not on ASC or CSC. It otherwise demonstrated no strong habitat preferences. *Laccaria lac-cata* (Scop.) Cooke and *Ramaria longispora* Marr and D.E. Stuntz 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 $p = 0.123$ with CWD, respectively). They were collected mostly from sites on the left side of the ordination and from a few sites on the right. Three of the four sites on which *Cortinarius brunneus* (Pers.) Fr. and *Cortinarius cinnamomeoluteus* P.D. Orton occurred are to the left of center, but these species showed no significant habitat preferences.

Table 7 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 ¹⁵N 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 (at $\alpha < 0.10$) in total C, total N, ¹⁵N, C/N ratio, CWD, and age. Differences between ordination groups were suggestive but nonsignificant for FWD and litter mass. When grouped by soil types, only total C and N were significantly different.

Figure 3 illustrates the spatial relationships of the units. The ordination group 1 sites were located east of Annie Canyon, except the disjunct ASC site in the northwest corner of CLNP. Of these, the AB and MC sites had a Union Peak – Sun Notch – Castlecrest soil series, but ASC and MVLC were Castlecrest gravelly ashy loam (Table 4). The ordination group 2 sites were located along Highway 62, west of Annie Canyon, and the soils at all sites were Castlecrest gravelly ashy loam.

A number of taxa were also correlated with total C and (or) total N. However, several other habitat attributes were negatively correlated with total C and N, such as C/N ratios, soil pH, and stand age (Table 4). Although no fungal taxa correlated with soil pH, one did correlate with C/N ratio, and three correlated with stand age (Table 6). 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 were also 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*, *C. caperatus*, *C. depressus*, *C. gentilis*, and *Ramaria cartilaginea* all correlated at $p < 0.15$.

$\delta^{15}\text{N}$ enrichments (‰) [‡]	Soil C/N ratio [‡]	Soil pH [‡]	Elevation (m)	Fuel (Mg·ha ⁻¹) [‡]			Stand age (years)	No. of collections	No. of species
				CWD	FWD	Litter			
3.50 (0.90)	31.2 (4.3)	4.7 (0.1)	1950	68.1 (48.2)	8.9 (2.5)	107.0 (12.5)	300	46	37
2.24 (0.78)	33.0 (5.5)	5.1 (0.2)	1950	43.5 (15.6)	3.8 (0.1)	42.1 (13.8)	300	44	32
4.02 (1.12)	41.4 (5.3)	4.8 (0.2)	1750	47.0 (15.0)	7.0 (0.5)	109.8 (14.0)	225	43	36
3.11 (1.02)	42.1 (5.9)	5.1 (0.4)	1890	25.4 (13.0)	8.3 (0.8)	111.0 (7.6)	300	55	40
1.56 (0.31)	38.1 (4.8)	5.4 (0.2)	1890	10.3 (4.0)	4.8 (1.4)	64.0 (12.0)	300	38	28
4.23 (0.84)	32.1 (5.2)	4.7 (0.3)	1850	20.5 (4.9)	10.0 (1.3)	157.0 (19.0)	300	91	64
3.11	36.4	5.0	1880	37.1	7.1	98.5	288	53	40
1.80 (0.65)	28.5 (2.2)	5.0 (0.3)	1850	18.9 (7.7)	5.8 (0.4)	62.4 (6.6)	300	49	39
3.15 (0.54)	30.5 (3.7)	4.7 (0.1)	1770	22.8 (3.8)	8.2 (1.2)	88.8 (5.5)	135	49	41
2.94 (1.14)	28.7 (3.5)	4.9 (0.3)	1770	14.4 (1.4)	4.9 (0.7)	72.6 (13.5)	135	52	42
1.61 (0.62)	28.9 (4.7)	4.8 (0.3)	1890	18.1 (8.1)	5.1 (2.2)	74.0 (12.0)	100	54	43
1.51 (0.59)	25.2 (2.1)	4.7 (0.2)	1830	2.0 (2.0)	0.3 (0.1)	38.0 (4.8)	100	36	25
1.63 (0.39)	25.8 (4.7)	5.1 (0.4)	1830	3.9 (2.6)	0.9 (0.4)	55.0 (9.7)	300	60	45
2.11	27.9	4.9	1823	13.4	4.2	65.1	178	50	39
2.61	32.15	4.9	1852	25.2	5.7	81.8	233	52	39

ABC was the only site in ordination group 1 to produce *C. depressus* or *C. gentilis*. It was also 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 *C. 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. The differences between ordination groups were suggestive but nonsignificant 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 ($p = 0.066$) than 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 was not significantly different from the occasional-use sites. The patterns of ^{15}N enrichment may be a function of site history, but the significance of differences between ordination groups (independent of site use) suggests that ^{15}N enrichment may be a function of wider geographic patterns possibly related to soil types.

Table 6 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 four 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.

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 positively correlated with ^{15}N enrichment also positively correlated with stand age and negatively correlated with total C and N (Table 5). *Suillus brevipes*, the only taxon that negatively correlated with ^{15}N , positively correlated with total C and N and negatively correlated with C/N ratio.

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 significantly influence 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.

The relatively large size of our survey plots, designed to capture an adequate sampling of fungal sporocarps and reduce the influence of individual host tree species associations, was not sensitive to the fine-scale spatial patterns of intense disturbance. The alternative — many smaller survey plots — may have better quantified microsite disturbance effects but would have diminished the comprehensiveness of the sporocarp inventory (Claridge et al. 2000).

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 correlated with ^{15}N enrichment. The nature of these correlations renders it difficult to decon-

Fig. 3. Map of sites by ordination group, illustrating geographic and soil chemistry relationships.

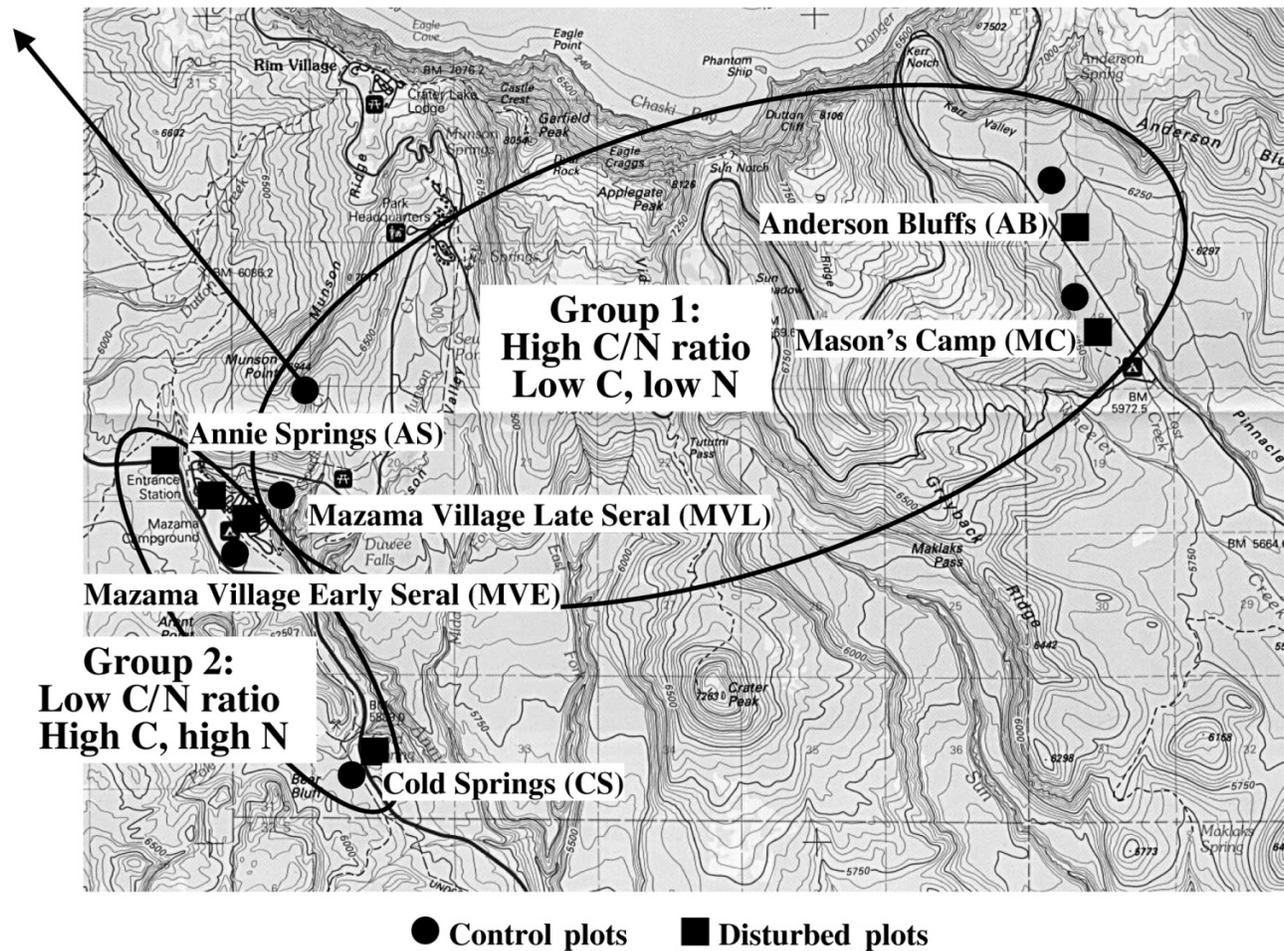


Table 5. Summary of ordination groups.

	Ordination group 1	Ordination group 2
Sites*	ABC, ABD, ASC, MCC, MCD, MVLC	ASD, CSC, CSD, MVEC, MVED, MVLD
Habitat attributes differing between ordination groups at $\alpha < 0.05$	C/N ratio > 31 , $\bar{x} = 36.4$ Total C $< 3.6\%$, $\bar{x} = 2.7\%$ Total N $< 0.12\%$, $\bar{x} = 0.071\%$ CWD > 10.3 , $\bar{x} = 37.1 \text{ Mg}\cdot\text{ha}^{-1}$ Age > 225 years, $\bar{x} = 287.5$ years	C/N ratio < 31 , $\bar{x} = 27.9$ Total C $> 2.7\%$, $\bar{x} = 4.1\%$ Total N $> 0.10\%$, $\bar{x} = 0.152\%$ CWD < 22.8 , $\bar{x} = 13.4 \text{ Mg}\cdot\text{ha}^{-1}$ Age < 300 years, $\bar{x} = 178.3$ years
Indicator species	<i>Cortinarius caperatus</i> , <i>Gastroboletus subalpinus</i> , <i>Gomphus floccosus</i> , <i>Ramaria cartilaginea</i> , <i>Ramaria rubrievanescens</i> , <i>Rhizopogon evadens</i> , <i>Russula vinosa</i>	<i>Boletus zelleri</i> , <i>Cortinarius depressus</i> , <i>Cortinarius gentilis</i> , <i>Cortinarius montanus</i> , <i>Suillus brevipes</i>

*Site key is provided in Table 1.

volve any one dominant soil chemistry factor. These suites of interrelationships and the associated fungal indicator taxa appear to follow broad geographic patterns (Fig. 3).

Griffiths et al. (2009) found correlations between elevation and a number of edaphic characteristics, including soil organic matter, labile C, mineralizable N, microbial activities, extractable ammonium, denitrification potentials, bulk density, pH, and soil temperature. In our study, elevation correlated only with ^{13}C , possibly a consequence of microclimate on soil respiration; however, our elevational gradient was only 240 m.

Williamson and Neilsen (2000) and Gomez et al. (2002) reported that the degree of mineral soil compaction from a disturbance was strongly related to the original bulk density, forest type, and soil parent material. They found that compaction resulting from ground-based harvest methods was below levels found to restrict root growth; however, the reduction in macropores and the effect of compaction on aeration and drainage had the potential to affect nutrient acquisition and, subsequently, tree growth. Mariani et al. (2006) found no effects of soil compaction on microbial communities in samples taken 3–7 years postdisturbance,

Table 6. Number of sites within each group that a taxon is present, R^2 strength of ordination vector correlation, and logistic regression correlations significant at $\alpha < 0.10$ between individual taxa and habitat attributes.

Fungal taxon*	No. of sites		R^2		Logistic regression correlations (p value)				
	Group 1	Group 2	Habitat attributes	Species	C	N	^{15}N	C/N ratio	Age
Coca	6	2	0.529	0.895	-0.097	-0.090			
Gasu	6	0	0.761	0.919	-0.074		0.099		0.077
Gofl	3	1	0.537	0.391					
Raca	5	2	0.603	0.566	-0.075	-0.080			
Raru	4	0	0.483	0.735					
Rhev	4	1		0.628					
Ruvi	5	1	0.684	0.484	-0.078	-0.080	0.093		0.077
Cobr	2	2		0.602					
Coci	2	2		0.607					
Hyva	1	3		0.448					
Lala	3	4		0.760					
Ralo	2	2		0.759					
Trsa	3	5	0.497			0.0622			
Boze	0	4		0.405					-0.084
Code	1	5	0.590	0.778	0.084				
Coge	1	5	0.459	0.731	0.093	0.088			
Como	1	4	0.572	0.698					
Subr	1	6	0.790	0.721	0.099	0.081	-0.054	-0.093	

*Fungal taxa key: Boze, *Boletus zelleri*; Cobr, *Cortinarius brunneus*; Coca, *Cortinarius caperatus*; Coci, *Cortinarius cinnamomeoluteus*; Code, *Cortinarius depressus*; Coge, *Cortinarius gentilis*; Como, *Cortinarius montanus*; Gasu, *Gastroboletus subalpinus*; Gofl, *Gomphus floccosus*; Hyva, *Hydnotrya variiformis*; Lala, *Laccaria laccata*; Raca, *Ramaria cartilaginea*; Rala, *Ramaria longispora*; Raru, *Ramaria rubrievanescens*; Rhev, *Rhizopogon evadens*; Ruvi, *Russula vinosa*; Subr, *Suillus brevipes*; Trsa, *Tricholoma saponaceum*.

Table 7. Two-tailed Tukey–Kramer HSD differences between site groupings.

	Compacted vs. control	Ordination group 1 vs. group 2	Union Peak vs. Castlecrest soil type
High bulk density	0.060	0.533	0.487
Low bulk density	0.265	0.177	0.353
C	0.588	0.009	0.019
^{13}C	0.544	0.147	0.294
N	0.980	0.003	0.005
^{15}N	0.014	0.083	0.987
C/N ratio	0.196	0.003	0.151
pH	0.105	0.394	0.155
Elevation	0.481	0.789	0.327
CWD	0.050	0.047	0.463
FWD	0.016	0.106	0.901
Litter	0.001	0.136	0.979
Age	0.988	0.024	0.116
Collections*	0.241	0.734	0.693
Species*	0.141	0.935	0.425

Note: Values in bold are significant at $\alpha < 0.10$.

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

suggesting that microbial communities might be more resilient to compaction perturbation than plant communities.

Many studies have investigated the effects of N deposition and fertilization on mycorrhizal species diversity and fruit-body production (reviewed in Wallenda and Kottke 1998; Erland and Taylor 2002; Treseder 2004). In most cases, increased N resulted in reduced mycorrhizal colonization; however, there is considerable variability in responses

between genera. Lilleskov et al. (2001) identified groups of nitrophilic and nitrophobic taxa, including the genera *Cortinarius*, *Hebeloma*, *Lactarius*, *Russula*, and *Tricholoma* in the nitrophobic group. We did not observe these patterns; in fact, two species of *Cortinarius* were in ordination group 2, with affinities toward higher N sites. Lilleskov et al. (2001) noted that the genus *Hebeloma*, in particular, has been characterized in other studies as a nitrophile (Sagara et al. 1993;

Tibbett et al. 1998; Carter and Tibbett 2003). Kraepelin and Michaelis (1997) reported that fruiting of *Hebeloma* increased after a lime treatment, perhaps as a result of increased pH or an attendant increase in N mineralization. These mixed findings suggest that ectomycorrhizal fruiting responses to soil conditions are neither simple nor unifactorial.

Pennanen et al. (1999), Nilsson et al. (2005), and Högberg et al. (2006) used phospholipid fatty acid analysis to detect shifts in mycorrhizal abundance across nutrient gradients. These studies agreed that with increasing soil N, the relative abundance of ectomycorrhizae decreased and other soil microbiota increased. This phenomenon is a widely accepted result of the host plants' decreased need for mycorrhizal assistance in nutrient acquisition in N-rich sites, which results in a reduction in belowground allocation of photosynthates (Mosse and Phillips 1971) and thus a potential decrease in soil C/N ratios. At our sites, soil N was one of the more significant factors correlating with fungal fruiting patterns (Table 7) but it also positively correlated with soil C (Table 3).

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

The 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 $\pm 2\%$ of atmosphere, and mineralization reactions are not isotopically discriminatory (Nadelhoffer and Fry 1994). 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 (Compton et al. 2007). 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) reported ^{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, ^{15}N enrichment was not correlated with total N or stand age but rather with fuels, particularly litter mass (Table 3); these two habitat attributes were the only ones directly correlated with the number of mycorrhizal species collected, although litter mass was not correlated with the likelihood of any species' occurrence.

As in this study, Toljander et al. (2006) reported a pattern of ectomycorrhizal root tip community structure reflecting a gradient from higher C/N ratios (36.6) and lower NH_4 (0.45 $\text{mmol}\cdot\text{kg}^{-1}$) to lower C/N ratios (16.9) and higher NH_4

(5.37 $\text{mmol}\cdot\text{kg}^{-1}$). Toljander et al. (2006) too encountered difficulties isolating the effects of individual parameters as a result of autocorrelation, particularly among NH_4 , pH, and soil base saturation.

Levels of soil N clearly affect the ectomycorrhizal community. In systems with high levels of N deposition or that are subjected to fertilization treatments, ectomycorrhizal diversity and abundance can be significantly decreased. In natural systems where N gradients are less extreme, the effects are much more subtle, with changes observed in the abundance or presence of some species (either nitrophilic or nitrophobic), while much of the community appears unaffected. It is possible, given a familiarity of the local mycoflora, that the presence or absence of certain species might serve as an indicator of soil N, much as lichens can serve as indicators of air quality (Denison and Carpenter 1973; Conti and Cecchetti 2001).

Conclusions

Our first hypothesis was that intense recreational site use influences aboveground 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 the 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 designed to prioritize thorough sampling of fungal fruiting data and disturbance at larger scales (1000 m^2) rather than to quantify the microsite effects of anthropogenic disturbances.

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 both site history and fungal fruiting patterns 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 did not adversely impact the quantities of sporocarps collected or the 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 concentrations, 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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