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Interaction of Fungal Sporocarp Production with Small Mammal Abundance and Diet in Douglas-fir Stands of the Southern Cascade Range

Abstract

Small mammal population densities are highly variable across forest stands and landscapes. The species composition and abundance of ectomycorrhizal fungi (EMF) may influence the ability of forests to provide suitable habitat for small mammals. Identification and interpretation of changes in the abundance of these organisms, or in their inter-relationships due to experimental harvest, require that we first identify the patterns and potential causes of natural variability in the pre-harvest communities. Pre-treatment data were gathered from the Watson Falls block of a green-tree retention experiment to establish baseline conditions. The six experimental treatments that comprise this block lie in two spatially distinct areas that differ in environment and forest composition. The initial variability in EMF, small mammals, and their relationships was documented. Three primary questions are addressed in this paper: (1) Are the abundance and species composition of EMF sporocarps similar between the two areas of the Watson Falls block? (2) How does sporocarp consumption vary among small mammal species and by area? (3) For common truffle genera, is sporocarp biomass correlated with the spore frequency of those genera in small mammal diets? The Watson Falls block was found to have spatial and temporal variation in EMF production, small mammal mycophagy, and small mammal abundance. However, truffles were consistently the primary food item in the diet of all three small mammal species in this study. Small mammals are potentially important agents of truffle dispersal into disturbed areas where EMF are locally extirpated. This study furthers knowledge of the role of small mammal mycophagy in the functioning of forest ecosystems.

Introduction

Ectomycorrhizal fungi (EMF) form symbiotic relationships with the roots of trees and other vegetation. Trees supply carbon from photosynthesis to the fungi, in turn, EMF absorb minerals and nutrients from the soil and transfer them to tree roots (Smith and Read 1997). Mycorrhizae are essential for survival and growth of most coniferous forest trees and other shrubs and herbaceous vegetation (Fogel and Trappe 1978).

Ectomycorrhizal fungal species vary in their abundance and phenology of fruiting (Fogel 1981; Hunt and Trappe 1987; Luoma 1988, 1991; Luoma et al. 1991, 1997; Amaranthus et al. 1994; North et al. 1997; States and Gaud 1997) and in the nutritional value of their fruit bodies (Fogel and Trappe 1978). Various abiotic and biotic factors influence the fruiting of EMF (Villeneuve et al. 1991). Sporocarps are non-uniform in distribu-

tion, varying from a few, scattered fruitbodies to concentrated clusters of numerous fruitbodies (North et al. 1997, States and Gaud 1997, Waters et al. 1997). In planned experiments, documentation of existing fruiting patterns is critical to the interpretation of changes that may result from manipulation of treatment units.

Small mammals are integral components of many forest ecosystems including the Douglas-fir (*Pseudotsuga menziesii*) forests that dominate much of the western Cascade landscape. Numerous species of forest-dwelling, small mammals rely on the fruiting bodies of EMF as a primary source of food (Fogel and Trappe 1978, Maser et al. 1986, Maser and Maser 1988, Hall 1991, Waters and Zabel 1995). A food-web linkage of particular interest is between the endangered northern spotted owl (*Strix occidentalis caurina*) and the northern flying squirrel (*Glaucomys sabrinus*). The northern spotted owl feeds primarily on flying squirrels over most of their range (Forsman et al. 1984, Thomas et al. 1990, Carey 1991). Northern flying

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squirrels, in turn, require truffles, below-ground fruiting bodies of EMF, as their primary food source (Maser et al. 1985, Carey 1995). Other mycophagous (fungus eating) small mammals, such as chipmunks (*Tamias* spp.) are prey for raptors (e.g., goshawks) and mammalian carnivores (e.g., marten and fisher) (Fogel and Trappe 1978, McIntire 1984, Hayes et al. 1986, Carey 1991).

The presence and abundance of EMF species may change during forest development (Trappe 1977, Mehus 1986, Termorshuizen 1991). Truffle fungi are primarily dispersed by small mammals that eat the sporocarps and subsequently disperse spore-packed fecal pellets (Fogel and Trappe 1978, Maser and Maser 1988). The level and pattern of structural retention in harvest units may influence small mammal species directly, thereby indirectly influencing spore dispersal of EMF. Green-tree retention may also influence the composition, abundance, and fruiting of EMF and thus indirectly influence the abundance of small mammals *via* effects on their food sources.

Studies of animal mycophagy are mainly based on stomach content or fecal pellet analysis (Fogel and Trappe 1978, Maser et al. 1978, Maser and Maser 1988, Carey 1995, Waters and Zabel 1995). These analyses can provide an accurate record of an animal's previous meal. Fecal sample analysis provides a non-lethal method for long-term and integrated studies of diet habits. Forest-dwelling small mammal species that depend upon fruiting bodies of EMF contain a diverse array of truffle genera in their fecal material (Maser et al. 1978). Small mammal population densities are highly variable across stands and landscapes (Carey et al. 1992, Rosenberg and Anthony 1992, Witt 1992) and the species composition and abundance of EMF fruiting bodies may influence the ability of forests to provide suitable habitat for small mammals. Identification and interpretation of changes in the abundance of these organisms, or of their inter-relationships due to forest harvest, require that we first identify the patterns and potential causes of natural variability in the pre-harvest communities.

The high diversity of EMF in forests of the Pacific Northwest suggests that habitats and environmental conditions are also diverse. While some EMF may thrive in intensively managed forests, most are likely adversely affected by such management (Amaranthus and Luoma 1997). A

diverse mosaic of host species, habitats, and structures promote EMF diversity at the scale of landscapes. Variation in communities of EMF will reflect variation in forest type, successional stage, and the distinctive assemblages of plants and microhabitats within each of these. Silvicultural practices can be used to create habitat conditions that maintain or increase EMF diversity. For example, leaving large trees following regeneration harvests ("green-tree" retention) maintains an energy source for certain EMF species and provides for future recruitment of coarse woody debris, an important habitat component for some EMF (Amaranthus et al. 1994).

Until recently, limited consideration has been given to the conservation of EMF, despite their known ecological importance. The Northwest Forest Plan (USDA and USDI 1994a) now directs forest managers to incorporate rare species, including fungi, into future forest management activities. The standards and guidelines of the Plan require that federal ecologists and botanists create and maintain databases of known sites of rare fungi, and that they develop species or area management plans for these taxa (USDA and USDI 1994b). The report lists 527 species of fungi that are thought to be closely associated with late successional forests; approximately 80% of these are thought to be EMF. Studies of the spatial and temporal distributions of EMF and of their consumption by small mammals in unmanaged forests are a necessary first step if we are to understand the consequence of future management practices for these critical elements of forest ecosystems.

In this paper we describe some of these relationships in forests that will be harvested as part of the Demonstration of Ecosystem Management Options (DEMO) study (Aubry et al. 1999). The strong contrasts in levels and patterns of canopy cover produced by the six retention-harvest treatments are likely to influence habitat features and environmental conditions that in turn will affect populations of EMF and small mammals. However, initial differences in the distribution and abundance of EMF and small mammals may have equally important effects on post-treatment responses.

The six experimental units that we consider in the current study (the Watson Falls block) lie in two spatially distinct areas that differ in envi-

ronment and forest composition. Thus, it is necessary to quantify the initial variability in EMF, small mammals, and their interactions to facilitate the separation of treatment-effects from any effects due to pre-harvest differences. To this end, we pose three fundamental questions about the spatial and temporal variation of EMF sporocarps and their consumption by small mammals prior to forest harvest: (1) Are the abundance and species composition of EMF sporocarps similar between the two areas of the Watson Falls block? (2) How does sporocarp consumption vary among small mammal species and by location? (3) For the common truffle genera, is sporocarp biomass correlated with the frequency of spores found in the fecal material of small mammals?

Similar studies will be conducted following harvest thus yielding information on how levels and patterns of green-tree retention alter the abundance and distribution of EMF and of the small mammals that consume these species. Both sets of studies are critical as forest managers seek to incorporate basic ecological knowledge into forest management policies and practices.

Methods

Experimental Design

The Demonstration of Ecosystem Management Options (DEMO) study consists of six green-tree retention treatments replicated at eight geographic locations (blocks) in western Oregon and Washington (Aubry et al. 1999). The treatments consist of four levels of live tree retention (15, 40, 75, and 100% of existing live-tree basal area), with two patterns of retention (aggregated and

dispersed) applied to the 15 and 40% retention treatments. The aggregated pattern consists of residual trees retained in 1-ha circular patches; the dispersed pattern consists of residual trees uniformly dispersed throughout the unit (see Aubry et al. [1999] for details).

Study Area

Three treatment units were established in each of the two primary study areas that comprise the Watson Falls block of the DEMO experiment (see Figure 3 of Aubry et al. [1999]). The two areas, named for local geographic features, Toketee Airstrip and Mowich Park, lie approximately 12 km apart with an elevational difference of about 350 m (Table 1). Both areas are comprised of 110- to 130-yr-old forests dominated by Douglas-fir that originated following wildfire. Other tree species vary in importance among treatment units (Table 1).

Watson Falls lies northwest of Crater Lake National Park within the zone of heavy deposition of volcanic ejecta that originated from the eruption of Mt. Mazama 7,000 yr B.P. (Baldwin 1981). Thus, soils are deep (1.0-2.4 m), well-drained, loamy sands derived from volcanic ash and pumice. Surface soils contain low levels of organic matter, clay compounds, nitrogen, calcium, and magnesium (Radtko and Edwards 1976). The terrain is flat to gently sloping. The climate is moderate, with warm dry summers and cool wet winters. Precipitation falls in equal proportions as rain and snow at the Airstrip units, but primarily as snow at the Mowich units. Annual precipitation averages ca. 1,525 mm (U.S. Weather Service records for Lemolo Lake).

TABLE 1. Ecological and physiographic characteristics of the six treatment units at Watson Falls. Data are from the Diamond Lake Ranger District, Toketee, Oregon and Halpern et al. (1999).

| Treatment Unit | Airstrip Units | | | Mowich Units | | |
|---------------------------------|---------------------------|---------------------------|---------------------------|---------------------|---------------------------|----------------------------|
| | 2 | 5 | 6 | 1 | 3 | 4 |
| Overstory species ¹ | PSME, ABCO, PIPO, PIMO | PSME, ABCO, PIPO, TSHE | PSME, ABCO, PIPO, TSHE | PSME, ABCO, TSHE | PSME, ABCO, TSHE, PIMO | PSME, ABCO, TSHE, ABMAS |
| Basal area (m ² /ha) | 36.1 | 51.6 | 45.4 | 43.7 | 47.7 | 60.3 |
| Mean DBH (cm) | 37.1 | 48.2 | 40.8 | 40.7 | 40.5 | 43.8 |
| Age (yr) | 110 | 130 | 130 | 110 | 130 | 110 |
| Slope (%) | 0-5 | 0-5 | 0-5 | 0-10 | 0-10 | 0-10 |
| Elevation (m) | 945 | 945 | 945 | 1311 | 1311 | 1189 |

¹Major tree species in order of decreasing dominance and coded as: ABCO = *Abies concolor*, ABMAS = *Abies magnifica* var. *shastensis*, PIMO = *Pinus monticola*, PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii*, TSHE = *Tsuga heterophylla*.

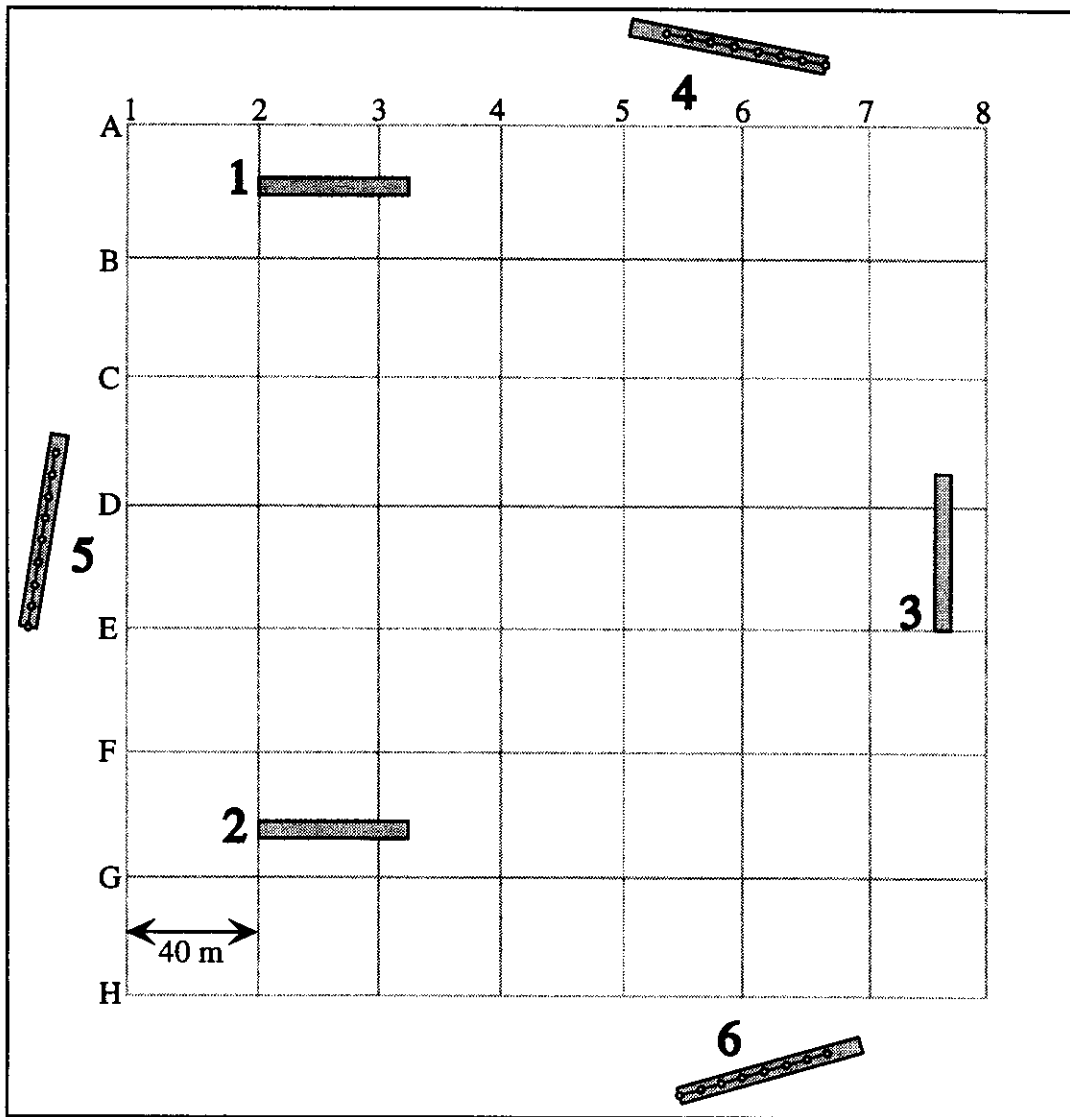


Figure 1. Schematic of sample plot layout for fungi. Plots were dispersed throughout each experimental unit. Three, permanent, 2 x 50 m mushroom sample plots (numbered 1–3) were located within the primary sampling grid (8 x 8 at 40-m spacing). Three transient, 2 x 50 m mushroom plots (numbered 4–6) were established at different locations around the grid and were replaced each sample season. Transects located down the center of the non-permanent mushroom plots contained, respectively, 8, 9, and 8, circular 4-m² truffle plots for a 100 m² total sample area. Truffle plots were placed at 6-m intervals along each transect.

Sampling of Fungal Sporocarps

Sporocarps of EMF were sampled from all treatment units during October 1993 and June 1994. These are the peak fruiting times for EMF in our region. Mushroom species were collected from 6 strip plots (2 x 50 m) per treatment unit for each seasonal sample (Figure 1). Three of the strip

plots were permanently installed and were placed systematically to maintain a dispersed sample pattern. The remaining three plots were also systematically located within each unit, but were used only once during each seasonal sample; three new locations were chosen the following season. Use of the temporary strip plots increased the area and

diversity of habitat sampled. All sporocarps of EMF mushrooms were collected from the plots and distinguishing field characteristics noted. In the field facility or laboratory, sporocarps were identified to genus or species, dried, and weighed to the nearest 0.01 g to determine biomass.

Truffles were collected from 25, circular 4-m² plots in each treatment unit, yielding a total sample area of 100 m² each season. Truffle plots were placed every 6 m along a transect within the three temporary mushroom strip plots (Figure 1). In each truffle plot, the forest floor was raked to a depth of 5–10 cm, exposing sporocarps in the upper soil layers. Distinguishing field characteristics such as handling reaction and odor were noted. In the laboratory, sporocarps were identified to species, dried, and weighed to the nearest 0.01 g to determine biomass.

Sampling of Arboreal Rodents and Small Mammals

Within each of the treatment units, arboreal rodents and small mammals were sampled using an 8 x 8 or 7 x 9 trapping grid with a 40-m spacing between grid points and a buffer of at least 50 m between stand edges and the trapping grid. Animal abundance was determined from first captures only.

Arboreal Rodents

Arboreal rodents were sampled using the methodology of Carey et al. (1991). Two Tomahawk 201 live traps were placed at each grid point. One trap was placed 1.5 m above ground on a tree, and the second at the ground next to a natural drift fence (e.g., log or snag). All traps were placed within 10 m of the grid point. Traps were covered with a waxed carton to protect animals from rain. A nest box containing polyester batting and bait (a mixture of peanut butter, molasses, and oats) was placed in each trap to provide shelter, minimize hypothermia, and prevent starvation.

Arboreal rodents were trapped for two consecutive 4-day periods in September 1993 and June 1994. Total number of trap nights per treatment unit per sample season was 1024 for treatment units with an 8 x 8 grid spacing and 1008 for those with a 9 x 7 spacing.

Small Mammals

Small mammals were sampled using Sherman live traps (8 x 9 x 23 cm) and non-fatal pitfall traps (two No. 10-tin cans, stacked and joined with duct tape). Sherman traps were placed 10 m apart on a 10 x 10 grid within the larger permanent grid system for a total of 100 traps per stand. We used a subset (36) of the permanent grid points for pitfall traps. Both types of traps were placed within 3 m of each grid point along a natural drift fence. Sherman traps were covered with a waxed carton sleeve to provide insulation and shelter and polyester batting was added to minimize hypothermia. A plastic collar nested in the top of the pitfall trap prevented animals from escaping. A waxed carton containing polyester batting was placed in the bottom of each pitfall trap to provide insulation. All traps were baited with a mixture of peanut butter, molasses, and oats.

Small mammals were trapped for two consecutive 4-day periods in October 1993. The total number of trap nights per stand was 1088 (800 for Sherman traps, 288 for pitfall traps).

Diet Analyses

Fecal pellets from trapped northern flying squirrels, Siskiyou chipmunks (*Tamias siskiyou*), and western red-backed voles (*Clethrionomys californicus*) were collected from individuals that had been captured for the first time during both 4-day trapping intervals, and from all captures on the first capture day of the second week (we assumed the 3-day period between trapping sessions was adequate for bait to pass through the animal). Fecal pellets were taken directly from individual animals or, if pellets fell during handling, they were collected only from clean, dirt-free surfaces to avoid introduction of extraneous spores or plant material into the sample. One to five fecal pellets were obtained from each individual and were placed in paper envelopes labeled with collection information. Fecal pellets of Siskiyou chipmunks and western red-backed voles were not collected during the spring sample period.

In the laboratory, two samples of pooled fecal pellets were prepared for each small mammal species from each of the six treatment units (following Method 2 of Colgan et al. [1997]). Each pooled sample consisted of pellets randomly selected from three to six individuals. Pooling reduces

the time required to collect and process samples, and is efficient for examining treatment-level responses where among-individual variation is not of interest. Each pooled sample was placed in a small vial with two or three drops of 95% ethanol to dissolve lipid layers of viruses. Four to five drops of distilled water were then added to rehydrate the samples for 48 hr at room temperature. Pellets were macerated and mixed thoroughly. Three drops of the resulting suspension were placed on a microscope slide. Two drops of Melzer's reagent (iodine, potassium iodide, and chloral hydrate in aqueous solution) were added and covered with a cover slip. Three slides were prepared in this manner for each pooled fecal sample.

For each of the 3 slides, 25 randomly selected fields of view were examined at 400x magnification with a compound microscope. Fungal spores were identified to genus according to Castellano et al. (1989). It is difficult to distinguish between the closely related genera *Rhizopogon* and *Truncocolumella* solely by spore morphology; thus these taxa were grouped in subsequent analyses. In effect, this grouping affects only fall data because *Truncocolumella* does not fruit in the spring (Luoma 1988). Plant material (e.g., seed parts, pollen, and other vegetative material identified by morphology and the presence of chloroplasts) was also identified. Frequency of each item of the diet (e.g., spore type or plant material) was calculated as the percentage of occurrence of a particular food type from the 75 possible fields in each pooled fecal sample.

Statistical Analyses

Statistical comparisons of EMF sporocarp biomass, small mammal abundance, or frequency of dietary items in small mammal fecal pellets were conducted using two-way or one-way analysis of variance (ANOVA). Main effects for these ANOVAs were area, animal species, or season. Data were variously transformed to more closely meet the assumptions of normal distribution and constant variance (Sabin and Stafford 1990). Sporocarp biomass was log (*Gautieria*, *Hysterangium*, *Rhizopogon/Truncocolumella*, total truffles) or square root (Boletaceae, Cortinariaceae, total mushrooms) transformed. Sporocarp biomass variables that could not be successfully transformed to meet the assumptions of normal distribution and constant variance (as measured by skewness and kurtosis) were rank transformed (Aphylo-

phorales, Russulaceae, other mushrooms, *Leucogaster*, other truffles). Northern flying squirrel and Siskiyou chipmunk abundance values were square-root transformed. Western red-backed vole abundance was log transformed. Dietary item variables were all rank transformed. Fisher's protected least significant difference was used as a multiple comparison procedure ($p \leq 0.1$) only when the overall ANOVA p value was ≤ 0.15 . Given the numerous ANOVAs conducted, findings of statistical significance should be interpreted with caution.

Abundance of truffles may affect the amount of plant material that mycophagous animals consume. Regression analysis was used to test the relationship between truffle sporocarp biomass produced in a unit and plant material frequency recorded from fecal pellet analysis of the three small mammal species. Plant material frequency values were log transformed.

Because the assumptions of normal distribution and constant variance could not be met by transformation of truffle spore frequency values, non-parametric correlation was used to test the relationship between truffle standing-crop biomass and mean frequency of truffle spores in fecal pellets. In all analyses, *Rhizopogon* and *Truncocolumella* sporocarp biomass was combined, consistent with the procedure used in identifying spores from fecal pellets (above).

Results

Fungal Biomass

Peak seasonal truffle standing crop biomass exceeded that of ectomycorrhizal mushroom biomass in both fall 1993 and spring 1994 (Table 2). Over 85% of the total EMF sporocarp standing crop biomass was composed of truffles. *Rhizopogon/Truncocolumella* had the greatest sporocarp biomass of all groups in fall 1993 (Table 2) and *Gautieria* in spring 1994 (Table 2).

Sporocarp biomass was different ($p \leq 0.10$) for some truffle or mushroom species groups between the Airstrip and Mowich areas (Table 2). Seasonal differences for Russulaceae, *Hysterangium*, *Leucogaster*, and *Rhizopogon/Truncocolumella* did not vary between areas (Table 2).

Sporocarp biomass did show an interaction between season and location (Airstrip and Mowich) for Boletaceae, Cortinariaceae, total mushrooms, *Gautieria*, other truffles, and total truffle biomass

TABLE 2. Mean standing-crop sporocarp biomass (g/ha dry weight) (\pm 1 SE) and ANOVA results in two study areas at Watson Falls and for the two seasons sampled, fall 1993 and spring 1994; n = 6.

| Fungal Group | Area | | | Season | | |
|-----------------------------------|-------------|-------------|-----------------------|------------|-------------|----------|
| | Airstrip | Mowich | <i>p</i> ¹ | Fall | Spring | <i>p</i> |
| Mushrooms | | | | | | |
| Aphylophorales | 128 (100) | 341 (147) | 0.19 | 252 (106) | 217 (157) | 0.31 |
| Boletaceae ² | 49 (28) | 58 (28) | 0.74 | 50 (28) | 58 (28) | 0.71 |
| Cortinariaceae ² | 28 (6) | 106 (29) | 0.01 | 36 (13) | 98 (31) | 0.02 |
| Russulaceae | 56 (53) | 174 (126) | 0.79 | 229 (123) | 1 (1) | 0.002 |
| Other mushrooms | 46 (20) | 29 (23) | 0.57 | 18 (9) | 57 (27) | 0.67 |
| Total mushrooms ² | 307 (99) | 708 (148) | 0.03 | 585 (102) | 430 (187) | 0.17 |
| Truffles | | | | | | |
| <i>Gautieria</i> ² | 508 (216) | 2278 (1440) | 0.82 | 77 (52) | 2710 (1318) | 0.002 |
| <i>Hysterangium</i> | 427 (197) | 913 (460) | 0.49 | 85 (55) | 1255 (365) | 0.007 |
| <i>Leucogaster</i> | 133 (76) | 420 (228) | 0.34 | 32 (32) | 521 (203) | 0.004 |
| <i>Rhizopogon/Truncocolumella</i> | 1509 (1054) | 1394 (513) | 0.62 | 2474 (971) | 428 (125) | 0.03 |
| Other truffles ² | 80 (38) | 1106 (666) | 0.15 | 68 (44) | 1117 (662) | 0.03 |
| Total truffles ² | 2655 (979) | 6111 (2260) | 0.11 | 2736 (984) | 6031 (2282) | 0.12 |

¹ *p* values from ANOVA based on transformed data.

² Significant area-by-season interaction precludes simple main effects comparisons. See Table 3 for detailed interaction effects.

(Table 3). Total ectomycorrhizal mushroom biomass was significantly lower in the Airstrip area in spring 1994 (Table 3). More than 92% of the sporocarp biomass in spring 1994 was from truffles and total truffle biomass was significantly greater in the Mowich area (Table 3).

Small Mammal Diets

Spores from a total of 11 truffle genera were detected in the fecal pellets of the three small mammal species. Four genera were encountered with frequencies $\geq 10\%$ (Table 4) and were considered the major food items for analytical purposes. In

contrast, the frequency of mushroom spores in fecal pellets was very low; thus, mushrooms were dropped from the analyses of dietary patterns. Spores from the mushroom groups Aphylophorales and Russulaceae were not detected in fecal pellets despite their common fruiting in all stands (Table 2).

Fall

In fall 1993, *Rhizopogon/Truncocolumella* truffles were the dominant food items in the diets of all three mammal species (Table 4) and showed no differences in occurrence among them (Table 5).

TABLE 3. Area by season interaction effects on mean standing-crop sporocarp biomass (g/ha dry weight) (\pm 1 SE) in two study areas at Watson Falls and for the two seasons sampled, fall 1993 and spring 1994. Fungal groups that do not share a superscript letter across areas and seasons are significantly different by Fisher's Protected LSD test ($p \leq 0.1$) based on transformed data; n = 3.

| Fungal Group | Airstrip | | | | Mowich | | | |
|------------------|-------------------|--------|-------------------|-------|-------------------|-------|-------------------|--------|
| | Fall | | Spring | | Fall | | Spring | |
| Mushrooms | | | | | | | | |
| Boletaceae | 89 ^a | (48) | 10 ^b | (6) | 10 ^c | (8) | 106 ^a | (40) |
| Cortinariaceae | 23 ^a | (12) | 33 ^a | (3) | 50 ^a | (23) | 163 ^b | (23) |
| Total mushrooms | 503 ^a | (95) | 111 ^b | (43) | 666 ^c | (191) | 749 ^a | (266) |
| Truffles | | | | | | | | |
| <i>Gautieria</i> | 133 ^{ab} | (100) | 883 ^a | (286) | 20 ^b | (20) | 4537 ^c | (2294) |
| Other truffles | 80 ^a | (80) | 79 ^a | (26) | 57 ^a | (57) | 2156 ^b | (1054) |
| Total truffles | 3030 ^a | (2079) | 2280 ^b | (571) | 2440 ^c | (657) | 9780 ^b | (3410) |

TABLE 4. Mean frequency (%) (± 1 SE) of truffle spores or plant fragments in fecal pellets from western red-backed voles, northern flying squirrels, and Siskiyou chipmunks at Watson Falls, fall 1993: $n=6$.

| Food Item | Frequency (± 1 SE) ^c | |
|-----------------------------------|---|-------|
| Truffles | | |
| <i>Gautieria</i> | 37.3 ^c | (4.8) |
| <i>Hysterangium</i> | 21.4 ^a | (4.4) |
| <i>Leucogaster</i> | 14.5 ^b | (3.4) |
| <i>Rhizopogon/Truncocolumella</i> | 99.7 ^c | (0.3) |
| Plant material | 63.1 ^d | (2.3) |

^cFood item frequency values that do not share a superscript letter are significantly different by Fisher's Protected LSD test ($p \leq 0.1$).

The importance of other fungal genera varied in the diets of small mammals. Northern flying squirrels had a significantly ($p \leq 0.1$) higher frequency of *Gautieria* spores in fecal pellets than did western red-backed voles or Siskiyou chipmunks (Table 5). Western red-backed voles had a significantly ($p \leq 0.02$) lower frequency of *Leucogaster* spores in fecal pellets than did Siskiyou chipmunks (Table 5). Significant area-by-animal interactions were found for *Hysterangium* and plant material (Table 6). *Gautieria* spores were more frequent in fecal pellets from the Mowich area and *Hysterangium* spores from the Airstrip area (Table 5).

For the three most frequent truffles as a group, the correlation between truffle standing crop and truffle dietary frequency was significant for all three mammal species (Table 7). Individually, however, none of the major truffle genera showed strong correlations between frequency of spore

occurrence in fecal pellets and sporocarp biomass within a treatment unit (Table 7). Total truffle standing crop within a unit did not correlate significantly with the frequency of plant material in the diets of the three mammal species, however there was an inverse correlation for western red-backed voles ($\rho = -0.60$, $p = 0.18$).

Spring

In spring 1994, *Gautieria*, *Hysterangium*, *Leucogaster*, and *Rhizopogon* (*Truncocolumella* does not fruit in spring) were major food items in the diet of northern flying squirrels, the only animal examined that season. No differences in the frequencies of truffle spores in fecal pellets were observed between the Airstrip and Mowich areas (Table 8). The frequencies of *Gautieria* and *Hysterangium* spores were higher in spring than in fall for northern flying squirrels (Tables 5 and 8). The Mowich area had lower *Rhizopogon/Truncocolumella* spore frequency in spring than fall (Tables 5 and 8).

For the four major spring food items as a group and individually, no strong correlation between truffle standing crop and spore frequencies were found (Table 9). For northern flying squirrels, the dietary frequency of plant material was negatively correlated with *Rhizopogon* sporocarp biomass ($r = -0.75$, $p = 0.08$).

Small Mammal Abundance

Western red-backed voles were most abundant (fall only) followed by Siskiyou chipmunks and northern flying squirrels ($p \leq 0.05$). Siskiyou chipmunks were more abundant in the Mowich area than the Airstrip area (Table 10).

TABLE 5. Mean frequency (%) (± 1 SE) of truffle spores or plant fragments in fecal pellets from three mammal species and ANOVA results in two study areas at Watson Falls, fall 1993. Food item values that do not share a superscript letter among animals are significantly different by Fisher's Protected LSD test ($p \leq 0.1$) based on transformed data.

| Food Item | Area (n = 18) | | | Animal (n = 12) | | | |
|-----------------------------------|---------------|------------|----------|-------------------------|---------------------------|--------------------------|----------|
| | Airstrip | Mowich | <i>p</i> | western red-backed vole | northern flying squirrel | Siskiyou chipmunk | <i>p</i> |
| Truffles | | | | | | | |
| <i>Gautieria</i> | 21.6 (5.2) | 59.9 (7.1) | 0.0004 | 33.0 ^a (5.2) | 64.7 ^b (15.0) | 28.3 ^a (10.9) | 0.15 |
| <i>Hysterangium</i> ¹ | 28.8 (6.3) | 10.7 (5.4) | 0.02 | 22.3 (5.7) | 20.9 (10.9) | 18.8 (9.7) | 0.47 |
| <i>Leucogaster</i> | 10.5 (3.2) | 20.3 (6.7) | 0.51 | 3.4 ^a (1.3) | 27.2 ^{ab} (10.7) | 39.7 ^b (10.5) | 0.02 |
| <i>Rhizopogon/Truncocolumella</i> | 100.0 (0.0) | 99.1 (0.7) | 0.15 | 99.9 (0.1) | 100.0 (0.0) | 98.7 (1.3) | 0.54 |
| Plant material ¹ | 58.4 (3.2) | 69.8 (2.6) | 0.0006 | 63.6 (1.6) | 51.7 (11.3) | 70.7 (3.5) | 0.08 |

¹Significant area by animal interaction precludes simple main effects comparisons. See Table 6 for detailed interaction effects.

TABLE 6. Area by animal interaction effects on the mean frequency (%) (± 1 SE) of *Hysterangium* spores or plant fragments in fecal pellets from three small mammal species in two study locations at Watson Falls, fall 1993. Values that do not share a superscript letter across areas and animals are significantly different by Fisher's Protected LSD test ($p \leq 0.1$) based on transformed data; $n = 6$.

| Food Item | Airstrip | | | Mowich | | |
|---------------------|-------------------------|--------------------------|-------------------------|-------------------------|--------------------------|--------------------------|
| | western red-backed vole | northern flying squirrel | Siskiyou chipmunk | western red-backed vole | northern flying squirrel | Siskiyou chipmunk |
| <i>Hysterangium</i> | 33.4 ^a (7.7) | 37.0 ^a (21.9) | 3.0 ^b (1.5) | 0.0 ^b (0.0) | 10.2 ^b (10.2) | 34.7 ^a (17.6) |
| Plant material | 63.1 ^a (2.2) | 20.5 ^b (15.1) | 66.3 ^a (4.2) | 64.7 ^a (2.0) | 72.6 ^a (8.4) | 78.0 ^c (3.6) |

TABLE 7. Spearman rank correlation, rho, between truffle standing-crop biomass and mean frequency of truffle spores in fecal pellets, ranked by treatment unit ($n = 6$) of the Watson Falls block, fall 1993; p values in parentheses.

| Food Item | Animal | | |
|-----------------------------------|-------------------------|--------------------------|-------------------|
| | western red-backed vole | northern flying squirrel | Siskiyou chipmunk |
| <i>Gautieria</i> | 0.58 (0.20) | 0.65 (0.15) | -0.28 (0.54) |
| <i>Hysterangium</i> | -0.34 (0.43) | -0.36 (0.43) | -0.09 (0.84) |
| <i>Rhizopogon/Truncocolumella</i> | 0.13 (0.77) | 0.50 (0.26) | -0.66 (0.14) |
| Pooled items | 0.70 (0.004) | 0.66 (0.007) | 0.64 (0.008) |

TABLE 8. Mean frequency (%) (± 1 SE) of truffle spores or plant fragments in northern flying squirrel fecal pellets and ANOVA results from two study areas at Watson Falls, spring 1994. Whole block food items that do not share a superscript letter are significantly different by Fisher's Protected LSD test ($p \leq 0.1$) based on transformed data.

| Food Item | Area ($n = 3$) | | | p | Whole block ($n = 6$) |
|---------------------|------------------|------------|------|--------------------------|-------------------------|
| | Airstrip | Mowich | | | |
| Truffles | | | | | |
| <i>Gautieria</i> | 91.9(8.1) | 96.5 (3.4) | 0.79 | 94.2 ^a (4.1) | |
| <i>Hysterangium</i> | 87.1(4.3) | 56.7(22.5) | 0.73 | 71.9 ^b (12.3) | |
| <i>Leucogaster</i> | 10.9(6.4) | 9.7 (5.5) | 0.85 | 10.3 ^c (3.8) | |
| <i>Rhizopogon</i> | 99.3(0.7) | 84.8(10.1) | 0.26 | 92.0 ^a (5.6) | |
| Plant material | 7.3(2.6) | 29.0(12.2) | 0.16 | 18.2 ^c (7.4) | |

TABLE 9. Spearman rank correlation, rho, between truffle standing-crop biomass and mean frequency of truffle spores in fecal pellets of northern flying squirrels, ranked by treatment unit ($n = 6$) of the Watson Falls block, spring 1994; p values in parentheses.

| Food Item | rho | (p) |
|---------------------|-------|---------|
| <i>Gautieria</i> | 0.09 | (0.84) |
| <i>Hysterangium</i> | -0.38 | (0.41) |
| <i>Leucogaster</i> | -0.64 | (0.15) |
| <i>Rhizopogon</i> | 0.52 | (0.25) |
| Pooled items | 0.23 | (0.26) |

Discussion

Sporocarp Abundance

Our results suggest that there are potentially large differences in the distribution and abundance of fungal sporocarps among our study sites, but that these differences may be apparent only during particular seasons. Truffles in particular showed strong seasonal effects. For example, the prolific spring fruiting of *Gautieria* and other minor truffle species at Mowich produced standing crops three to four times greater than those observed in the same locations in fall or in either season at

the Airstrip sites. Similar seasonal variation in truffle production has been noted at the H. J. Andrews Experimental Forest, 100 km to the north of Watson Falls (Luoma 1991).

Truffle biomass greatly exceeded mushroom biomass during both sample periods. Similarly, in a study of 15 Douglas-fir stands from southwestern Oregon, truffle species were seven of the ten most abundant producers of sporocarps (D. L. Luoma, unpubl. data). These below-ground fruiting fungi are insulated from desiccation and freezing effects that can prevent mushrooms from reaching spore maturation. Although fall is generally

TABLE 10. Number of captures per 100 trap nights (± 1 SE) of three mammal species in the two study locations at Watson Falls, and for the two seasons sampled, fall 1993 and spring 1994; $n = 6$ except $n = 3$ for the Airstrip vs. Mowich comparison of western red-backed voles.

| Animal | Area | | p^1 | Season | | p |
|--------------------------|-----------|-----------|-------|-----------|-----------------|------|
| | Airstrip | Mowich | | Fall | Spring | |
| western red-backed vole | 5.0 (2.1) | 3.1 (0.7) | 0.23 | 4.1 (0.8) | ND ² | — |
| northern flying squirrel | 0.5 (0.2) | 0.8 (0.3) | 0.37 | 0.9 (0.3) | 0.3 (0.1) | 0.23 |
| Siskiyou chipmunk | 1.5 (0.1) | 3.9 (0.7) | 0.005 | 2.2 (0.5) | 3.2 (0.9) | 0.21 |

¹ p values from two-way ANOVA based on transformed data.
²ND = No data.

when mushroom production is greatest (Fogel and Hunt 1979; North et al. 1997; D. L. Luoma, unpubl. data), fall mushroom biomass was low in this study. In subsequent years, mushroom biomass on the Watson Falls block was 8-10 times greater than in fall 1993 (D. L. Luoma, unpubl. data). We hypothesize that weather patterns are largely responsible for the low mushroom production in 1993. Unusually droughty conditions persisted from late August through mid-October that year.

Generally in our region, annual and seasonal truffle production are less variable than mushroom production (North et al. 1997; D. L. Luoma, unpubl. data). Truffles also fruit over a longer period of time (Fogel and Hunt 1979, North et al. 1997). For example, at one 3-ha ponderosa pine site in southwest Oregon, truffles have been found every week of the year (J. M. Trappe, unpubl. data). Both the seasonally-extended availability and greater biomass of truffles increase their dependability as a food source for small mammals.

Mycophagy

Our finding that northern flying squirrels consumed *Gautieria* more frequently than did western red-backed voles or Siskiyou chipmunks provides field-based support for a similar pattern observed by Zabel and Waters (1997) who found that flying squirrels preferred *Gautieria* in "cafeteria-style" feeding trials. Their study did not include *Rhizopogon*, which we found to be nearly ubiquitous in fecal pellets and which had the greatest sporocarp standing crop during fall 1993. *Rhizopogon* and *Gautieria* sporocarps may be particularly important food sources in these forests.

That all three small mammal species consumed *Gautieria* less frequently in the Airstrip units is not easily explained by variation in standing crop

alone, which if anything, was slightly higher in the Airstrip units during fall. The significantly higher number of Siskiyou chipmunks in the Mowich units could have increased predation rates on *Gautieria* in that area and thereby lowered standing-crop biomass. Spatial patterns of consumption may be a consequence of interactions between sporocarp availability, small mammal abundance, and food item preferences leading to complex competitive effects among small mammal species that vary spatially and temporally.

In the fall, the biomass of ectomycorrhizal mushrooms equaled or exceeded that of the truffle genera *Gautieria* and *Hysterangium*. Yet, despite the comparable abundance of mushroom sporocarps, truffle genera were significantly more frequent in the diets of all three small mammal species. This suggests that truffles are a preferred food in these Douglas-fir stands. No spores of the mushroom groups Russulaceae or Aphyllophorales were found in the diet analysis of any of the three small mammal species even though their sporocarp biomass exceeded that of all truffle genera except for *Rhizopogon/Truncocolumella*. Thus, EM mushrooms do not appear to be a dietary staple for these small mammal species in the Watson Falls block.

Both *Gautieria* and *Hysterangium* appear to be consumed, to some extent, in proportion to their seasonal abundance. In contrast, although *Rhizopogon/Truncocolumella* biomass decreased sharply in the spring, it remained an important component of the diet of flying squirrels. The results of other research and our own observations lead us to speculate that *Gautieria* and *Rhizopogon* may be equally preferred as food by northern flying squirrels. When maintenance of small mammal abundance and diversity are goals, management that maintains sporocarp production by truffle fungi may be crucial for success.

Dietary Correlations

In our study, the positive correlation between frequency of *Gautieria* spores in northern flying squirrel fecal pellets and *Gautieria* biomass lends further support to the hypothesis that northern flying squirrels have a preference for this genus. Colgan (1997) found that despite the reduced fruiting of *Gautieria* in thinned stands, flying squirrels trapped in those stands were continuing to utilize *Gautieria* as a dominant food source. He hypothesized that flying squirrel preference for *Gautieria* could further reduce standing crop biomass in those stands (beyond that induced by the thinning) forcing flying squirrels to obtain *Gautieria* outside the thinned treatment areas. The much larger, contiguous treatment areas of the DEMO experiment will reduce the influence of this type of edge effect.

The significant correlation between truffle standing-crop biomass and frequency of truffle spores in fecal pellets for the pooled food items must be viewed with some caution. The correlation was mainly the result of a few high *Rhizopogon/Truncocolumella* sporocarp biomass values coinciding with high dietary frequency values while *Gautieria* and *Hysterangium* tended to have lower biomass and spore frequency values. As an individual food item, there is no correlation between truffle standing-crop biomass and frequency of truffle spores in fecal pellets for *Rhizopogon/Truncocolumella* because these are eaten ubiquitously, regardless of variation in peak-season standing-crop biomass.

Negative correlations between the Siskiyou chipmunk and *Gautieria* may indicate that increased competition for truffles reduces sporocarp standing-crop biomass. North et al. (1997) have demonstrated predation effects on truffle standing crop in northwestern Washington. In spring, the negative correlation between fungal biomass and spores of *Leucogaster* in the diet (Table 8) again suggests that mycophagy may affect sporocarp standing-crop biomass. When truffle biomass is lowered, consumption of plant material may increase, however unexplored complexities involving animal abundance, competitive ability, and food preference limit our ability to generalize from this study.

Small Mammal Abundance

Truffle abundance probably has an important influence on the abundance of mycophagous small

mammals. In addition to higher Siskiyou chipmunk abundance at Mowich in fall, were higher *Gautieria* consumption by all three animals studied and reduced *Gautieria* standing-crop biomass. However, factors other than truffle abundance could also affect the densities of small mammal species in these stands. Variation in tree basal area, snags, downed trees, and tree cavities may influence the availability of cover, food, and nesting areas (Gilbert and Allwine 1991). The movements of animals from adjacent stands and variation in local predation rates can also influence small mammal abundance (Carey 1991, Lehmkuhl and Ruggiero 1991). These potential effects were not analyzed in the current study but will be considered by other researchers in subsequent analyses of wildlife patterns (Lehmkuhl et al. 1998). Further exploration of the sources of between-area differences will be an important part of our baseline, pre-harvest analysis; the patterns and causes of these differences will be of fundamental importance to understanding variation in the relationships that emerge following imposition of the DEMO harvest treatments.

Conclusions

We identified significant spatial and temporal variation in EMF production, small mammal mycophagy, and small mammal abundance in the pre-harvest forests of the Watson Falls block. However, truffles were consistently the primary food item in the diet of all three small mammal species studied. Small mammals are potentially important dispersal agents of truffles into disturbed areas where EMF are locally extirpated. Although this study represents only a "snap shot" in time, future analyses will examine responses to various levels and patterns of green-tree retention over multiple years, thus broadening the scope of inference for our findings.

Northern flying squirrels and Siskiyou chipmunks nest in trees or use trees as avenues for travel (Carey 1991). Arboreal rodents may be affected by forest management activities that change the pattern and structure of forest canopies. Trees also provide the energy sources for EMF and their fruiting bodies. Therefore, disturbances that influence the level and pattern of live trees retained through harvest are also likely to influence the diversity, abundance, and distribution of EMF and their fruiting bodies. Future analyses of post-harvest patterns will provide

valuable insights into the effects of retention harvest on EMF and small mammal abundance. Given the functional importance of these groups in our forest ecosystems, the results of our work will have important implications for how retention harvests may be implemented in the future.

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