Short-term effects of fire and forest thinning on truffle abundance and consumption by *Neotamias speciosus* in the Sierra Nevada of California

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Abstract: In many western North American forests, prescribed burning and mechanical thinning are widely used to reduce fuels and restore stand conditions after a century of fire suppression. Few studies have followed the relative impacts of these treatments on the production and consumption of truffles in forest ecosystems, particularly in the Sierra Nevada of California. Using a full-factorial completely randomized design, we examined the short-term impacts of prescribed burning (no burn and burn), mechanical thinning (no thin, light thin, and heavy thin), and combinations of these treatments on the production of truffles and their consumption by lodgepole chipmunks (*Neotamias speciosus* Merriam) in a mixed-conifer forest of the southern Sierra Nevada of California. Truffle frequency, biomass, and species richness were lower in thinned or burned plots than controls, as was the frequency and generic richness of truffles in the diet of *N. speciosus*. Truffle frequency, biomass, and species richness, and truffle consumption by *N. speciosus* were lower in heavily thinned and thinned and burned plots than in those exclusively burned. These results suggest that either thinning or burning can reduce short-term truffle production and consumption, and potentially the dispersal of ectomycorrhizal spores by small mammals. Moreover, truffles decreased with treatment intensity, suggesting heavy thinning and higher burn intensity, particularly when applied together, can significantly affect short-term truffle abundance and small mammal consumption.

Résumé : Dans plusieurs forêts de l'ouest de l'Amérique du Nord, le brûlage dirigé et l'éclaircie mécanisée sont largement utilisés pour réduire les combustibles et restaurer les peuplements après un siècle de suppression des feux. Peu d'études ont examiné l'impact de ces traitements sur la production et la consommation de truffes dans les écosystèmes forestiers, particulièrement dans la Sierra Nevada en Californie. À l'aide d'un dispositif factoriel complètement aléatoire, nous avons étudié les impacts à court terme du brûlage dirigé (brûlé et non brûlé), de l'éclaircie mécanisée (pas d'éclaircie, éclaircie légère et éclaircie forte) et des combinaisons de ces traitements sur la production de truffes et leur consommation par les tamias (*Neotamias speciosus* Merriam) dans une forêt mélangée de conifères située dans la partie sud de la Sierra Nevada en Californie. La richesse en espèces, la biomasse et la fréquence des truffes, de même que la fréquence et la richesse en genre de truffes dans la diète de *N. speciosus*, étaient plus faibles dans les parcelles brûlées ou éclaircies que dans les parcelles témoins. La richesse en espèces, la biomasse et la fréquence des truffes ainsi que la consommation de truffes par *N. speciosus* étaient plus faibles dans les parcelles fortement éclaircies et les parcelles éclaircies et brûlées que dans les parcelles brûlées seulement. Ces résultats indiquent que l'éclaircie ou le brûlage peuvent à court terme réduire la production et la consommation de truffes et possiblement la dispersion des spores des champignons ectomycorhiziens par les petits mammifères. De plus, la diminution des truffes est fonction de l'intensité du traitement, ce qui indique qu'une éclaircie forte et un brûlage de forte intensité, particulièrement lorsque ces traitements sont combinés, peuvent significativement affecter l'abondance de truffes et la consommation par les petits mammifères à court terme.

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Introduction

Fire is an integral component of many ecosystems throughout the world (Dickman and Rollinger 1998), and in forests it facilitates tree regeneration, nutrient cycling, and forest succession (Attiwill 1994). However, decades of fire suppression in many North American forests have altered these processes, increasing drought stress (Ferrell 1996; Ferrell et

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al. 1994), pest outbreaks (Mattson and Hack 1987), and wildfire intensity (Husari and McKelvey 1996; Dickman and Rollinger 1998). To reduce fuels and crown fire risk, two treatments are often used: mechanical thinning alone in wildland urban interface areas, and thinning and prescribed fire in more remote locations. It is unclear, however, how thinning, fire, and their interaction influence the ecological processes and trophic structure that maintain ecosystem "health" and function.

An important functional component of forest ecosystems are ectomycorrhizal fungi (EMF), required by most temperate forest conifer species for increased water and nutrient uptake (Molina et al. 1992). In return, EMF receive carbohydrates from tree photosynthesis. EMF fruiting bodies, especially belowground truffles, are frequently consumed by many small mammals (Fogel and Trappe 1978; Maser et al. 1978) for their high caloric (Smith 1968) and protein content (Miller and Halls 1969). Viable fungal spores pass through the mycophagist's digestive system (Kotter and Farentinos 1984; Cork and Kenagy 1989; Colgan and Claridge 2002) and are dispersed to new soil patches where they facilitate conifer succession (Terwilliger and Pastor 1999) and promote EMF diversity (Johnson 1996).

Much is known about truffle production and consumption by small mammals in wet Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of western Washington and Oregon (Luoma et al. 1991; Colgan et al. 1997; Carey et al. 2002; Smith et al. 2002). Recently, several studies have examined truffle production in dry mixed-conifer and ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forests of interior Washington State, California, and Arizona (States and Gaud 1997; Waters et al. 1997; Lehmkuhl et al. 2004). However, few parallel studies exist for forests in the Sierra Nevada of California (e.g., Pyare and Longland 2001*a*), and no studies have examined fire or forest management effects on truffle production or consumption in this region.

The purpose of this study was to examine the short-term effects (1–3 years) of fire and thinning on truffle production and consumption by lodgepole chipmunks (*Neotamias speciosus* Merriam) in a region (Sierra Nevada of California) and forest type (mixed conifer) previously unexamined with respect to forest management impacts on truffle production or consumption. We focused on *N. speciosus* with an omnivorous diet (Best et al. 1994), because their opportunistic diet may better reflect the availability of different truffle genera in treated stands than dietary specialists like the northern flying squirrel (*Glaucomys sabrinus* Shaw). In addition, *N. speciosus* was the most abundant small mammal species in our treatment plots. Specifically, we evaluated the effects of burning, two levels of thinning, and thinning followed by burning on truffle production as well as consumption by *N. speciosus*. Before and after treatments, we assessed burning and thinning effects on the frequency, biomass, species diversity, and species composition of truffles, as well as truffle frequency and generic diversity in the diet of *N. speciosus*. We also examined changes in forest stand structures (canopy cover, litter depth, and tree density) that previous studies (e.g., North and Greenberg 1998; Lehmkuhl et al. 2004) suggest are associated with truffle production and consumption following management treatments.

Methods

Study area

The study was conducted at Teakettle Experimental Forest, a 1300-ha, mixed-conifer forest in the southern Sierra Nevada, Fresno Co., California. Teakettle Experimental Forest (1800–2400 m elevation), characterized by a Mediterranean-influenced montane climate, with hot, dry summers, receives precipitation almost exclusively as snow in the winter (Major 1990). Mean annual precipitation is 110 cm at 2100 m, and mean summer rainfall (June–September) during 1999–2002 was 0.9 ± 0.3 cm. Teakettle Experimental Forest is an old-growth forest characterized by a multilayered canopy and numerous large (>100 cm diameter at breast height; dbh) and old (>200 years) trees, snags, and decayed logs. Dominant trees are white fir (*Abies concolor* (Gord & Glend.) Lindl.), red fir (*Abies magnifica* A. Murray), sugar pine (*Pinus lambertiana* Douglas), Jeffrey pine (*Pinus jeffreyi* Balfour), and incense cedar (*Calocedrus decurrens* (Torrey) Florin).

Experimental design and treatments

This research is part of the Teakettle Experiment and use a full factorial set of treatments in a completely randomized design. Two levels of burning (no burn or prescribed burn) were crossed with three levels of thinning (none, light thin and heavy thin) producing six treatments: (1) light thin only; (2) heavy thin only; (3) light thin followed by burn; (4) heavy thin followed by burn; (5) burn only; and (6) no burn or thin (control). Within Teakettle Experimental Forest, 18 replicate 4-ha plots were established, and all plots but one were randomly assigned to each treatment. The single exception was a plot that was randomly assigned to one of the three unthinned treatments because it contained a perennial stream around which Forest Service regulations did not permit tree harvest. All plots are separated by untreated buffer zones of 50–150 m. The size and spatial placement of plots were determined following variogram and cluster analysis of mapped sample quadrats (North et al. 2002). In July–September of 2000 and July–August of 2001, 12 plots were experimentally thinned following two prescriptions: light-intensity CASPO (California Spotted Owl guidelines) and high-intensity shelterwood thinning. Under CASPO thinning, no trees >76 cm diameter were harvested and at least 40% of the canopy cover was left in place after harvest. With shelterwood thinning, all trees >25 cm DBH were removed except for approximately 22 dominant, evenly spaced trees per ha. Shelterwood guidelines followed practices used on several National Forests in the Sierra Nevada before CASPO regulations and were modeled on common silvicultural prescriptions (Smith 1986). In early November 2001, after the first substantial fall rain, 12 plots were prescribed burned. At this time, average daytime temperature was 13 °C and relative humidity ranged from 25% to 70%. The percentage of ground cover burned was approximately 35%–70% and 20%–40% in thinned and unthinned plots, respectively.

Measurements

In each of the eighteen 4-ha plots, all trees and snags >5 cm DBH and shrubs were measured. Trees and shrubs were identified to species and snags were assigned a decay class following Cline et al. (1980). The position coordinates (x, y) and the elevation (z; m above mean sea level) of each stem were measured using a surveyor's total station (Criterion 400 and Topcon 300). All logs >20 cm diameter and >2 m in length were measured. Understory light conditions were estimated at each sample point using hemispherical photographs that were analyzed using SCANOPY (Regent Instruments Inc., Québec, Que.) software. From each photograph, two metrics were calculated: direct and diffuse photosynthetically active photon flux density (PPFD; $\mu mol \cdot s^{-1} \cdot m^{-2}$). PPFD was calculated using the latitude, longitude, and elevation of the study area and the tracking angle of the sun over the course of a year. PPFD values were used as an approximation of understory light conditions. Percent soil volumetric water content was measured in June–August 2002 using time domain reflectometry following methods described by Gray and Spies (1995). Stand conditions by treatment are given in Table 1.

Truffle sampling

In June and August of 2000 and June of 2001, pretreatment frequency, species richness, and biomass of truffles were estimated for each treatment plot by placing five 4-m^2 circular quadrats immediately outside the treatment plots (to minimize pretreatment soil disturbance). After treatments, nine sample points were established within each plot in a 3 × 3 grid with 50 m spacing between points and a 50-m buffer from the plot boundary. A single 4-m^2 circular quadrat was placed at the first eight grid points per plot (including one quadrat at the ninth grid point in one of the three plots), giving a total sample area of 32 m^2 per plot (36 m^2 for the third replicate), 100 m^2 per treatment (three replicates per treatment; 32 + 32 + 36 m^2), and 600 m^2 total per season (six treatments). Within each quadrat, litter depth was measured by digging two shallow pits at the edge of each quadrat and taking two depth measurements of the combined litter and humus layers. In June and July–August of 2002 and 2003, quadrats were sampled for truffles by searching through the litter, humus, and upper 5 cm of mineral soil using a four-tined rake. All collected truffles were counted, placed in wax bags, dried for 24 h at 60 °C, weighed to the nearest 0.01 g, and identified to species. Truffle collections were used to estimate frequency, species richness, and total biomass of truffles in treatment and control plots. Owing to the small size of truffle collections for each season, collections from June and July–August were pooled.

Following Waters et al. (1997), secotioid, epigeous fungi (*Hymenogaster* and *Martellia*) were grouped with truffles in fungal collections, because these taxa are mycorrhizal and primarily producers of subterranean fruiting bodies. The peridium, gleba, columella, and spores of fresh specimens were examined microscopically, tissues were reinflated with 3% potassium hydroxide, and Melzer's reagent (I, K, and chloral hydrate; Castellano et al. 1989) was used to characterize dextrinoid (reddish brown) and amyloid (blue-black) reactions. We used keys by Smith (1966), Smith and Smith (1973), Smith and Zellner (1966), and Arora (1986) to identify species. Samples were also compared with an extensive collection of voucher specimens (878 individuals of 87 species) collected from a nearby 1-ha sampling site (North 2002). Using the keys and the voucher collection, all but 1 genus (*Rhizopogon*) was readily identified to species. For *Rhizopogon*, we checked our identifications (from macroscopic characteristics and spore keys) with DNA sequencing methods used in a related study (Izzo et al. 2005) that used our sporocarp and fecal samples.

Truffle consumption by *Neotamias speciosus*

Neotamias speciosus was censused in all treatment plots with Tomahawk live traps (model 201; 40 cm × 13 cm × 13 cm). Traps were attached 1.5 m high on the trunk of a large (>70 cm DBH) tree at each 50-m grid point in a plot (n = 9 traps per plot). In 1999–2000 (pretreatment) and 2002–2003 (post-treatment), traps were placed in each plot for three consecutive days in early summer (June) and four consecutive days in mid-summer (July–August), for a total of 63 trap-nights per plot per year. Traps were baited with a mixture of peanut butter and rolled oats, and a small cardboard shelter, filled with polyester stuffing material, was placed in each trap to provide animals with thermal insulation. Captured animals were uniquely marked with numbered ear tags, and standard measurements (mass, gender, reproductive condition) were recorded.

Fresh fecal samples were opportunistically collected from captured *N. speciosus*. Samples were placed into individual envelopes, labeled, and stored in a dry location at room temperature for 1–6 weeks. Following the methods of Colgan et al. (1997) and Pyare and Longland (2001*a*), small portions of all pellets in a single fecal sample (approximate total weight = 25 mg) were assessed for truffle spores. Samples were mixed with 3 mL of distilled water, and a single drop was applied to each of three slides. One drop of Melzer's reagent was added to each slide, and 25 systematically located fields of view were examined at 400× magnification (total of 75 fields of view per sample). All fungal spores present were identified to genus using a synoptic key (Castellano et al. 1989). Frequency of occurrence was calculated separately for each genus. The frequencies of two dietary genera of secotioid, epigeous fungi (*Gymnomyces* and *Martellia*) were combined, since they were indistinguishable based on spore characteristics alone. The frequency of occurrence of nonsecotioid, epigeous genera was also noted. Fecal samples collected from individuals that were captured in more than one treatment plot (4.4% of samples) were excluded from analysis.

Analysis

All pretreatment truffle variables (frequency, species richness, biomass, dietary generic richness, and dietary frequency) were analyzed with three-way mixed model analysis of variance (ANOVA) to test for differences among treatments and between pretreatment years (2 years). No significant pretreatment or annual differences (all $P > 0.05$) were found for these variables. Data were evaluated for normality with the Kolmogorov–Smirnov test and for homoscedasticity with Levene's test (Zar 1984). Truffle species richness was square-root transformed, and truffle frequency and biomass, dietary generic richness of truffle spores, *Elaphomyces* dietary frequency, and tree basal area were log-transformed to

Table 1. Mean (±SE) values of stand structure variables measured in treatment plots at Teakettle Experimental Forest (2002–2003).

	No burn			Burn		
Stand variable	No thin (control)	Light thin*	Heavy thin†	No thin	Light thin*	Heavy thin†
Tree basal area (m^2/ha)	54.3a (4.5)	45.3a (2.0)	22.6b (3.8)	59.7a (9.2)	44.0a (1.5)	22.6b (1.5)
Tree density (no./ha)	348.3a (21.3)	336.7ab (32.0)	235.3ab (27.4)	455.9ab (99.5)	334.8ab (41.8)	311.3b (36.9)
PPFD ($\mu mol \cdot s^{-1} \cdot m^{-2}$)	1.82a (0.05)	1.28b (0.10)	0.88c (0.03)	1.75a (0.05)	1.25b (0.07)	0.73c (0.04)
Shrub cover (%)	17.6a (2.4)	5.7ab (2.5)	1.5b (0.8)	15.8a (3.9)	6.8ab (2.3)	2.5b (0.6)
Log volume (m^3/ha)	215.2a (39.2)	172.5ab (25.1)	152.6ab (16.0)	94.5bc (4.1)	70.8c (15.3)	54.9c (16.0)
Soil volumetric water content (%)	10.2a (2.8)	12.7a (0.5)	13.9a (0.4)	10.9a (1.3)	10.6a (1.2)	10.7a (0.6)
Litter depth (cm)	5.2a (0.5)	4.0a (0.2)	4.2a (0.2)	2.3b (0.5)	0.6c (0.4)	0.1c (0.1)

Note: Within a row, values with different letters are significantly different ($P < 0.05$) using Tukey's honestly significant difference test. PPFD, photosynthetically active photon flux density; an approximation of understory light conditions.

*Light (CASPO) thinning, no trees >76 cm diameter were harvested, and at least 40% of the canopy cover was left in place after harvest.

†Heavy (shelterwood) thinning, all trees >25 cm DBH were removed except for approximately 22 dominant, evenly spaced trees per hectare.

meet parametric assumptions of normality and homoscedasticity. All analyses were conducted with Statistica 6.0 (StatSoft Inc., Tulsa, Oklahoma) using an α level of 0.05.

Multivariate analysis of variance (MANOVA) and two-way model 1 ANOVAs were used to test for the effect of fire (two levels), thinning (three levels), and post-treatment year (2 years) on truffle production (species richness, frequency, and biomass) and consumption by *N. speciosus* (dietary generic richness and frequency). Owing to the presence of a single outlier in truffle biomass (one quadrat/plot per year contained an extreme biomass cluster of *Elaphomyces granulatus* Fr., equal to 30% of the total biomass of truffle samples from all plots in both years), a second ANOVA substituting the extreme 99-g value with a 35-g value (equal to the remaining truffle biomass after removal of the *E. granulatus* cluster from the single quadrat) also was used to test for the effect of fire and thinning on truffle biomass. Since the results from this second analysis were qualitatively similar to the earlier analysis, only the results from the first analysis (using the 99-g value) are presented below. A single MANOVA was used to test the null hypothesis that low-intensity (CASPO) and high-intensity (Shelterwood) thinned plots were similar with respect to dietary generic richness and frequency of truffles. Additionally, MANOVAs were used to evaluate whether dietary generic richness and frequency were similar between burned compared with thinned plots and exclusively burned compared with thinned and burned plots. Two-factor model 1 ANOVAs were used to examine if the three most common truffle genera in diet samples (*Rhizopogon*, *Geopora*, and *Elaphomyces*) were similar among plots both burned and thinned and those exclusively burned. Since very few spring fecal samples were available (n = 9 for May to early June), these samples were excluded from analysis. Tukey's honestly significant difference (HSD) test was calculated for all stand variables and dietary truffle taxa, as well as truffle frequency, biomass, species richness, dietary frequency, and dietary generic richness to evaluate responses of specific variables to burning and thinning treatments. In addition, 95% confidence intervals (CI) were calculated for truffle frequency, biomass, species richness, dietary frequency, and dietary generic richness.

Indicator species analysis (ISA; Dufrene and Legendre 1997) using species of truffles was used to identify significant species associations with burning and thinning treatments. ISA combined information on relative abundance and site fidelity of each species to estimate indicator values (IV) for each species in each group. ISA P values were calculated as the proportion of 1000 randomized trials with an IV equal to or greater than the observed IV: P = (1 + number of runs = observed)/(1 + number of randomized runs).

Results

A total of 108 and 98 truffles were collected from treatment plots in 2002 and 2003, respectively (288 sample plots per year). A total of 10 species of truffles were encountered, with 1–6 species per treatment (Table 2). Species frequencies of truffles in all treatment and control plots were low (range: 0%–2.6%). Across treatments, *Elaphomyces granulatus* had the greatest biomass, while *Rhizopogon subcaerulescens* had the greatest frequency of occurrence.

Truffle frequency, biomass, and species richness were reduced by either burning or thinning, with no treatment interactions or difference between years of sampling (Tables 2 and 3). Truffle frequency was 2.3 times greater in unburned (15.5% ± 3.8% (95% CI)) than burned (6.7% ± 3.8%) plots, as well as 1.5 and 5.1 times greater in unthinned (18.2% ± 4.6%) than light-thinned (11.7% ± 4.6%) and heavy-thinned (3.5% ± 4.6%) plots, respectively. Truffle biomass was 12.1 times greater in unburned (1651.7 ± 1738.4 g/ha (95% CI)) than burned (136.1 ± 116.6 g/ha) plots, as well as 1.9 and 7.6 times greater in light-thinned (1623.9 ± 2707.8 g/ha) than unthinned (843.1 ± 718.7 g/ha) and heavy-thinned (214.6 ± 359.9 g/ha) plots, respectively. Truffle species richness was 2.5 times greater in unburned (1.8 ± 0.4 (95% CI)) than burned (0.7 ± 0.4) plots, as well as 1.3 and 4.6 times greater in unthinned (1.9 ± 0.5) than light-thinned (1.5 ± 0.5) and heavy-thinned (0.4 ± 0.5) plots, respectively. Truffle frequency, biomass, and species richness were not different between plots that were either thinned or burned (Wilks' λ = 0.865, $F_{[3,22]}$ = 1.146, P = 0.353), but these variables were lower in heavy- compared with light-thinned treatments (Wilks' λ = 0.617, $F_{[3,22]}$ = 4.556, P = 0.013; frequency: $F_{[1,24]}$ = 12.784, P = 0.002; biomass: $F_{[1,24]}$ = 4.421, P = 0.046; species richness: $F_{[1,24]}$ = 13.004, P = 0.001) as well as thinned and burned compared with burned only treatments (Wilks' λ = 0.595, $F_{[3,22]}$ = 4.990, P = 0.009; frequency: $F_{[1,24]}$ = 16.065, P < 0.001; biomass: $F_{[1,24]}$ = 3.343,

Table 2. Truffle biomass (g/ha) found among treatment plots at Teakettle Experimental Forest (2002–2003).

Species or genus	No burn: No thin (control)	No burn: Light thin	No burn: Heavy thin	Burn: No thin	Burn: Light thin	Burn: Heavy thin	Total biomass (% frequency) across treatments
Elaphomyces granulatus Fr.	—	2487.5 (62)	81.0 (3)	—	—	—	428.09 (3.3)
Gautieria monticola Harkn.	107.5 (2)	5.3 (1)	—	41.0 (1)	3.5 (3)	—	26.22 (1.7)
Geopora cooperi Harkn.	—	58.0 (1)	—	17.3 (1)	—	—	12.54 (0.7)
Martellia californica Singer & A. H. Smith	7.8 (1)	38.5 (8)	261.0 (5)	—	—	—	51.21 (0.7)
Hydnotrya cerebriformis Harkn.	252.5 (17)	102.5 (7)	—	44.5 (2)	—	7.7 (1)	69.14 (3.7)
Hymenogaster gilkeyae Zeller & Dodge	428.0 (9)	4.0 (1)	—	15.0 (2)	3.8 (1)	—	72.85 (2.0)
Hysterangium setchellii E. Fisch.	6.3 (1)	—	—	84.8 (4)	—	—	15.15 (0.7)
Leucophleps spinispora Fogel	48.3 (3)	—	—	—	—	—	8.04 (0.3)
Melanogaster tuberiformis Corda	—	31.0 (5)	—	—	—	—	5.17 (0.7)
Rhizopogon subcaerulescens A. H. Smith	482.5 (18)	464.5 (22)	72.0 (2)	67.8 (5)	23.8 (2)	—	185.09 (5.3)
Truffle biomass, all species combined (g/ha)	1339.0a	3202.1a*	414.0ab	347.3ab	45.8b	15.3b	
Truffle % frequency	21.1a	19.4ab	6.0bc	15.3abc	3.9cd	1.0d	
Truffle species richness	2.3a	2.5a	0.7b	1.5ab	0.5b	0.2b	

Note: Species within light- and heavy-thinned plots are pooled as “thinned”. Values in parentheses are the total number of sporocarps collected in each treatment type, with the exception of the last column (total biomass of all truffle species across all treatments) which indicates % frequency of all truffle species combined. For summary values in the last three rows, values within a row with different letters are significantly different ($P < 0.05$) using Tukey’s honestly significant difference test. Species with <5 g total biomass are not included.

*Sixty-five percent of the total biomass is attributed to a single cluster of *E. granulatus* found in a single 4-m^2 truffle plot (1% of the total sampled area).

P = 0.080; species richness: $F_{[1,24]} = 10.623$, $P = 0.003$; Table 2).

No truffle species were found in all treatment types (Table 2), although *R. subcaerulescens* was found in all treatments except for the heavy-thin followed by burning. Other species were limited to particular treatments, such as *E. granulatus* (exclusively in plots thinned but not burned) or *Leucophleps spinispora* (exclusively controls). *Elaphomyces granulatus* was positively associated with thinning treatments (IV = 11.6, $P = 0.026$). *Elaphomyces granulatus* (IV = 10.8, $P = 0.004$), *R. subcaerulescens* (IV = 13.8, $P = 0.030$), and *H. cerebriformis* (IV = 10.4, $P = 0.037$) were negatively associated with burning, and *E. granulatus* (IV = 23.2, $P = 0.002$) and *H. cerebriformis* (IV = 18.0, $P = 0.009$) were negatively associated with burn plus thin treatments. Most truffle species were most abundant in control plots, but a few widespread species were more common in thinned (*Martellia californica*) or burned plots (*Hysterangium setchellii*).

The abundance of truffle genera in the diet of *N. speciosus* was lower in burned or thinned plots than controls, with no treatment interactions (Tables 4 and 5). Dietary frequency of truffles was 1.4 times greater in unburned (83.5% ± 6.7% (95% CI)) than burned (60.6% ± 6.7%) plots, as well as 1.2 and 1.4 times greater in unthinned (83.9% ± 7.9%) than light-thinned (69.9% ± 7.9%) and heavy-thinned (62.3% ± 7.9%) plots, respectively. Dietary generic richness of truffles was 1.8 times greater in unburned (1.6 ± 0.2 (95% CI)) than burned (0.9 ± 0.2) plots, as well as 1.5 and 1.7 times greater in unthinned (1.7 ± 0.2) than light-thinned (1.1 ± 0.2) and heavy-thinned (1.0 ± 0.2) plots, respectively. There was no difference in dietary generic richness and frequency between plots that were either thinned or burned (Wilks’ $\lambda = 0.994$, $F_{[1,22]} = 0.062$, $P = 0.940$) or between heavy- and light-intensity thinning (Wilks’ $\lambda = 0.952$, $F_{[1,22]} = 0.526$, $P = 0.599$). However, plots that were both burned and thinned were lower in dietary generic richness and frequency than plots exclusively burned (Wilks’ $\lambda = 0.513$, $F_{[1,22]} = 9.964$, $P = 0.001$; frequency: $F_{[1,22]} = 14.956$, $P < 0.001$; generic richness: $F_{[1,22]} = 18.439$, $P < 0.001$). There was no difference in the dietary frequency of *Rhizopogon* ($F_{[1,22]} = 1.501$, $P = 0.233$), *Geopora* ($F_{[1,22]} = 3.126$, $P = 0.091$), and *Elaphomyces* ($F_{[1,22]} = 4.106$, $P = 0.055$) between plots both burned and thinned and those exclusively burned (Table 5).

Discussion

Treatment effects of truffle abundance and species diversity

Burning can reduce several stand variables associated with truffle production, particularly litter depth (Waters et al. 1994; North and Greenberg 1998), log volume (Amaranthus et al. 1994), and soil moisture (Waters et al. 1997). Burning reduced litter depth and log volume (but not soil moisture), as well as the frequency, biomass, and species richness of truffles at Teakettle Experimental Forest. Decaying woody debris in the form of organic litter and decayed logs are important reservoirs of moisture and nutrients that may provide conditions favorable for fruiting fungi (Amaranthus et al. 1994), especially in forests where the soils are relatively dry (Clarkson and Mills 1994). Removal of decayed woody debris in burned only and thinned followed by burned plots

Table 3. MANOVA and ANOVAs for effects of burning, thinning, and year on truffle production at Teakettle Experimental Forest (2002–2003).

Dependent variable	Factor	Wilks' λ	*F*	df	*P*
MANOVA					
Truffle frequency, biomass, and species richness	Burn	0.527	6.578	3,22	0.002
	Thin	0.472	3.340	6,44	0.008
	Burn × thin	0.759	1.084	6,44	0.387
	Year	0.949	0.393	3,22	0.760
	Burn × year	0.907	0.754	3,22	0.532
	Thin × year	0.686	1.524	6,44	0.193
	Burn × thin × year	0.842	0.659	6,44	0.684
ANOVAs					
Truffle frequency	Burn		14.836	1	<0.001
	Thin		9.632	2	<0.001
	Burn × thin		9.632	2	0.218
Truffle biomass	Burn		12.477	1	0.002
	Thin		3.653	2	0.045
	Burn × thin		1.059	2	0.359
Truffle species richness	Burn		14.970	1	<0.001
	Thin		10.684	2	<0.001
	Burn × thin		2.208	2	0.127

Table 4. MANOVA and ANOVAs for effects of burning, thinning, and year on truffle consumption by *Neotamias speciosus* at Teakettle Experimental Forest (2002–2003).

Dependent variable	Factor	Wilks' λ	*F*	df	*P*
MANOVA					
Dietary frequency and richness	Burn	0.401	15.653	2,21	0.001
	Thin	0.472	4.786	4,42	0.003
	Burn × thin	0.900	0.570	2,21	0.686
	Year	0.979	0.229	4,42	0.797
	Burn × year	0.870	1.572	2,21	0.231
	Thin × year	0.949	0.277	4,42	0.891
	Burn × thin × year	0.777	1.414	4,42	0.246
ANOVAs					
Dietary frequency	Burn		24.729	1	<0.001
	Thin		7.736	2	0.002
	Burn × thin		0.707	2	0.502
Dietary generic richness	Burn		35.305	1	<0.001
	Thin		12.743	2	<0.001
	Burn × thin		1.128	2	0.338

may have decreased the abundance of truffles in these plots compared with controls. Other stand variables associated with truffle production (e.g., tree density, soil moisture) were not different between burned only and control plots. Interestingly, truffle biomass and frequency did not differ between burned and unburned sites in northeastern California, possibly because burning had no effect on the abundance of decayed logs and a marginal effect (1 cm decrease) on organic litter depth (Waters et al. 1994).

Mechanical thinning also can reduce several stand variables associated with truffle production, including tree density (Waters et al. 1994; Colgan et al. 1999), total basal area (States and Gaud 1997), and canopy cover (States and Gaud 1997; Lehmkuhl et al. 2004). In this study, thinning decreased canopy cover and tree basal area (heavy-thin only) as well as the frequency, biomass, and species richness of truffles. Denser canopies and greater tree basal area in control compared with thinned plots create a moister understory microclimate (S. Ma, unpublished data) that may provide conditions favorable for truffle production in relatively dry forests (States and Gaud 1997; Lehmkuhl et al. 2004). Additionally, the greater tree basal area in unthinned plots would support a higher density of fine roots, possibly providing more sites for EMF colonization (Pietikäinen and Fritze 1995) and greater truffle production. In northeastern California, there was no difference in truffle frequency or biomass between heavy-, moderate-, and unthinned white and red fir stands (Waters et al. 1994). Similarly, in eastern Washington State there was no difference in truffle richness or biomass between young and mature mixed-conifer forest (Lehmkuhl et al. 2004). In wetter Douglas-fir stands of western Oregon and Washington, results of the effect of forest management

Table 5. Mean generic richness and percent frequency of truffle spores in diet of *Neotamias speciosus* at Teakettle Experimental Forest (2002–2003).

	No burn			Burn		
Genus or group	No thin (control)	Light thin	Heavy thin	No thin	Light thin	Heavy thin
Generic richness	2.0a	1.4a	1.4a	1.4ab	0.8bc	0.6c
Rhizopogon	47.6a	46.5ab	40.3ab	24.6ab	13.9ab	13.2b
Melanogaster	6.6	11.5	6.9	11.0	6.9	13.9
Elaphomyces	27.2	11.2	9.3	21.5	4.9	2.8
Leucophleps	10.0	1.4	6.9	12.2	6.0	1.9
Hymenogaster	11.4	14.4	11.7	7.6	7.0	2.1
Glomus	10.2	6.9	2.0	19.9	6.9	2.0
Gymnomyces and *Martellia*	5.9	8.5	2.0	2.1	11.4	0
Geopora	39.1	16.7	31.4	24.5	4.9	12.8
All genera combined	91.7a	82.4a	76.4ab	76.2ab	57.4bc	48.2c

Note: Values with different superscript letters are significantly different ($P < 0.05$) using Tukey's honestly significant difference test. Genera with <5% total frequency are not included.

Table 6. Summary of studies examining the effects of forest management treatments on truffles.

Study	Forest type	Dominant truffles	Biomass response
Luoma et al. 1999	DF	*E. granulatus*, *G. monticola*	MF>OG>MY
North et al. 1997	WH, DF	*E. granulatus*	OG=MF>MY
This study	MC	*E. granulatus*, *R. subcaerulescens*	C=LT>HT
Colgan et al. 1999	DF	*R. vinicolor*	C>VT
Amaranthus et al. 1994	DF	*R. vinicolor,* *R. parksii**	MF>MY
Clarkson and Mills 1994	DF, WF	*Melanogaster* sp., *Hysterangium* sp.	MF>MY
Waters et al. 1994	WF	*Gymnomyces* spp.	C=LT=HT
Waters et al. 1997	WF, RF	*G. monticola*	OG=MF
Lehmkuhl et al. 2004	GF, DF, PP	*G. monticola*, *H. coriaceum*	MF=MY
Smith et al. 2002	DF	*G. monticola*, *H. crassirhachis*	MY=MF>OG
Carey et al. 2002	DF	*R. vinicolor*	HT=LT

Note: DF, Douglas-fir; WH, Western hemlock; MC, mixed conifer; WF, white fir; RF, red fir; GF, grand fir; PP, Ponderosa pine; OG, old growth; MF, mature forest; MY, managed young; C, control; LT, light thin; HT, heavy thin; VT, variable thin.

*Relative abundance of truffles is based on presence or absence data in different treatment stands.

history on truffle biomass have been mixed, with some showing greater biomass in young (30–50 years) than old-growth (>400 years) stands (e.g., Smith et al. 2002) or lower biomass in variable-thinned compared with control stands (e.g., Colgan et al. 1999; Table 6). These differences in biomass may be due to dissimilarities in the dominant truffle taxa collected in each study: where *E. granulatus* or *R. vinicolor* dominated collections, thinning generally reduced truffle biomass, but in studies where *G. monticola* or *Martellia* spp. was dominant, thinning either increased or had no effect on truffle abundance. Notably, *G. monticola* and *M. tuberiformis* were most abundant in mature (60–100 years postdisturbance; Luoma et al. 1991), rotation-age (45–50 years; Smith et al. 2002), or managed young (<30 years; Clarkson and Mills 1994; Smith et al. 2002) compared with old-growth stands (>200 years).

The presence of *E. granulatus* was associated with plots that were thinned (light intensity) but not burned. This species has been associated with thick organic litter layers with a high root density (North and Greenberg 1998) in unburned microsites (North et al. 1997) of mixed stands of western hemlock and Douglas-fir. In this study, burning may have reduced the abundance of *E. granulatus* by reduction or removal of the litter layer. However, *E. granulatus* was not detected in controls, even though these plots had the highest litter depth, tree density, and basal area. *Elaphomyces granulatus* sometimes produces high-biomass clusters of sporocarps (Vogt et al. 1981; Luoma et al. 1991; North et al. 1997), making interpretation of study results problematic (Smith et al. 2002). Similarly, in this study a single light-intensity thinned plot quadrat contained several high biomass clusters of *E. granulatus* that represented 30.2% of the total truffle biomass for all plots in both years. The irregular and patchy distribution of *E. granulatus* in this study may have influenced the probability of detection of this species in control plots.

Both *R. subcaerulescens* and *H. cerebriformis* were negatively associated with plots that were burned, particularly those thinned prior to burning. *Rhizopogon subcaerulescens* has been observed to increase following burning, but only several years (Bruns et al. 2002); possibly production of this species decreases initially following burning then increases after several years. *H. cerebriformis* often is associated with decayed wood (e.g., rotting logs and woody debris; Arora 1986). The volume of logs was reduced in all burn treatments in our study, suggesting that the absence of decayed wood material may have resulted in lower abundance of *H. cerebriformis* in burned compared with unburned plots. Interestingly, *H. cerebriformis* was abundant in both mature and old-growth forest stands that had similar cover of decayed logs and organic soil depth (Waters et al. 1997).

High-intensity management treatments had a greater negative impact on truffle production than low-intensity treatments in our study. Intensive shelterwood thinned plots had lower truffle biomass, frequency, and species richness than less intensive CASPO thinned plots. In addition, plots that were thinned prior to burning had lower truffle frequency and species richness than plots treated with burning alone. These results likely are due to the greater impact that intensive treatments have on multiple stand features associated with truffle production (e.g., tree basal area, canopy cover, litter depth). For instance, plots subjected to thinning followed by burning had a lower litter depth and log volume than those thinned alone (Table 1). Consequently, truffle species that are positively associated with organic litter depth (Amaranthus et al. 1994; North and Greenberg 1998) may be more negatively impacted by thinning followed by burning than burning alone, because thinning adds fuels that increase the intensity and coverage of the fire.

Treatment effects on truffle consumption by *Neotamias speciosus*

Several explanations can potentially explain the reduced frequency and generic richness of truffles consumed by *N. speciosus* in burned, thinned, or thinned followed by burned plots compared with controls. Decreased availability of truffles in thinned or burned plots likely reduced truffle consumption by *N. speciosus* following these treatments. Decreased biomass of decayed logs and other woody debris from thinned followed by burned plots may have reduced the frequency of truffle consumption by *N. speciosus*, since small mammals may use decayed wood as a visual cue for locating truffles (Pyare and Longland 2001*b*). Additionally, animals foraging in areas with low shrub cover (primarily heavy-thin followed by burn plots) may have been at greater predation risk (Carey 1995) and spent more time being vigilant and less time foraging for favored food items (Lima and Valone 1986), such as fruits, seeds, and fungi (Best et al. 1994).

Although this study was conducted in a relatively dry forest type that has a unique stand structure and composition (North et al. 2004), patterns of truffle consumption by chipmunks (*Neotamias* spp.) were consistent with previous work conducted in wet Douglas-fir forests of western Oregon and Washington State. Townsend's chipmunks (*Neotamias townsendii*) consumed more fungal taxa in old-growth than thinned forest stands of southwestern Oregon (Carey et al. 1999). Fungal consumption by *N. townsendii* was reduced in clearcut forest relative to intact or burned forest stands in central Washington State (Gunther et al. 1983). In southern Oregon, the frequency and mean generic richness of truffles consumed by Siskiyou chipmunks (*Neotamias siskiyou* Howell) was greater in control plots than in sites that were thinned followed by burned (McIntire 1984).

Implications for forest management

Current fuel management policies in California's National Forests use a combination of commercial timber harvest, noncommercial fuel reduction thinning, and prescribed burning (Sierra Nevada Forest Plan Amendment 2001). Our results suggest that as the intensity of the treatment increases, truffle frequency, biomass, species richness, and consumption by *N. speciosus* decrease. The shelterwood treatments had the most significant decrease in truffles, possibly because there were few trees remaining to support EMF that produce sporocarps. Additionally, intensive thinning can open canopies and increase the drying of undestory fuels, resulting in increased fire hazard and intensity (van Wagtendonk 1996). However, less intensive treatments may be more consistent with historical conditions and reduce the potential for hot, catastrophic crown fires that can substantially reduce tree basal area and coarse woody debris (e.g., Waters et al. 1997). We are not aware of any studies that have examined truffle abundance shortly after a catastrophic crown fire; however, studies in clearcuts and heavily harvested stands suggest that truffle production is severely reduced with a sharp decline in tree basal area and coarse woody debris (Amaranthus et al. 1994; Clarkson and Mills 1994; States and Gaud 1997). The burn only or light-intensity thin only treatments that retained all large, overstory trees and a tree basal area >45 m^2/ha as well as coarse woody debris in the form of decayed logs (>90 m^3/ha) and litter (>2 cm depth), may provide an EMF legacy important for maintaining some truffle production and speeding dispersal and recolonization of EMF spores. Long-term (>2 years) postburning and thinning data will be necessary to determine the efficacy of these two management practices, whether individually or in combination.

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