TRUFFLE ABUNDANCE IN RECENTLY PRESCRIBED BURNED AND UNBURNED FORESTS IN YOSEMITE NATIONAL PARK: IMPLICATIONS FOR MYCOPHAGOUS MAMMALS

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ABSTRACT

Truffles are an important food resource for wildlife in North American forests, but decades of fire exclusion have altered the availability of this resource. In Yosemite National Park, resource management policies seek to restore essential forest processes such as fire while minimizing adverse ecological impacts that may result from burning decades of accumulated fuels. Burning can impact truffles through heat stress, elimination of soil organic layers, and damage to tree hosts, but these effects may be dependent on time lags between fires and fire frequency. We examined truffle abundance, and species diversity and composition in four paired burned and unburned sites (8 sites total) in Yosemite to determine the short-term effect of fire on truffles and its implications for truffle-consuming mammals. Burned and unburned sites had similar truffle biomass and species richness, but truffle frequency was greater in unburned than burned sites. Truffle species composition was distinctively different between burned and unburned sites, although seven species were found exclusively in both burned and unburned sites. Truffles were positively associated with litter depth in burned and unburned sites, although this association was stronger in burned sites. Prescribed burning may enhance the regional diversity of truffles for mycophagous mammals across the forest landscape without impacting total abundance in Yosemite National Park.

Keywords: ectomycorrhizal fungi, litter depth, prescribed fire, Sierra Nevada, truffles
A diverse and important functional component of forest ecosystems are ectomycorrhizal fungi (EMF), which are required by most temperate forest conifer species for increased water and nutrient uptake (Molina et al. 1992). The EMF fruiting bodies, especially below-ground truffles, form the base of a complex food web in forests (Johnson 1996, North et al. 1997) and are a major part of the diet of many mammals (Fogel and Trappe 1978, Maser et al. 1978). In Sierra Nevada forests, truffles are the primary food of northern flying squirrels (Glaucous sabrinus; Pyare and Longland 2001, Meyer et al. 2005b), which in turn constitute the main prey of California spotted owls (Strix occidentalis occidentalis) (Williams et al. 1992). Truffles also comprise a frequent 92 % of the diet of fisher (Martes pennanti) and 44 % of the diet of American marten (Martes Americana), key management species in Sierra Nevada forests (Zielinski and Duncan 2004). Viable fungal spores pass through the digestive system of mycophagous (i.e., fungus consuming) mammals and are dispersed to new soil patches where they facilitate conifer succession (Terwilliger and Pastor 1999) and promote EMF diversity (Johnson 1996, Izzo et al. 2005).

Prescribed burning can reduce both EMF (Stendell et al. 1999, Smith et al. 2005) and truffle abundance, diversity, and consumption by small mammals (Meyer et al. 2005a) in the short-term (<2 years). Truffle abundance returns to pre-burn levels nine years after burning, although changes in species composition often persist for more than a decade (Waters et al. 1994). The abundance of EMF and richness of truffle species peaks in areas with well-developed surface litter and organic material (Amaranthus et al. 1994, Stendell et al. 1999, Claridge et al. 2000, Lehmkuhl et al. 2004, Smith et al. 2005) and a higher density of large-diameter trees with greater canopy closure (States and Gaud 1997, Lehmkuhl et al. 2004). Consequently, forest stands unharvested and unburned for long periods (>100 years) often have greater truffle abundance than recently harvested and burned stands (Meyer et al. 2005). Burning can directly impact truffle-producing EMF through heat stress (Dahlberg et al. 2001, Smith et al. 2005) and indirectly by damaging tree hosts and impacting tree root biomass (Stendell et al. 1999, Smith et al. 2005).

Yosemite National Park, in the central Sierra Nevada of California, contains a highly diverse flora and fauna (Davis and Stoms 1996, Burns et al. 2003) that are historically adapted to fire (Shaffer and Laudenslayer 2006, van Wagtendonk and Fites-Kaufman 2006). For the past three decades, Yosemite has maintained an active fire management program using prescribed and managed wildland fires, particularly in mixed-conifer forests of the western slope (National Park Service 2004). This management policy has created a heterogeneous landscape of burned and unburned stands throughout Yosemite’s mixed-conifer zone, and may increase biotic diversity across the forest landscape (Martin and Sapsis 1992, Huntzinger 2003). However, the effects of this management program on truffles and the implications for forest food webs have not been previously examined.

Our research objective was to determine the effects of recent prescribed burning on patterns of truffle abundance (frequency, biomass), diversity (species richness), and species composition in Yosemite National
Park. We define recent as equal to or less than eight years, which is the minimum median fire return interval in mixed-conifer forests of the Sierra Nevada (Skinner and Chang 1996). Specifically, we examined three hypotheses concerning the effect of fire on truffles: 1) truffle abundance and diversity are lower in recently burned sites compared to sites unburned for >75 years; 2) truffle abundance and diversity are positively associated with organic litter depth and tree (>30 cm dbh) proximity in recently burned sites, but are not associated with these variables in unburned sites; and 3) recently burned sites have a distinct species composition compared to unburned sites.

METHODS

Study Area and Design

We selected four paired research sites at four separate prescribed burn locations in the southwest corner of Yosemite National Park: Yosemite West (burned in 1998), Turner Ridge (burned in 1999), Big Creek (burned in 2005), and Mariposa Grove (burned in 1999 and 2002). Each burn site was in a separate watershed. Within each site, we selected a burned and unburned sample location using a random set of locations defined by the Yosemite National Park fire management vegetation map (National Park Service 2004). Burned sites were selected based on the following criteria: 1) prescribed burned in the past eight years, 2) burned site ≥5 ha in size, 3) located between 1300 m and 1800 m elevation (primary elevation range of mixed-conifer forest in Yosemite), and 4) located >200 m from a road and >100 m inside a burned stand (to minimize edge effects). We selected paired unburned sites that were located within 500 m from burned areas at the same elevation, aspect, slope, and forest type, and where fire has been absent for >75 years (75 years is the extent of the Yosemite National Park fire history record at the onset of this study; National Park Service 2004). All sample sites burned at low severity with the exception of 7 % of sample sites that burned at moderate severity, especially in the Mariposa Grove site. The frequency of tree species at all sites included 41 % white fir (Abies concolor), 20 % incense cedar (Calocedrus decurrens), 17 % sugar pine (Pinus lambertiana), 13 % ponderosa pine (Pinus ponderosa), 4 % Jeffery pine (P. jeffreyi), 4 % black oak (Quercus kelloggii), and 1 % Pacific dogwood (Cornus nuttallii). Common shrubs included Arctostaphylos patula, Ceanothus cordulatus, Ceanothus integerrimus, Chamaebatia foliolaris, Chrysolepis sempervirens, Corylus cornuta californica, Cornus nuttallii, Quercus berberidifolia, and Ribes roezlii. Average canopy closure was 78 % in both burned and unburned sites (based on digital hemispherical photos [Jennings et al. 1999]).

Truffle and Stand Measurements

Beginning at a random point in our study area, we placed 25 4 m$^2$ circular quadrats every 10 m in a five by five grid at each study site. From June 14 through July 6, 2006, (Turner Ridge, Yosemite West, Mariposa Grove) and June 10 through June 30, 2007 (Big Creek), we sampled quadrats for truffles by searching through the organic litter, humus, and upper 5 cm of mineral soil (5 cm to 20 cm total depth) using a four-tined rake, yielding a total sample area of 800 m$^2$ (4 paired sites × 100 m$^2$). All truffles were collected and counted, placed in wax bags, dried for 24 h at 60 °C, weighed to the nearest 0.01 g, and identified to species. We used truffle collections to estimate frequency, biomass, and species richness of truffles in burned and unburned sites. All truffle voucher specimens were stored and catalogued in the USDA Forest Service Sierra Nevada Research Center in Davis, California,
USA, or in the Yosemite Museum, Yosemite National Park, California, USA.

Based on our review of the truffle literature for dry interior forests (States and Gaud 1997, Waters et al. 1997, North 2002, Lehmkuhl et al. 2004, Meyer and North 2005, Meyer et al. 2005a), we selected and measured the following microsite variables in each 4 m² quadrat: distance to nearest tree (>30 cm dbh), litter depth (includes litter and humus layers), distance to nearest shrub (>30 cm height), and char height. We measured distance to the nearest tree from the center of each quadrat. To measure litter depth, we dug three shallow pits at the edge of each quadrat (at 0˚, 120˚, and 240˚ from the center point) and took two depth measurements at each pit of the combined organic litter and humus layers. We measured char height on all sampled nearest trees to estimate fire intensity or potential heat stress (Borchert et al. 2002). We also estimated canopy closure at the center of ten randomly chosen quadrats at each site using hemispherical photographs that were analyzed using Gap Light Analyzer 2.0 software.

Statistical Analysis

We used dependent t-tests to examine the effect of burning on truffle frequency, biomass, and species richness, as well as litter depth, tree distance, shrub distance, and canopy closure. We also conducted these dependent t-tests to examine the effect of burning on truffle and forest variables using only data from sites sampled in 2006 (i.e., Turner Ridge, Mariposa Grove, and Yosemite West). The results that included all sites were similar to the analyses that excluded Big Creek (2007); therefore, we only present the former results. We evaluated data for normality with the Kolmogorov-Smirnov test and for homoscedasticity with Levene’s test. We used logistic regression to relate microsite variables (i.e., litter depth, tree distance, shrub distance) to truffle occurrence. To reduce model over-fitting, we only included significant \( P < 0.10 \) predictors in our logistic regression analyses, and tested for multicollinearity by examining potential correlation between independent factors in each model. For each significant parameter in the logistic regression model, we calculated odds-ratios and their confidence intervals based on a Quasi-Newton estimation method in Statistica 6.1 (StatSoft, Tulsa, Oklahoma, USA). We interpreted the odds-ratio estimates as the odds of truffle occurrence given a one unit change in a microsite parameter after being adjusted for the effects of other parameters in the model. We used a sensitivity analysis of each treatment type to evaluate the performance of the reduced logistic regression model and to assess model accuracy in successfully predicting occurrence of truffles among sample points (Hosmer and Lemeshow 2000). All statistics were conducted with Statistica 6.1 and an \( \alpha \) level of 0.10.

RESULTS

A total of 47 (40.83 g) and 63 (71.59 g) truffles were collected from burned and unburned sites, respectively. The greatest truffle biomass was collected from Yosemite West (4.45 kg ha\(^{-1}\)), followed by Turner Ridge (3.76 kg ha\(^{-1}\)), Mariposa Grove (1.73 kg ha\(^{-1}\)), and Big Creek (1.33 kg ha\(^{-1}\)). Truffle species richness was greatest at Turner Ridge (15 species), followed by Mariposa Grove (8 species), Yosemite West (7 species), and Big Creek (4 species). The total cumulative richness was 15 species at both burned and unburned sites; total richness among all sites was 22 species. Truffle species richness \( t = -1.124, df = 3, P = 0.343 \) and biomass \( t = -1.216, df = 3, P = 0.311 \) were similar between burned and unburned areas, but truffle frequency was greater in unburned (29 ± 6 % [SE]) than burned areas (17 ± 8 %; \( t = -5.196, df = 3, P = 0.014 \); Table 1). Truffle species composition was
distinctively different between burned and unburned sites, although seven species were found exclusively in both burned and unburned sites (Table 2). Ten and twelve truffle species were more abundant in burned and unburned areas, respectively.

Litter depth ($t = -3.416$, df = 3, $P = 0.076$) was greater in unburned than burned sites, but tree distance ($t = 0.065$, df = 3, $P = 0.811$), shrub distance ($t = -0.800$, df = 3, $P = 0.507$), and canopy closure ($t = 0.179$, df = 3, $P = 0.869$) were similar between treatments (Table 1). Char height was different among burned sites ($F_{1,4} = 3.260$, $P = 0.046$), and was greater at Mariposa Grove than at Yosemite West (Bonferroni: $P = 0.043$). The occurrence of truffles was positively associated with litter depth in burned and unburned sites (although this association was stronger in burned sites) and negatively associated with tree distance in burned sites (Table 3). The selected logistic regression models correctly classified 77 % and 89 % (burned sites) and 45 % and 66 % (unburned) of truffle-present and truffle-absent stations, respectively.

### Table 1. Truffle abundance and diversity, and mean values of microsite variables at four burned and four unburned paired sites in Yosemite National Park, California. Yosemite West was burned in 1998, Turner Ridge in 1999, Big Creek in 2005, and Mariposa Grove in 1999 and 2002.

| Site and Treatment | Frequency (%) | Species Richness | Biomass (kg ha$^{-1}$) | Litter depth (cm) | Distance to tree (m)$^a$ | Canopy closure (%) | Char height (m) |
|-------------------|---------------|------------------|------------------------|-------------------|--------------------------|-------------------|----------------|
| Yosemite West Burn | 24            | 5                | 1.69                   | 2.0               | 2.7                      | 78                | 1.2            |
| Yosemite West No Burn | 32        | 4                | 2.76                   | 6.3               | 2.9                      | 75                |                |
| Turner Ridge Burn  | 36            | 10               | 2.37                   | 4.4               | 3.3                      | 82                | 1.8            |
| Turner Ridge No Burn | 44        | 9                | 1.39                   | 6.4               | 2.6                      | 79                |                |
| Mariposa Grove Burn | 8             | 2                | 0.05                   | 1.3               | 3.8                      | 76                | 2.9            |
| Mariposa Grove No Burn | 24        | 8                | 1.68                   | 7.5               | 7.5                      | 81                |                |
| Big Creek Burn      | 0             | 0                | 0.00                   | 1.1               | 2.4                      | 77                | 1.1            |
| Big Creek No Burn   | 33            | 4                | 1.33                   | 7.6               | 2.3                      | 75                |                |

$^a$Distance to nearest tree (>30 cm dbh).

### Table 2. Biomass of truffle species at 4 burned and 4 unburned sites in Yosemite National Park, California (June and July 2006, 2007).

| Species                  | Biomass (kg ha$^{-1}$) |
|--------------------------|------------------------|
| $Alpova$ trappei         | 0.462                  |
| $Balsamia$ magnata       | 0.028                  |
| $Cortinarius$ verrucisporus | 0.055               |
| $Elaphomyces$ granulatus | 0                       |
| $Endogone$ lactiflua     | 0.221                  |
| $Gastroboletus$ ruber    | 0.209                  |
| $Gautieria$ monticola    | 0.321                  |
| $Genabea$ cerebriformis  | 0.006                  |
| $Gilkeya$ compacta       | 0.002                  |
| $Geopora$ cooperi        | 0.595                  |
| $Gymnomyces$ brunescens  | 0.343                  |
| $Hydnotrya$ cerebriformis| 0.129                  |
| $Hydnotrya$ variifromis  | 0.282                  |
| $Hysterangium$ coriaceum | 0.088                  |
| $Leucogaster$ cribrinus  | 0.103                  |
| $Leucophleps$ spinispora | 0.304                  |
| $Macowanites$ luteolus   | 0.365                  |
| $Pyrenogaster$ atroblea  | 0.025                  |
| $Radiigera$ taylorii     | 0.432                  |
| $Rhizopogon$ ponderosus  | 1.152                  |
| $Rhizopogon$ subcaeruleus | 0.635                |
| $Truncocolumella$ citrine| 0.077                  |
| Unidentified (immature)  | 0.013                  |
Our study was conducted with limited sampling over one season (summer) and four sites in a single region and forest type of Yosemite National Park, and we do not know how applicable our results are to a broader range of forests in the Sierra Nevada. In our study, sites that burned eight years before our sampling (i.e., Turner Ridge, Yosemite West) had similar truffle biomass, frequency, and richness as nearby unburned stands. However, sites burned more recently (i.e., Mariposa Grove, 4 yr; Big Creek, 2 yr) had lower truffle abundance and richness compared to nearby unburned sites (Table 2). These results suggest that the time since burning is important in determining fire effects on truffles. The two sites burned eight years before sampling had more time for ectomycorrhizal fungi communities to reestablish following burning than the two sites burned 2 yr to 4 yr ago. Additionally, unlike the sites burned more recently, sites burned eight years before sampling had thicker litter layers, and these thicker layers were positively associated with truffles across all burned sites. In mixed-fir forests of northeastern California, the biomass and frequency of truffles did not differ between prescribed burned and unburned sites, nine years after burning (Waters et al. 1994). In contrast, the frequency, biomass, and species richness of truffles were greater in unburned mixed-conifer stands than stands burned one year to two years before sampling in the southern Sierra Nevada (Meyer et al. 2005a).

Burning can influence several microsite variables associated with truffle production, including litter depth (Waters et al. 1994, North and Greenberg 1998) and tree density (Kobziar et al. 2007). Decaying woody debris in the form of organic litter is an important reservoir 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, Meyer and North 2005). Reduced decayed woody debris following burning may have decreased the abundance of truffles in our burned sites compared to unburned sites. In mixed-conifer forests of the southern Sierra Nevada, truffles were generally greater in unburned stands with thicker litter layers than burned or unburned stands with thinner litter layers (Meyer et al. 2005a). Interestingly, the probability of capturing truffle-consuming northern flying squirrel (Glaucomys sabrinus) was greater as litter depth increased in burned mixed conifer stands of the southern Sierra Nevada (Meyer et al. 2007).

The negative association of truffles with tree distance in burned sites may be a result of increased fungal fruiting near large trees. In unburned Douglas-fir (Pseudotsuga menziesii) stands of western Oregon, truffle abundance peaks at 2 m from the base of a tree where roots and mycorrhizae may form dense clusters and give rise to enhanced truffle production (Fogel 1976). Similarly, in our burned but not our unburned sites, the probability of truffle occurrence increased with proximity to a large-diameter tree and was greatest at a tree distance of <2.5 m.

| Treatment | Independent variable | Estimate (SE) | $\chi^2$ | Odds ratio$^a$ (95 % CI) | $P$ |
|-----------|---------------------|--------------|--------|---------------------|-----|
| Burned    | Litter depth        | 0.96 (0.37)  | 6.901  | 2.6 (1.2 to 5.5)    | 0.009 |
|           | Tree distance       | -0.96 (0.44) | 4.705  | 0.4 (0.2 to 0.9)    | 0.030 |
| Unburned  | Litter depth        | 0.21 (0.12)  | 2.885  | 1.2 (1.0 to 1.7)    | 0.089 |

$^a$ Effect of a 1 cm increase in litter depth or 1 m distance to the nearest tree on the probability of truffle occurrence.

**DISCUSSION**

Table 3. Results of logistic regression models relating microsite variables with the occurrence of truffles in Yosemite National Park, California (2006).
Several of the most abundant truffles at our study sites included *Rhizopogon subcaerulescens*, *Gautieria monticola*, and *Geopora cooperi*. These species had greater overall biomass in the unburned sites than burned sites, and were notably reduced in sites burned two years to four years before sampling. These three species also had greater overall biomass in unburned stands than prescribed burned stands in the southern Sierra Nevada (Meyer et al. 2005a). These genera were among the most frequently occurring truffle genera in northern flying squirrel diets in the southern Sierra Nevada (Meyer et al. 2005b) and in Yosemite National Park (*Rhizopogon* and *Gautieria* only; M. Meyer, University of California, Merced, unpublished data). The reduction of frequently consumed truffle genera within burned sites could potentially diminish foraging habitat quality for mycophagous small mammals (Meyer et al. 2005a), decrease relative abundance of northern flying squirrels in burned compared to unburned stands (Roberts 2008), or cause flying squirrels to forage more selectively in patches with greater probability of truffle occurrence (i.e., patches with thicker litter; Meyer et al. 2007).

A primary goal of Yosemite National Park's fire management program is to reduce fuel levels and restore fire-dependent ecosystem processes and biodiversity (National Park Service 2004). To meet the goal of enhancing the biodiversity of truffle-producing EMF and the wildlife species dependent on these taxa, we recommend: 1) the continuation of active prescribed burning programs in Yosemite National Park to enhance habitat quality for wildlife and promote key ecosystem processes, 2) prescribed fire return intervals of ≥8 yr, when feasible, to allow adequate time for truffle abundance to rebound from burning in mixed-conifer stands, and 3) managing fire for heterogeneous fuel consumption so that patches of litter (>3 cm depth) and overstory host trees are retained. Such recommendations may substantially benefit truffle-producing fungi and the mycophagous mammals dependent on these key forest ecosystem components in Yosemite National Park.

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LITERATURE CITED

Amaranthus, M., J.M. Trappe, L. Bednar, and D. Arthur. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research 24: 2157-2165.
Borchert, M., D. Schreiner, T. Knowd, and T. Plumb. 2002. Predicting postfire survival in Coulter pine (*Pinus coulteri*) and gray pine (*Pinus sabiniana*) after wildfire in central California. Western Journal of Applied Forestry 17: 134-138.
Burns, C.E., K.M. Johnson, and O.J. Schmitz. 2003. Global climate change and mammalian species diversity in U.S. national parks. Proceedings of the National Academy of Sciences 100: 11474-11477.

Claridge, A.W., S.C. Barry, S.J. Cork, and J.M. Trappe. 2000. Diversity and habitat relationships of hypogeous fungi. II. Factors influencing the occurrence and number of taxa. Biodiversity and Conservation 9: 175-199.

Clarkson, D.A., and L.S. Mills. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. Northwest Science 68: 259-265.

Dahlberg, A., J. Schimmel, A.F.S. Taylor, and H. Johannesson. 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. Biological Conservation 100: 151-161.

Davis, F.W., and D.M. Stoms. 1996. Sierra vegetation: A gap analysis. Pages 671-690 in: D.C. Erman, editor. Sierra Nevada Ecosystem Project: Final Report to Congress, Volume 2, University of California, Davis, Wildland Resources Center Report 37.

Fogel, R. 1976. Ecological studies of hypogeous fungi. II Sporocarp phenology in western Oregon, USA, Douglas-fir stand. Canadian Journal of Botany 54: 1152-1162.

Fogel, R., and J.M. Trappe. 1978. Fungus consumption (mycophagy) by small mammals. Northwest Science 52: 1-31.

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression. Wiley Press, New York, New York, USA.

Huntzinger, M. 2003. Effects of fire management practices on butterfly diversity in the forested western United States. Biological Conservation 113: 1-12.

Izzo, A.D., M. Meyer, J.M. Trappe, M. North, and T.D. Bruns. 2005. Hypogeous ectomycorrhizal fungal species on roots and in small mammal diet in a mixed-conifer forest. Forest Science 5: 243-254.

Jennings, S.B., N.D. Brown, and D. Sheil. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72: 59-73.

Johnson, C.N. 1996. Interactions between mammals and ectomycorrhizal fungi. Trends in Ecology and Evolution 1: 503-507.

Kobziar, L., J. Moghaddas, and S.L. Stephens. 2007. Tree mortality patterns following prescribed fires in a mixed conifer forest. Canadian Journal of Forest Research 36: 3222-3238.

Lehmkuhl, J.F., L.E. Gould, E. Cazares, and D.R. Hosford. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management 200: 49-65.

Martin, R.E., and D.B. Sapsis. 1992. Fires as agents of biodiversity: pryodiversity promotes biodiversity. Pages 150-157 in: R.R. Harris, D.E. Erman, and H.M. Kerner, editors. Proceedings of the symposium on biodiveristy in northwestern California. University of California, Berkeley, Wildland Resources Center Report 29.

Maser, C., J.M. Trappe, and R.A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59: 799-809.

Meyer, M.D., and M.P. North. 2005. Truffle abundance in riparian and upland mixed-conifer forest of California’s southern Sierra Nevada. Canadian Journal of Botany 83: 1015-1020.

Meyer, M.D., M. North, and D.A. Kelt. 2005a. Short-term effects of fire and forest thinning on truffle abundance and consumption in the southern Sierra Nevada of California. Canadian Journal of Forest Research 35: 1061-1070.
Meyer, M.D., D.A. Kelt, and M. North. 2005b. Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada. Canadian Journal of Zoology 83: 1581-1589.

Meyer, M.D., D.A. Kelt, and M.P. North. 2007. Microhabitat associations of northern flying squirrels in burned and thinned forest stands of the Sierra Nevada. American Midland Naturalist 157: 202-211.

Molina, R., H.B. Massicotte, and J.M. Trappe. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. Pages 357-423 in: M. Allen, editor. Mycorrhizal functioning: an integrative plant-fungal process. Chapman Hall, New York, New York, USA.

National Park Service. 2004. Yosemite fire management plan, final version. 2004. Yosemite National Park, El Portal, California, USA.

North, M. 2002. Seasonality and abundance of truffles from oak woodlands to red fir forests. Pages 91-98 in: J. Verner, editor. Proceedings of a symposium on the Kings River sustainable forest ecosystems project: progress and current status. USDA Forest Service General Technical Report PSW-GTR-183.

North, M., and J. Greenberg. 1998. Stand conditions associated with truffle abundance in western hemlock/Douglas-fir forests. Forest Ecology and Management 112: 56-66.

North, M., J. Trappe, and J. Franklin. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology 78: 1543-1554.

Pyare, S., and W.S. Longland. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82: 681-689.

Roberts, S. L. 2008. The effects of fire on California spotted owls and their mammalian prey in the central Sierra Nevada, California. Dissertation, University of California, Davis, USA.

Shaffer, K.E., and W.F. Laudenslayer, Jr. 2006. Fire and animal interactions. Pages 118-144 in: N.G. Sugihara, J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California’s ecosystems. University of California Press, Berkeley, California, USA.

Skinner C.N., and C. Chang. 1996. Fire regimes, past and present. Pages 1041-1070 in: D.C. Erman, editor. Sierra Nevada Ecosystem Project: Final Report to Congress, Volume II. University of California, Davis, Wildland Resources Center Report 37.

Smith, J.E., D. McKay, G. Brenner, J. McIver, and J.W. Spatafora. 2005. Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest. Journal of Applied Ecology 42: 526-535.

States, J.S., and W.S. Gaud. 1997. Ecology of hypogeous fungi associated with ponderosa pine. I. Patterns of distribution and sporocarp production in some Arizona forests. Mycologia 89: 712-721.

Stendell, E.R., T.R. Horton, and T.D. Bruns. 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. Mycological Research 103: 1353-1359.

Terwilliger, J., and J. Pastor. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos 85: 83-94.

van Wagendonk, J.W., J. Fites-Kaufman. 2006. Sierra Nevada bioregion. Pages 264-294 in: N.G. Sugihara, J.W. van Wagendonk, J. Fites-Kaufman, K.E. Shaffer, and A.E. Thode, editors. Fire in California’s ecosystems. University of California Press, Berkeley, USA.
Waters, J.R., K.S. McKelvey, C. Zabel, and W.W. Oliver. 1994. The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi. Canadian Journal of Forest Research 24: 1516-1522.

Waters, J.R., K.S. McKelvey, D.L. Luoma, and C.J. Zabel. 1997. Truffle production in old-growth and mature fir stands in northeastern California. Forest Ecology and Management 96: 155-166.

Williams, D.F., J. Verner, H.F. Sakai, and J.R. Waters. 1992. General biology of the major prey species of the California spotted owl. Pages 207-221 in: J. Verner, K.S. McKelvey, B.R. Noon, R.J. Gutiérrez, G.I. Gould, Jr., and T.W. Beck, editors. The California spotted owl: a technical assessment of its current status. USDA Forest Service General Technical Report PSW-GTR-133.

Zielinski, W.J., and N.P. Duncan. 2004. Diets of sympatric populations of American martens (Martes americana) and fishers (Martes pennanti) in California. Journal of Mammalogy 85: 470-477.