# Truffle abundance in riparian and upland mixed-conifer forest of California's southern Sierra Nevada

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**Abstract:** We compared the abundance, diversity, and composition of truffles in riparian and upland areas within a mixed-conifer forest of the Sierra Nevada of California. We sampled for truffles in a single watershed over two seasons (spring and summer) and 4 years to determine whether truffles were more abundant and diverse in riparian than upland sites in old-growth, mixed-conifer forest. Truffle frequency, biomass, and species richness were greater in riparian sites than in upland sites in both spring and summer samples. Species composition of truffles also was different between sites, with nine and one species found exclusively in riparian and upland sites, respectively. Distance between the center of truffle plots to logs and trees was lower and soil moisture was greater in riparian sites compared with upland sites, suggesting that log density, tree proximity, and soil moisture may influence truffle production in these habitats. Our study underscores the importance of riparian areas for truffles, a primary food source for northern flying squirrels (*Glaucomys sabrinus*) in the Sierra Nevada of California.

*Key words:* truffles, riparian, Sierra Nevada.

**Résumé :** Les auteurs ont comparé l'abondance, la diversité et la composition des truffes, dans les portions ripariennes et plus élevées d'une forêt coniférienne mixte de la Sierra Nevada, en Californie. Pour localiser les truffes, les auteurs ont effectué les échantillonnages dans un seul bassin versant, au cours de deux saisons (printemps et été), pendant quatre ans, le but étant de déterminer si les truffes sont plus abondantes et plus diversifiées près des rives que sur les terrains plus élevés, dans cette forêt coniférienne mixte surannée. La fréquence, la biomasse et la richesse en espèces est plus grande près des rives que sur les terrains plus élevés, au printemps aussi bien qu'en été. La composition en espèces de truffes diffère également selon les sites, avec neuf et un espèces, localisées exclusivement près des rives et sur les terrains élevés, respectivement. La distance entre le centre des colonies de truffes, par rapport aux morceaux de bois et aux arbres, est plus faible, et l'humidité du sol supérieure, dans les sites riverains comparativement aux sites élevés, ce qui suggère que la densité du bois mort, la proximité des arbres, et l'humidité du sol peuvent influencer la production des truffes dans ces habitats. Les études sous-estiment l'importance des sites ripariens pour les truffes, une source de nourriture de base pour le grand polatouche (*Glaucomys sabrinus*), dans le Sierra Nevada, en Californie.

*Mots clés :* truffes, riparien, Sierra Nevada.

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## Introduction

Mychorrizal fungi are important components in forest ecosystems; they facilitate water and nutrient uptake in forest trees (Molina et al. 1992), reduce the incidence of forest pathogens (Marx 1972), and provide a carbon source for soil microbes, invertebrates, and other organisms (Ingham and Molina 1991). The sporocarps of these fungi are a major food source for many mammals in temperate forests throughout the world (Fogel and Trappe 1978; Johnson 1996). Mychorrizal fungi form sporocarps that mature above- and below-ground, known as epigeous and hypogeous fungi, respectively. Hypogeous fungal sporocarps ("truffles") are particularly important to the diet of fungal specialists, such as the northern flying squirrel (*Glaucomys sabrinus* Shaw) in North America (Maser et al. 1978) and the northern bettong (*Bettongia tropica* Wakefield) in northeastern Australia (Vernes et al. 2001).

Many factors at different spatial scales can influence the abundance of truffles in forests. Within a forest stand, truffle abundance varies with presence of decaying logs or litter (Amaranthus et al. 1994; North and Greenberg 1998), canopy cover (States and Gaud 1997), and density of trees (Colgan et al. 1999). Among stands, truffle abundance changes with forest stand structure (North et al. 1997, Smith et al. 2002), composition (Loeb et al. 2000), and age (Vogt et al. 1981; Luoma et al. 1991). Across landscape or regional scales, truffle production varies along elevation (North 2002) and moisture gradients (O'Dell et al. 1999; Claridge et al. 1999). Only two studies have examined truffle abundance in drier interior forests of western North

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America, and both have suggested moisture may limit truffle abundance seasonally (States and Gaud 1997) or locally (Lehmkuhl et al. 2004).

Riparian areas surrounding perennial streams have a more moderate microclimate (Chen et al. 1999) and higher soil moisture, and support a more productive and diverse assemblage of plant and animal species than nearby non-riparian areas (upland; McComb et al. 1993; Gomez and Anthony 1998; Waters et al. 2001). However, little is known about the importance of riparian habitat for fungi, particularly for truffles. Both epigeous and hypogeous sporocarp production has been positively correlated with increased moisture at larger landscape scales (e.g., O'Dell et al. 1999; Lehmkuhl et al. 2004), but within stand differences between riparian and upland forest have not been examined.

In an earlier study of northern flying squirrel habitat use at the Teakettle Experimental Forest, a location near the southern extent of the squirrel's range, we found the squirrels to be strongly associated with riparian habitat (Meyer 2003). In this study our goal was to examine the importance of riparian areas for the abundance and richness of truffles in a mixed-conifer forest of the Sierra Nevada. We compared truffle production in riparian and upland habitats to test whether the frequency, biomass, and species richness of truffles differ by habitat or season. We also evaluated the importance of stand variables associated with truffle production between riparian and upland sites.

## Materials and methods

### Study area

This study was conducted at Teakettle Experimental Forest, a 1300-ha, mixed-conifer forest in the southern Sierra Nevada, Fresno Co., California, USA. Teakettle is at 1800–2400 m elevation and characterized by a strongly Mediterranean-influenced montane climate, with hot, dry summers and precipitation that falls almost exclusively as snow during winter (Major 1990). Average annual precipitation is 110 cm at 2100 m, and average summer (June–August) rainfall during this study (2000–2004) was 0.3 ± 0.2 cm. Dominant forest trees included white fir (*Abies concolor* [Gord & Glend.] Lind.), red fir (*Abies magnifica* A. Murray), sugar pine (*Pinus lambertiana* Douglas), Jeffrey pine (*Pinus jeffreyi* Balfour), and incense cedar (*Calocedrus decurrens* [Torrey] Florin). Our study site focused on a 2.4 km stretch of Teakettle Creek's main fork and tributaries within the Teakettle Experimental Forest that was relatively homogenous with respect to stand structure and composition. Teakettle forest is an unlogged, old growth forest characterized by a multilayered canopy and numerous large (>100 cm diameter at breast height (dbh)) trees, snags, and decayed logs (North et al. 2002). Creek width along the main fork and tributaries averaged 2.4 ± 0.2 (SE) m during June–August 2001 and 2002.

### Truffle and vegetation sampling

At our study site, twenty-five 4-$m^2$ circular quadrats were placed every 20 m along a 480 m transect that followed a perennial creek. Another parallel transect was placed in an adjacent upland stand, 100 m from the creek transect. Initial placement of transects along a drainage was established at a random point in the study area bordering Teakettle creek. From 12 to 23 June and 2 to 16 August of 2000–2002 and 2004, we sampled quadrats for truffles by searching through the litter, humus, and upper 5 cm of mineral soil using a four-tined rake, yielding a total sample area of 200 $m^2 \cdot year^{-1}$ (2 seasons × 100 $m^2$) or 800 $m^2$ for all years (2 seasons × 4 years × 100 $m^2$). We avoided sampling in the same plot location from previous years of sampling (2000–2002). 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. We used truffle collections to estimate frequency, biomass, and species richness of truffles in riparian and upland stands. All truffle voucher specimens were stored and catalogued in the USDA Forest Service Sierra Nevada Research Center Herbarium in Davis, California.

We examined the peridium, gleba, columella, and microscopic features of spores of fresh specimens, reinflated tissues with 3% potassium hydroxide, and used Melzer's reagent (I, K, and chloral hydrate; Castellano et al. 1989) to characterize dextrinoid (reddish brown) and amyloid (blue-black) reactions. We used keys by Smith (1966), Smith and Smith (1973), Smith and Zeller (1966), and Arora (1986) to identify species. We used the taxonomic classification system of Bidartondo and Bruns (2002) to classify species of *Rhizopogon*. 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). Following Waters et al. (1997), we grouped secotioid fungi (produces epigeous sporocarps that remain closed; *Hymenogaster*, *Martellia*, and *Macowanites*) with truffles in fungal collections, because these taxa are mycorrhizal and primarily producers of subterranean fruiting bodies.

Surveying the literature for associations between forest structure and truffle abundance (Fogel 1976; Luoma et al. 1991; Amaranthus et al. 1994; Clarkson and Mills 1994; States and Gaud 1997; Waters et al. 1997; North and Greenberg 1998; Lehmkuhl et al. 2004), we measured the following stand variables in each 4-$m^2$ quadrat: canopy cover, distance to nearest tree (>30 cm dbh), litter depth, distance to nearest shrub (>1 m height), and distance to nearest log (>20 cm diameter and >2 m in length; an effort to distinguish large logs from finer fuels accumulated from fire suppression; M. Meyer, personal observation). Measurement distance to the nearest log and tree were taken from the center of each quadrat. Litter depth was measured by digging three shallow pits at the edge of each quadrat (at 0°, 120°, and 240°) and taking two depth measurements of the combined litter and humus layers. Canopy cover was estimated at the center of each quadrat using hemispherical photographs that were analyzed using Gap Light Analyzer 2.0 (Simon Fraser University, Burnaby, British Columbia, Canada) software. We also measured volumetric soil water content for the 0–15 cm layer of riparian and upland stands using time domain reflectometry (model No. 1502C, Tektronix Inc., Beaverton, Oregon, USA; Gray and Spies 1995). Time domain reflectometry was measured twice in June and August 2002 (four total per station) at a subset of 10 sample stations next to (<10 m) truffle plots.

### Statistical analysis

All variables were evaluated for normality with the

Kolmogorov–Smirnov test and for homoscedasticity with Levene's test. Soil volumetric water content was log-transformed to meet the assumption of homoscedasticity. All statistics were conducted with Statistica 6.1 (StatSoft Inc., Tulsa, Oklahoma, USA) and an $\alpha$ level of 0.05. We used a multivariate analysis of variance (MANOVA) and two-way analysis of variance (ANOVA) to test for the effect of habitat (riparian, upland) and season (spring, summer) on truffle frequency, biomass, and species richness. Since each of these dependent variables did not differ among years ($P > 0.10$), we pooled truffle data from 2000 to 2002 and 2004. We used ANOVAs with a Bonferroni-adjusted experiment-wise error rate to examine significant differences between stand structure variables in riparian and upland areas in each watershed. We used Pearson's product-moment correlation to examine the association between rainfall from June to August and truffle biomass (June and August collections pooled) in riparian and upland stands. For this test, we used an $\alpha$ level of 0.10.

## Results

Riparian habitat had significantly greater percentage soil moisture than upland habitat in June and August (1.7 and 2.3 times greater, respectively). The distance of logs and live trees was significantly closer to the center of truffle plots in riparian areas (2.3 and 5.0 m, respectively) than in upland sites (3.1 and 7.4 m, respectively; Table 1). We collected a total of 313 and 76 truffles from riparian and upland areas, respectively. Total species richness of truffles ($n = 19$) was greater in riparian ($n = 18$) than upland areas ($n = 10$). Comparing spring and summer samples, the frequency of truffles was 2.8 and 3.2 times greater, biomass was 2.9 and 4.0 times greater, and species richness was 3.7 and 3.3 times greater in riparian than upland quadrats, respectively, (all differences were significant; Tables 2 and 3). Truffle frequency differed significantly between seasons (1.7 and 2.0 times greater in spring than summer in riparian and upland sites, respectively), and there was no significant interaction between habitat and season. Nearly half (53%) of all truffle species were rarely encountered and had a frequency of occurrence of 1% or less in both riparian and upland sites (Table 4). Riparian and upland sites had similar truffle species composition, although nine species were found exclusively in riparian plots, only one species (*Hymenogaster subolivaceus*) was found exclusively in upland areas (Table 4). Eight out of ten species that occurred in both sites had greater biomass in riparian than upland habitat. Across sites, *Rhizopogon ellenae* A.H. Smith had the greatest biomass followed by *Hydnotrya cerebriformis* Harkn. and *Elaphomyces granulatus* Fr. Truffle biomass was positively correlated with June–August rainfall in upland ($r^2 = 0.811$, $P = 0.099$) but not riparian ($r^2 = 0.001$, $P = 0.956$) sites.

**Table 1.** Means ± 95% CI for stand variables in riparian and upland sample locations at the Teakettle Experimental Forest (Fresno Co., California).

| Variable | Riparian | Upland |
|---|---|---|
| Litter depth (cm) | 3.1±0.2 | 2.4±0.2 |
| Soil volumetric water content (%) | | |
| June | 21.6±3.3* | 12.7±0.8* |
| August | 18.3±3.1* | 7.8±0.4* |
| Log distance (m)[a] | 5.0±0.4* | 7.4±0.6* |
| Tree distance (m)[a] | 2.3±0.2* | 3.1±0.2* |
| Shrub distance (m)[a] | 2.3±0.2 | 3.0±0.3 |
| Canopy coverage (%) | 69.5±5.2 | 59.9±3.4 |

**Note:** *, statistically significant difference ($P < 0.05$) between riparian and upland samples.

[a]Distances were measured between the plot center and the nearest log, tree, or shrub.

**Table 2.** Means ± SE for frequency, total biomass, and species richness of truffles found in riparian and upland habitats during spring (June) and summer (August) 2000–2002 and 2004.

| | Spring | | Summer | |
|---|---|---|---|---|
| | Riparian | Upland | Riparian | Upland |
| Frequency (%) | 50.0±3.5 | 18.0±6.8 | 29.0±9.1 | 9.0±4.4 |
| Biomass ($kg \cdot ha^{-1}$) | 1.97±0.22 | 0.67±0.42 | 2.31±1.19 | 0.58±0.31 |
| Species richness | 8.5±1.0 | 2.3±0.5 | 5.0±1.5 | 1.5±0.6 |

**Note:** All riparian and upland values were significantly different.

## Discussion

Since our sampling was conducted in a single riparian and upland forest, we do not know how applicable our results may be to a broader range of forests in the Sierra Nevada. Despite this limitation, truffle production was clearly greater in riparian than upland forest across four years and two seasons. Truffle biomass (0.67 $kg \cdot ha^{-1}$) and species richness ($n = 10$) in our upland stand were similar to the biomass (0.57 $kg \cdot ha^{-1}$) and species richness ($n = 9$) of truffles in a mixed-conifer stand near (approx. 6 km away) our study site (North 2002). Truffle biomass at our upland site also was similar to Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) stands of western Washington (0.48 $kg \cdot ha^{-1}$; Colgan et al. 1999) and Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands of northern Arizona (0.72 $kg \cdot ha^{-1}$), while biomass at our riparian site (2.0 $kg \cdot ha^{-1}$) was similar to red and white fir stands of northeastern California (2.4 $kg \cdot ha^{-1}$; Waters et al. 1997), Douglas-fir stands of southwestern Oregon (2.8 $kg \cdot ha^{-1}$; Luoma et al. 2004), and mixed-conifer stands of eastern Washington (4.1 $kg \cdot ha^{-1}$; Lehmkuhl et al. 2004).

Several factors could explain the increased abundance of truffles in riparian compared with upland forest stands. Decayed logs and organic litter 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; Lehmkuhl et al. 2004). At Teakettle, greater soil moisture in riparian compared with upland areas may have enhanced truffle production. Several studies at larger temporal and spatial scales have found truffle abundance associated with moisture over landscapes (Claridge et al. 1999), habitats (Luoma et al. 1991; Lehmkuhl et al. 2004), and seasons (Fogel 1976; States and Gaud 1997). In this study, upland truffle biomass was positively correlated with summer rainfall, indicating that outside riparian areas, moisture may limit biomass during the drier summer months in the Sierra Nevada (North 2002). Riparian truffle biomass also may

**Table 3.** Results of MANOVA and ANOVAs for effects of habitat and season on truffle production at Teakettle Experimental Forest (2000–2002 and 2004).

| Variable | Factor | Wilk's λ | *F* | *P* |
|---|---|---|---|---|
| **MANOVA: truffle frequency, biomass, and species richness** | | | | |
| | Habitat | 0.278 | 9.335 | 0.003 |
| | Season | 0.271 | 5.579 | 0.016 |
| | Habitat × season | 0.623 | 2.302 | 0.139 |
| **ANOVAs** | | | | |
| Truffle frequency | Habitat | | 16.691 | 0.002 |
| | Season | | 5.556 | 0.036 |
| | Habitat × season | | 0.889 | 0.364 |
| Truffle biomass | Habitat | | 5.284 | 0.040 |
| | Season | | 0.038 | 0.849 |
| | Habitat × season | | 0.108 | 0.748 |
| Truffle species richness | Habitat | | 24.401 | <0.001 |
| | Season | | 4.636 | 0.052 |
| | Habitat × season | | 1.941 | 0.189 |

**Table 4.** Total biomass (kg·ha$^{-1}$) and frequency (%) of truffle species in riparian and upland habitats and totals for both habitats over all seasons (June and August) and years (2000–2002 and 2004).

| | Biomass | | | Frequency | |
|---|---|---|---|---|---|
| Truffle species | Riparian | Upland | Total | Riparian | Upland |
| *Rhizopogon ellenae* A.H. Smith | 4.91 | 1.38 | 6.23 | 6.5 | 2.5 |
| *Hydnotyra cerebriformis* Harkn. | 3.11 | 0.64 | 3.75 | 10.5 | 3.5 |
| *Elaphomyces granulatus* Fr. | 1.26 | 1.99[a] | 3.25 | 1.5 | 1.0 |
| *Gautieria monticola* Harkn. | 2.85 | 0 | 2.85 | 4.5 | 0 |
| *Melanogaster tuberiformis* Corda | 2.44 | 0.12 | 2.56 | 6.0 | 1.0 |
| *Leucophleps spinispora* Fogel | 1.12 | 0.86 | 1.98 | 2.5 | 0.5 |
| *Rhizopogon pedicellus* A.H. Smith | 0.45 | 0.72 | 1.17 | 1.0 | 0.5 |
| *Hymenogaster idahoensis* A.H. Smith | 0.76 | 0.06 | 0.82 | 3.0 | 0.5 |
| *Leucogaster rubescens* Zellner & C.W. Dodge | 0.80 | 0 | 0.80 | 2.5 | 0 |
| *Hysterangium setchellii* Fischer | 0.67 | 0.08 | 0.75 | 3.5 | 0.5 |
| *Trappea darkeri* (Zeller) Castellano | 0.52 | 0 | 0.52 | 0.5 | 0 |
| *Martellia californica* Singer & A.H. Smith | 0.46 | 0.04 | 0.50 | 1.0 | 0.5 |
| *Geopora cooperi* Harkn. | 0.45 | 0 | 0.45 | 1.0 | 0.5 |
| *Hymenogaster subolivaceus* A.H. Smith | 0 | 0.37 | 0.37 | 0 | 1.0 |
| *Genebea cerebriformis* (Harkness) Gilkey | 0.26 | 0 | 0.26 | 0.5 | 0 |
| *Macowanites luteolus* A.H. Smith & Trappe | 0.09 | 0 | 0.09 | 0.5 | 0 |
| *Endogone lactiflua* Berk. | 0.04 | 0 | 0.04 | 0.5 | 0 |
| *Thraxterogaster pingue* (Zeller) Singer & A.H. Smith | 0.04 | 0 | 0.04 | 0.5 | 0 |
| *Gymnomyces cinnamomeus* Singer & A.H. Smith | 0.02 | 0 | 0.02 | 0.5 | 0 |
| Unknown | 0.16 | 0.01 | 0.17 | 4.0 | 1.0 |

[a]78% of total biomass attributed to a single cluster of *E. granulatus* found in a single 4-m$^2$ truffle plot (0.5% of the total sampled upland area).

benefit from higher tree densities. Truffle biomass in Douglas-fir stands of western Oregon peaks at a distance of 2 m from the base of a tree (Fogel 1976), similar to the average tree distance in our riparian sample plots (2.3 m).

The three most abundant truffle species in our study, *R. ellenae*, *H. cerebriformis*, and *E. granulatus*, are often associated with decayed woody debris (e.g., rotting logs and organic litter; Arora 1986; North and Greenberg 1998; Meyer et al. 2005). In our study, logs were closer to the center of truffle sample plots in riparian than upland sites, consistent with an analysis finding higher log density in riparian versus upslope areas at Teakettle Experimental Forest (J. Innes, Sierra Nevada Research Center, personal communication, 2004). The higher log density may have contributed to the greater abundance of *R. ellenae* and *H. cerebriformis* in riparian than upland areas. Although the total biomass of *E. granulatus* was 58% greater in upland than riparian plots, this was due to the presence of a single high-biomass cluster of *E. granulatus* that represented the majority of the upland biomass of this species. *Elaphomyces granulatus* sometimes form large clusters of sporocarps (Vogt et al. 1981; Luoma et al. 1991; North et al. 1997), which can bias biomass esti-

mates (Smith et al. 2002) but have less influence on frequency. In our study, *E. granulatus* had similar frequency between riparian (1.5%) and upland (1%) habitats.

There was no significant difference in truffle production among years ($P = 0.6$), contrasting with previous studies showing high annual variation in production (e.g., Luoma et al. 1991; States and Gaud 1997; Waters et al. 1997; North 2002; Smith et al. 2002). Elevated precipitation may substantially increase the production of truffles across seasons or years (States and Gaud 1997; North 2002), particularly in dry interior montane forests of western North America (Lehmkuhl et al. 2004). However, lower than average summer precipitation (0.3 cm) and soil moisture (average of 8%) in the absence of extreme precipitation events (i.e., El Nino Southern Oscillation) may have reduced annual variation in truffle production during our study. Additionally, previous studies of truffles in interior montane forests (e.g., States and Gaud 1997; North 2002; Lehmkuhl et al. 2004) did not sample in riparian stands, where a stable microclimate (Chen et al. 1999) may reduce annual precipitation effects on truffle production.

California's Sierra Nevada contains a diverse assemblage of truffle species that occur over a range of forest types (North 2002). There have been few truffle studies, however, in this region or other dry montane forests (however see States and Gaud 1997; North 2002) where the seasonal and within-stand differences in soil moisture could influence availability of this important food source. We found truffle richness and biomass significantly vary across a relatively small spatial scale (100 m distance) in mixed-conifer forest of the Sierra Nevada. Our results are limited in both geographic scope (tributaries in one watershed) and time (2 seasons over 4 years), but are consistent with patterns of northern flying squirrel microhabitat use in this location (Meyer 2003). Future research examining small-scale differences in truffle abundance in other dry montane forests would help determine whether this important food source is concentrated in moist, riparian habitats.

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