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Effects of Forest Management on Truffle Abundance and Squirrel Diets

Abstract

Thinning and retention of biological legacies (large live, dead, and fallen trees and their associated biota) during clearcutting are two practices to promote development of late-seral attributes in second-growth forests. We evaluated the effects of these practices on production of truffles and use of truffles as food by northern flying squirrels and Townsend's chipmunks in 55-65-yr-old Douglas-fir forests in the Puget Trough of Washington. Truffles were collected at 6-wk intervals from March 1993 through December 1995. Feces were collected from flying squirrels and chipmunks in fall and spring, 1991-1995, and relative frequencies of truffle genera and vascular plant parts therein were determined. Mean standing crop biomass of truffles did not differ between thinned and legacy forests. However, dominant genera of truffles in the soil and in feces did. Truffles in soil and in flying squirrel diets were more diverse in legacy than in thinned forest. *Gautieria*, a consistently important component of flying squirrel diets, but not chipmunk diets, was more abundant in legacy than in thinned forest. *Melanogaster*, eaten by both chipmunks and flying squirrels, was more abundant in thinned than in legacy forest, as were vascular plants. Chipmunks consumed large amounts of vascular plant material. Flying squirrels also consumed plant parts in thinned forest, but they did not consume measurable amounts of plant materials in legacy forest. Flying squirrels consumed a greater diversity of truffles than we found with intensive random sampling. The ability of flying squirrels to find truffles, their propensity to ingest all species of truffles, their excretion of viable spores, and their wide travels makes them important in maintaining the diversity of ectomycorrhizal fungi.

Introduction

Mycorrhizal fungi enhance the ability of trees to absorb water and nutrients from soil and they move photosynthetic carbohydrates from trees to the mycorrhizosphere. In turn, this carbon supports a vast array of microbes, insects, nematodes, bacteria, and other organisms in the soil (Fogel 1988, Ingham and Molina 1991). Sporocarps of hypogeous ectomycorrhizal fungi (hereafter referred to as truffles) are food for diverse animals worldwide (Fogel and Trappe 1978, Maser et al. 1978, Viro and Sulkava 1985, Malajczuk et al. 1987, Blaschke and Baumler 1989, Launchbaugh and Umess 1992, Claridge and May 1994, Carey 1995). Truffles attract animals by producing aromatic compounds (Fogel and Trappe 1978). Most truffles consumed by animals in temperate forests are formed by ectomycorrhizal fungi in symbiotic association with the roots of Pinaceae, Fagaceae, Betulaceae, Myrtaceae, and Salicaceae (Molina et al. 1992).

Animals consume all or part of a truffle (Fogel and Trappe 1978) including spores, bacteria, and yeasts that live in the truffle (Li et al. 1986). These spores, yeasts, and bacteria pass through the digestive tract unharmed and are deposited in feces in new locations (Trappe and Maser 1976). Precipitation then moves fecal contents into the soil where the fungi colonize new roots (Trappe and Maser 1976). The mammals that disseminate spores also serve as prey for owls, raptors, and mustelids (Carey et al. 1999a, Carey 2000a). Thus, this food web of trees, truffles, and mammals may be considered a keystone complex (Daily et al. 1993) particularly indicative of forest ecosystem function in the Pacific Northwest (Carey et al. 1999a).

The major mycophagists in the Pacific Northwest are the northern flying squirrel (*Glaucomys sabrinus*), Douglas' squirrel (*Tamiasciurus douglasii*), and Townsend's chipmunk (*Tamias townsendii*). The Douglas' squirrel and Townsend's chipmunk are known to store and eat various foods besides truffles, including conifer seed. As adaptations to seasonal food shortages, the Douglas'

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squirrel maintains small territories and stores conifer cones. The chipmunk maintains small home ranges in shrubby areas that provide food (berries, nuts, and seeds) and cover from predation and sometimes hibernates in winter (Carey 2001). The flying squirrel seems to depend more on truffles than the other squirrels and its densities seem correlated jointly with truffle biomass and diversity (Carey 1995). Flying squirrel densities in old forests vary regionally, in a manner opposite to what would be expected based on total truffle abundance alone. Densities in natural forests in the North Cascades (0.2/ha) and Olympic Peninsula (0.5/ha) of Washington, where truffle biomass is unusually high (North et al. 1997), were low compared to the Western Cascades (2.3/ha) and Coast Ranges (1.9/ha) of Oregon (Carey 1995) where truffle abundance is moderate (Luoma 1991), and similar to those in managed forests in the Puget Trough of Washington (0.5-0.8/ha) (Carey 2001), where truffle abundance is low (Colgan et al. 1999). The lack of correspondence between abundance of flying squirrels and truffles may be due to differences in seasonal production of truffles, nutritional value of different species of truffles, and lack of correlation between abundance and diversity of truffles. For example, in areas of Washington where truffle biomass was high, diversity was low with 95% of biomass in one species, *Elaphomyces granulatus* (North et al. 1997).

The ecology of truffle production is poorly understood. Peak truffle production in the Pacific Northwest occurs during spring and fall but varies markedly from year to year (Fogel 1976, Hunt and Trappe 1987, Luoma et al. 1991) and with forest type and age (Vogt et al. 1981; Luoma 1989, 1991; Luoma et al. 1991; O' Dell et al., 1992; Amaranthus et al. 1994; Pilz and Molina 1996). In the Olympic and North Cascade mountains of Washington, truffle biomass was five times greater in old growth (4.0-4.5 kg/ha) than in second-growth managed forest (North et al. 1997). In the Western Cascades of Oregon, however, truffle biomass was <1 kg/ha in old growth, but >2 kg/ha in second growth (Jane E. Smith, USDA Forest Service, personal communication). In naturally young Douglas-fir (*Pseudotsuga menziesii*) forest in a nearby study, biomass (1.2 kg/ha) was similar to that in old growth (1.6 kg/ha) (Luoma 1991). Truffles were abundant in second-growth Douglas-fir in the Oregon Coast Range, 2.3-5.4 kg/ha (Fogel 1976 and 2.0-3.2kg/ha (Hunt and Trappe 1987).

Thus, truffle production varies greatly in space and time. Some truffles are available year-round, but there have been no definitive studies of truffle abundance in summer and winter (Fogel 1976, Hunt and Trappe 1987, North et al. 1997).

Most studies of mycophagy have lasted < 1 yr and do not explain how the functional relationship between squirrels and truffles is maintained in winter and summer, seasons when truffles may be scarce. Nor do these few studies explain how the flying squirrel can compete for truffles with Douglas' squirrels and Townsend's chipmunks in winter, when food (except stored food) generally is scarce and truffles still are the principal food of flying squirrels. For flying squirrels, truffle production during winter may be critical (Carey 1995). Flying squirrels are not only at high risk from predators while foraging for truffles on the ground (Wilson and Carey 1996) but also at risk to rapid loss of metabolic heat because of their habits of nocturnal activity, arboreal travel and gliding, and their high surface area relative to body mass. Flying squirrels must employ an optimal foraging strategy that allows them to minimize time on the ground and time of exposure to low temperatures. They also change dens regularly as an additional predator-avoidance strategy (Carey et al. 1997). The benefits of being able to locate and extract truffles quickly to avoid predation and minimize energy expenditure is somewhat offset by the low nutritive value of truffles and travel time to foraging sites (Cork and Kenagy 1989, Claridge et al. 1999, Carey 2000a).

The nutritional value of truffles for squirrels is low (Cork and Kenagy 1989, Claridge et al. 1999). Nevertheless, the three common squirrels in the Pacific Northwest feed on truffles throughout the year, primarily the genera *Rhizopogon*, *Melanogaster*, and *Hysterangium* (Maser et al. 1978, 1985, 1986; Carey, 1995; Carey et al. 1999a). These truffle genera are heavily consumed by mycophagists in general (North et al. 1997). Truffle diversity may be important in providing an adequate diet for mycophagists because truffles may differ in nutrient content (Claridge et al. 1999). Truffle species richness does not vary regionally, but apportionment of biomass among species does. Forty-three species occurred across western Washington (North et al. 1997), but a single species (*Elaphomyces granulatus*) accounted for 95% of biomass. Forty-

seven species occurred across the Western Cascades of Oregon, with five species accounting for 73 % of the biomass (Luoma 1991). Diets of squirrels may reflect differential consumption of truffles. Even where biomass of *Elaphomyces* was high (North et al. (1997), *Rhizopogon* dominated in squirrel diets (Carey 1995). The food value of *Elaphomyces* is near the minimum on which squirrels are able to maintain themselves as a sole source (Cork and Kenagy 1989) and flying squirrels lose weight on a diet of *Rhizopogon vinicolor* (Claridge et al. 1999). Thus, a diet of multiple fungi may be important to mammalian mycophagists (Claridge et al. 1999).

Management may affect truffle production, but the effects are not clear. Management seems to affect production of truffles by different species differently. Production of truffles by *Gautieria* (and *Hysterangium*) is reduced by thinning in the short-term (Colgan et al. 1999). Fruiting of *Melanogaster*, like *Hysterangium setchellii*, is favored by thinning (Colgan et al. 1999). Several factors may underlie low truffle production by certain species in thinned forest. Species that form hyphal mats may be more susceptible to mechanical damage by logging operations. Thinning may change microenvironment to the detriment of these species. *Hysterangium* and *Gautieria* were significantly less frequent in shelterwood stands in California 17 and 20 yr after timber harvest (Waters et al. 1994). Similarly, *Hysterangium* spores were infrequent in feces of Siskiyou chipmunks (*T. siskiyou*) in shelterwood stands in southwestern Oregon (McIntire 1984). *Gautieria* mats were common only in the rooting zone of retained oldgrowth trees 2 yr after a shelterwood harvest in the Oregon Western Cascades (Aguileria et al. 1993). Shelterwood harvests remove a greater proportion of trees than does thinning and considerable time may be required after disturbance for some fungal taxa to recover and fruit. Reduced biomass of *E. granulatus* in managed compared to natural old forests may be a consequence of reduced organic layers and root density in managed forests (North and Greenberg 1998). Other species, such as *Rhizopogon parksii*, are not associated with organic layers at the cool, moist end of the Western Hemlock Zone (North et al. 1997, North and Greenberg 1998). At the opposite extreme (hot, dry) in southwestern Oregon, there is a close association between truffles of various species and decaying logs on the forest floor (Amaranthus et al. 1994). Concerns about the 150 Carey, Colgan, Trappe, and Molina effects

of forest management on fungi led to special protection for fungal species thought to be associated with late-successional forests (FEMAT 1993, USDA and USDI 1994, Castellano et al. 1999). Most of these species, however, were newly described with little information on their ecologies. Concern about the effects of forest management on the spotted owl (*Strix occidentalis*) and its primary prey, the northern flying squirrel also a consumer of truffles and disperser of truffle spores—was the primary motivation behind massive changes to federal land management in the Pacific Northwest (FEMAT 1993).

Our objective was to determine the effects of forest management on production of truffles and on diets of northern flying squirrels and Townsend's chipmunks in second-growth Douglas-fir forests in the Puget Trough of Washington. Specifically, we compared two alternative strategies for managing second-growth forests on long rotations (>70 yr) for late-seral attributes: 1) management with multiple thinnings to grow large trees and well-developed understories quickly, and 2) management with retention of biological legacies (old live, dead, and fallen trees and their associated biota) at harvest with no further management intervention.

Methods

Study Area

We studied four even-aged blocks of Douglas-fir forest totaling =150 ha chosen from 6,000 ha of second-growth forest on that part of Fort Lewis Military Reservation in Thurston County, in the southern Puget Trough of Washington. These forests were located in the Western Hemlock (*Tsuga heterophylla*) Zone wherein Douglas-fir often is dominant in young managed stands, but where Douglas-fir, western hemlock, and western redcedar (*Thuja plicata*) often are codominant in old natural forest (Franklin and Dyrness 1973). Soils were gravely sandy loams in glacial outwash plains. Topography was flat to gently rolling, 100143 m above sea level. Average annual precipitation was 91 cm. Two blocks had been clearcut ca. 1927 and lightly thinned twice (1972 and late 1980s) to final retained densities of about 200 trees/ha (≈ 7 m between trees), hereafter referred to as thinned forest (Carey et al. 1999b). Thinned forest had 2-3% cover of coarse woody debris, few (<1/ha) residual old-growth trees, and dense understories

of salal (*Gaultheria shallon*), western brackenfern (*Pteridium aquilinum*), and western swordfern (*Polystichum munitum*). Two blocks were clearcut ≈ 1937 with retention of about six old-growth trees/ha and 10% cover of coarse woody debris, but received no further silvicultural treatment. Hereafter we refer to these blocks as legacy forest. Understories in legacy forest were variable and dominated by ground mosses. Salal and swordfern were patchily abundant in conjunction with canopy openings caused by laminated root rot (*Phellinus weirii*). We randomly selected 8 of the 16 available 13-ha stands, 2 per block, 4 from the legacy forest and 4 from the thinned forest. Within blocks, stands were >80 m apart; the forests were 4 km apart. Each stand had a central, square, surveyed sampling grid marked with plastic pipe and colored flagging (Carey et al. 1999b). Each grid consisted of 64 points (40 m apart) that were trapping stations for squirrels (Carey 2001) and references for locating fungal transects.

Fungal Sampling and Analysis

We sampled the forest floor for fungal sporocarps (truffles and mushrooms) 12 times (about every 6 wk) between April 1993 and December 1995. The December 1994 session, however, was interrupted by snow, thus 920 plots were sampled. We randomly chose a grid point, starting distance from the point, and direction for each sampling transect for each stand for each sampling occasion. Each transect consisted of 10 circular 4 m² microplots 10-m apart in each of the stands to be sampled (Luoma et al. 1991). First, mushrooms (primarily Boletaceae and *Russula* spp.) used as food by small mammals and obvious truffles were collected from the surface of each plot. Each plot was raked with hand tools to a depth of ≥ 5 cm into mineral soil to expose truffles. Each collection (one to several sporocarps of the same species in close proximity to one another on a single plot) was placed in a wax paper bag with a tag recording plot number, stand number, and other pertinent information. Field characteristics used in identification of sporocarps were noted. Plots were marked with plastic pin flags and the litter and duff were replaced. No plots were sampled twice. All fungal samples were dried the day of collection with a forced air dehydrator set at 49°C (Colgan 1997), transported to the Forestry Sciences Laboratory in Corvallis, Oregon, for identification, and weighed to the nearest 0.01 g. Voucher specimens were placed in the Mycological Herbarium at Oregon

State University.

We calculated the frequency of encounter for each species found on the microplots. We measured taxonomic diversity as number of truffle species and as number of truffle genera. Biomass values were calculated for each transect as kg/ha dry weight transformed with $\log_e(\ln)$ to improve normality. Biomass was compared by using analysis of variance (ANOVA) and Fisher's protected least significant difference (PLSD) with the significance level of $P \leq 0.05$. We limited comparisons among diets and transects to genera composing $>3\%$ relative frequency in feces or $>3\%$ of biomass collected from plots.

Feces Collection and Analysis

Flying squirrels and chipmunks were live-trapped with standard methods (Carey et al. 1991), including two four-night sessions with 128 Tomahawk 201 traps/stand (two/grid point) in spring and fall, from fall 1991 to fall 1995. Fecal pellets were collected only at the first capture of an individual within a session to avoid feces containing ingested bait (peanut butter, molasses, and oats). One to five fecal pellets were collected from the anus and placed into a small glass vial which was sealed immediately to minimize contamination of by fungal spores in or around the trap site. We examined feces with the pooling method (Colgan et al. 1997). Briefly, samples from three to six animals of each species were randomly selected from the group of animals captured during one trapping period on one trapping grid. Pooled samples were macerated in small vials with approximately 1 ml of tap water (approximately four times the volume of the pellets) and shaken thoroughly. Then one drop of suspension was transferred to each of five microscope slides. One drop of Melzer's reagent (iodine, potassium iodide, and chloral hydrate in aqueous solution) was added, and the solution was covered with a 22 x 22-mm cover slip. We examined 25 randomly selected fields of view/slide at 400x magnification and recorded the items present in each field. Truffle spores were identified to genus according to Castellano et al. (1989). Mushroom spores were identified to family. Vascular plant fragments and insect parts were recorded. Miscellaneous and unidentifiable items occurring in $<5\%$ of the fields were grouped as unknown. Mean relative frequencies (RF) and standard errors (SE) of dietary items Truffle Abundance

and Squirrel Diets 151 were calculated by species of squirrel over trapping periods for each treatment. Abundances in plots were converted to ranks and compared to ranks in diets of chipmunks and flying squirrels with Spearman rank order correlations.

Results

We collected 590 truffles from 920 plots (3,680 m²). We found 28 species: 19 in thinned forest, 7 of which were only in thinned forest, and 21 in legacy

TABLE 1. Percent frequencies of sporocarps of hypogeous fungal species occurring with $\geq 3\%$ relative frequency in plots in legacy forest and thinned forest in the Puget Trough, Washington, April 1993 through December 1995

Species ^a	Legacy	Thinned
<i>Rhizopogon vinicolor</i>	8.9	5.9
<i>Tuber monticola</i>	3.0	2.2
<i>Hysterangium coriaceum</i>	2.4	1.5
<i>Hysterangium crassirhachis</i>	2.1	1.1
<i>Gautieria monticola</i>	1.5	0.2
<i>Endogone lactiflua</i>	1.4	0.6
<i>Hysterangium setchellii</i>	1.1	2.4
<i>Melanogaster tuberiformis</i>	0.2	1.3
<i>Leucophleps magnata</i>	0.2	0.6
<i>Rhizopogon hawkera</i>	–	3.3
<i>Rhizopogon villosulus</i>	–	0.9

^aTaxa occurring with $< 3\%$ relative frequency included: *Elaphomyces granulatus*, *Endogone pisiformis*, *Genabea cerebriiformis*, *Genea intermedia*, *Glomus macrocarpum*, *Hymenogaster sp.*, *Hymenogaster sublilacinus*, *Leucogaster candidus*, *L. citrinus*, *L. gelatinosus*, *L. rubescens*, *Leucophleps spinispora*, *Rhizopogon vulgaris*, *Truncocolumella citrina*, *Tuber anniae*, and two species new to science.

TABLE 2. Relative frequencies of fungal sporocarp genera in soil, and spores and vascular plant parts in feces of *Glaucomys sabrinus* and *Tamias townsendii*, in thinned and legacy forest, 1991-1995.

Dietary components	<i>Glaucomys sabrinus</i>				<i>Tamias townsendii</i>	
	Legacy		Thinned		Legacy	Thinned
	Soil ^a	Diet ^a	Soil ^a	Diet ^a	Diet ^a	Diet ^a
<i>Rhizopogon</i>	40	22	47	31	27	20
<i>Hysterangium</i>	24	12	17	8	7	12
<i>Melanogaster</i>	1	10	6	20	–	9
<i>Gautieria</i>	6	13	1	6	–	–
<i>Leucogaster</i>	4	6	1	–	8	7
<i>Leucophleps</i>	3	5	3	–	15	10
<i>Elaphomyces</i>	1	6	–	–	–	–
No. truffle genera	7	7	4	5	5	4
Plant material	–	–	–	8	21	18

^aA dash (-) indicates the taxa was not detected, or in the case of vascular plants in the soil columns, not recorded.

forest, 9 of which were only in legacy forest (Table 1). *Rhizopogon vinicolor* was the most frequent species and *Rhizopogon* was the most frequent genus in both forest types (Table 1). Three other species of *Rhizopogon* were found only in thinned forest. *Gautieria monticola* was seven times more frequent in legacy than in thinned forest. *Melanogaster tuberiformis* was six times more frequent in thinned forest. There were more species of *Leucogaster*, a genus important to both flying squirrels and chipmunks, in legacy than in thinned forest. Truffle collections were dominated ($> 3\%$ relative frequency) by seven genera in legacy forest and five genera in thinned forest (Tables 1 and 2).

All species frequencies, however, were low, ranging from 0 to 8.9% of plots in any forest type (Table 1) and, thus, variances associated with mean standing crop biomasses were high. Standing crop biomass did not differ significantly between forest types for the 3 yr we sampled and averaged 0.48 kg/ha. Mean standing crop biomass ranged from 0 to 1.8 kg/ha over sampling periods with greatest values in spring and lowest values in winter, but 95% confidence intervals about the means overlapped for all sampling periods (Figure 1). The biomass of truffle collections totaled 176.1 g with 93.8 g from thinned forest and 82.9 g from legacy forest.

We collected 467 fecal samples from chipmunks and 185 from flying squirrels. The pellets of both species contained spores from families of hypogeous Ascomycetes, Basidiomycetes, and Zygomycetes and epigeous Ascomycetes and Basidiomycetes. *Rhizopogon* was the dominant fungus

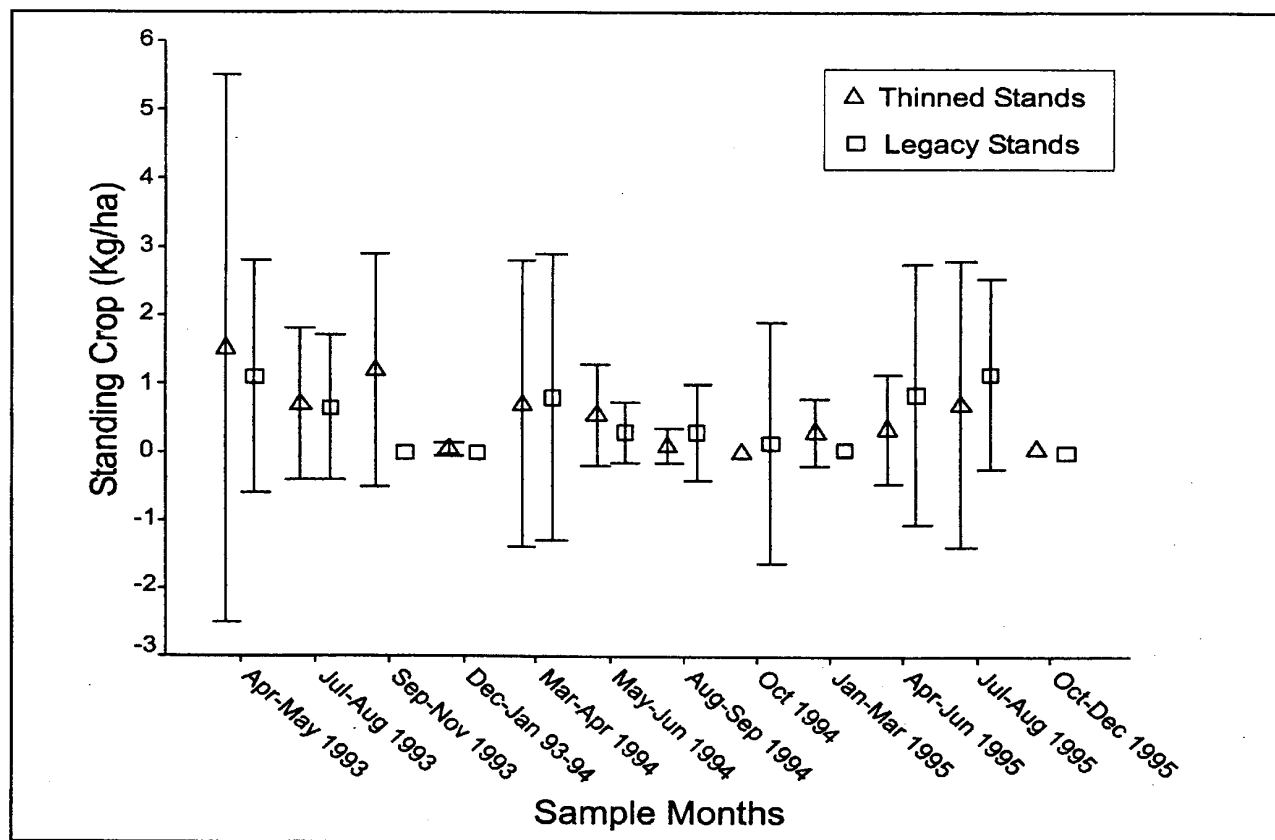


Figure 1. Means and 95% confidence intervals for estimated truffle biomass in second-growth Douglas-fir (*Pseudotsuga menziesii*) stands thinned twice with conventional thinning and never-thinned stands with biological legacies of old live tree, standing dead trees, and fallen trees from previous stands. December 1993-January 1994 sampling was interrupted by snowfall and could not be completed.

TABLE 3. Means and (standard errors) of relative frequencies of dietary fungal genera $\geq 3\%$ relative frequency and vascular plant parts for *Glaucomys sabrinus* and *Tamias townsendii* thinned and legacy forests, 1991-1995.

	<i>Glaucomys sabrinus</i>		<i>Tamias townsendii</i>	
	Legacy	Thinned	Legacy	Thinned
<i>Rhizopogon</i> ^a	22 (1)	31 (5)	27 (4)	20 (5)
<i>Hysterangium</i>	12 (2)	8 (3)	7 (2)	12 (2)
<i>Melanogaster</i>	10 (2)	20 (4)	—	9 (1)
<i>Gautieria</i>	13 (4)	6 (2)	—	—
<i>Leucogaster</i>	6 (2)	—	8 (1)	7 (1)
<i>Leucophleps</i>	5 (3)	—	15 (4)	10 (2)
<i>Elaphomyces</i>	6 (3)	—	—	—
Plant material	—	8 (3)	21 (4)	18 (7)

^a May include related taxa not distinguishable by spores alone

in the diets of both species in both forest types (Tables 2 and 3). Flying squirrels consumed *Gautieria*, even in thinned forest where we found no *Gautieria* sporocarps, and *Elaphomyces*, genera not present in the feces of chipmunks. *Leucophleps* had greater importance in chipmunk diets than in flying squirrel diets. Chipmunks consumed substantial amounts of vascular plant parts in both forest types, but flying squirrels consumed them primarily in thinned forest. Flying squirrel diets were more diverse in legacy than in thinned forest (seven vs. five frequent genera). Diet items were strongly correlated ($P < 0.001$) with abundance in plots for both flying squirrels ($r_s = 0.84$) and chipmunks ($r_s = 0.77$). Seasonal diets were correlated with seasonal abundances. We found in fecal pellets two genera of truffles, *Pachyphleous* and *Radiigera*, that we did not encounter in the field.

Discussion

Impacts of Management on Truffle Biomass in the Western Hemlock Zone

Management history had no discernable effect on truffle production in second-growth forest in the Puget Trough (Tables 1, 2). Compared to natural forests in Olympic Peninsula and North Cascades in Washington (North et al. 1997) and the Western Cascades in Oregon (Luoma 1991), Puget Trough second growth produced low biomasses of truffles (1-4.5 kg/ha vs. 0.5 kg/ha). Biomasses in the Puget Trough were similar to managed forests elsewhere in Washington, averaging 0.5 kg/ha over seasons, but ranging up to 1.8 kg/ha (Figure 1) versus 0.8 kg/ha (North et al. 1997). Second-growth forests in Oregon produced higher biomasses, averaging 2-5 kg/ha (Fogel 1976, Hunt and Trappe 1987, Jane E. Smith, USDA Forest Service, personal communication). However, effects of forest management on truffle production in Oregon have been inconsistent (Fogel 1976, Hunt and Trappe 1987, Luoma 1991, North et al. 1997, Jane E. Smith, USDA Forest Service, personal communication). The overall effects of forest management on truffle biomass remain unclear.

Impacts of Management on Truffle Diversity

Species diversity was slightly greater in legacy than in thinned forest. A total of 28 species was present on plots totalling 3,680 m² in this study on Fort Lewis, but 48 species were present on 14,720 m² that included eight nearby experimental stands of similar age (Colgan et al. 1999). Thus, species richness seems to reach an asymptote of about 48 species with widespread sampling in the Pacific Northwest (Luoma 1991, North et al. 1997, Colgan et al. 1999). Six species accounted for 80% of the biomass in the Puget Trough, 5 for 73% in Oregon (Luoma 1991), and 1 species for 93% in the Olympic Peninsula and North Cascades in Washington (North et al. 1997). Truffle diversity in managed Puget Trough forests was similar to diversity in natural forests across the Western Hemlock Zone.

Management affected truffle diversity on Fort Lewis. More genera occurred in soil and in feces in legacy than in thinned forest. Four genera common in flying squirrel diets across the Pacific Northwest, *Gautieria*, *Leucogaster*, *Leucophleps*, and *Elaphomyces* (Carey 1995, Carey et al. 1999a), were

less prevalent in soil and feces in thinned than in legacy forest. Production of truffles by *Gautieria* (and *Hysterangium*) was reduced by thinning in the short-term (Colgan et al. 1999). Apparently with conventional thinning, that effect is long lasting (Tables 1, 2) but not universal for species of *Hysterangium*. For example, *H. coriaceum* and *H. crassirhachis* were more abundant in legacy and *H. setchellii* was more abundant in thinned forest. *Leucogaster citrinus* and *Elaphomyces granulatus* are thought to be associated with late-successional forest (USDA and USDI 1994, Castellano et al. 1999). These two species occurred in legacy forest but not in thinned forest. Fruiting of *Melanogaster*, like *H. setchellii*, was favored by thinning (Colgan et al. 1999). *Melanogaster* truffles were six times more frequent in soil and twice as abundant in flying squirrel feces in thinned than in legacy forest. Three of four *Rhizopogon* species occurred only in thinned forest. Several species of *Rhizopogon* are common in early stages of forest development and are often abundant on tree roots following disturbance (Molina et al. 1999). Seventy-one epigeous (mushroom-producing) fungi thought to be associated with late-successional forests were found on the Puget Trough sites (Carey et al. 1999b). Thus, it appears that many fungi thought to be associated with late-successional forest can persist in managed stands, particularly stands with legacies from old-growth forest. Management does not decrease the diversity of fungi; rather, it may promote a diversity of fungi.

Truffles and Squirrels

Our study was the first multiyear study of mycophagy in the USA. Diets were similar to those reported previously (Maser et al. 1978, 1985, 1986; Carey 1995; Carey et al. 1999a). Our sampling intensity for plots was high compared to most studies, yet flying squirrels found as many genera during one 2-wk period as we found in 3 yr. Flying squirrels moved farther than chipmunks to forage (Carey 1995, 2000a). This mobility and a widely dispersed, but clumped, distribution of *Gautieria* truffles may explain the lack of consumption by chipmunks and the rarity of *Gautieria* in our soil samples compared to the prevalence of *Gautieria* in the flying squirrel diet. Squirrels used many species in proportion to their occurrence. Animals

that forage by smell will detect the odor nearest to them first and the truffles species with the most uniform and frequent distribution should dominate the diet, as *Rhizopogon* does. *Rhizopogon* may not produce as large a localized biomass of truffles as *Elaphomyces* (North et al. 1997), or even the most nutritious truffles (Claridge et al. 1999), but *Rhizopogon* produces truffles with high frequency at local scales in natural and managed forests over a wide geographic area (Table 2; Carey 1995, Molina et al. 1999). High mobility of flying squirrels compared to chipmunks and Douglas' squirrels (Carey 2001) and their willingness to consume all species of truffles explains their ability to compete with chipmunks and Douglas' squirrels for a limited truffle resource.

Total taxonomic diversity of truffles differs little among five of the six physiographic provinces in western Oregon and Washington (the Southern Cascades of Washington have not been studied). The Olympic Peninsula and North Cascades forests, however, seem to have been dominated more by a single species than elsewhere. Flying squirrel diets were rich in Puget Trough legacy forests (seven commonly occurring truffle genera) compared to similarly managed forests on the Olympic Peninsula (four genera) and similar in diversity to diets in old-growth forests on the peninsula (six genera). Diets in thinned forests in the Puget Trough had the same number of genera (four) as diets in the legacy forests on the Olympic Peninsula. Flying squirrel diets in the Puget Trough and on the Olympic Peninsula had fewer genera than flying squirrel diets from the warmer, drier, southern Oregon Coast Range (12 genera in old growth and 9 genera in extensively managed forests) (Carey 1995, Carey et al. 1999a).

Flying squirrel abundance varied with truffle abundance in northeastern California (Waters and Zabel 1995). In southwestern Oregon, flying squirrels foraged where coarse woody debris was abundant (Carey et al. 1999a) and coarse woody debris was positively correlated with truffle abundance (Amaranthus et al. 1994). However, on the Olympic Peninsula, flying squirrel abundance was correlated more with understory development (Carey 1995) and abundance of mast-bearing trees (*Acer circinatum* and *A. macrophyllum*)—ancillary sources of high quality food—than with coarse woody debris (Carey and Harrington 2001). In contrast, flying squirrels were 1.6 times more abundant in the legacy than

in thinned forest, whereas chipmunks were 4.4 times more abundant in thinned forest (Carey 2000b, 2001). The value of shrubs as food and cover explains differences in chipmunk abundance (Carey 2000b, 2001), but not differences in flying squirrel abundance, given that (1) truffle biomass was equal in the two forest types, (2) flying squirrels consumed all species of truffles (Colgan 1997), (3) truffles are nutritionally poor (Cork and Kenagy 1989, Claridge et al. 1999), and (4) vascular plant parts consumed by flying squirrels (Thysell et al. 1997) have high nutritive value (Cork and Kenagy 1989). Locally, flying squirrel abundance may be determined by (1) availability of dens (Carey et al. 1997; Carey 2001), (2) habitat-mediated predation (Carey et al. 1992; Wilson and Carey 1996), (3) competition with chipmunks and Douglas' squirrels in environments simplified by forest management (Carey and Harrington 2001), and (4) ancillary food sources (Ransome and Sullivan 1997, Thysell et al. 1997, Carey and Harrington, 2001). Our results support the hypothesis that simultaneously high populations of northern flying squirrels, Townsend's chipmunks, and Douglas' squirrels in the Douglas-fir keystone complex—a characteristic of old, natural forests (Carey 1995)—results from ecological processes of development of habitat breadth and niche diversification (Carey et al. 1999a) and not from a single limiting factor (Carey 2001, Carey and Harrington 2001).

Acknowledgments

Funding was provided by the U.S. Army, Fort Lewis Military Reservation, the USDA National Research Initiative Competitive Grants Program (Grant No. 9401095), and the USDA Forest Service, Pacific Northwest Research Station. We thank >80 volunteers who contributed >2,000 hours to sampling truffle plots, often under adverse conditions. Special thanks to D. Thysell for field and logistical assistance and to M. Myrdall, P. Molina, and J. Eblin for data entry. Many thanks to A. Claridge, D. McKay, J. Smith, M. Kiel, C. Cray, D. Luoma, and D. Pilz who each contributed in numerous ways. We thank A. Claridge, R. Forbes, D. Luoma, F. Rhoades, and M. Vavrek for careful reviews of an early manuscript.

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Received 7 September 2001

Accepted for publication 14 December 2001