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Stand conditions associated with truffle abundance in western hemlock/Douglas-fir forests

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Abstract

Truffles are a staple food source for many forest small mammals yet the vegetation or soil conditions associated with truffle abundance are unknown. We examined the spatial distribution of forest structures, organic layer depth, root density, and two of the most common western North American truffles (*Elaphomyces granulatus* and *Rhizopogon parksii*), in managed-young, natural-mature and old-growth western hemlock (*Tsuga heterophylla*)/Douglas-fir (*Pseudotsuga menziesii*) stands in Washington State. Forest conditions, *E. granulatus* and *R. parksii* sporocarp locations were mapped and analyzed using ARC/INFO. Spatial patterns were assessed with univariate and bivariate Ripley's K analysis, which measures the scale at which one and two sets of points, respectively, are 'attracted' or 'repelled'. *R. parksii* truffles were not associated with organic layer depth, root density or forest structure. *E. granulatus* truffles were distributed in widely-spaced, high-biomass clusters which are significantly associated with thick organic layers with a high density of fine roots. *E. granulatus* truffles were significantly distanced from trees at 1–2 m. No other associations were found between *E. granulatus* truffles, logs, ferns or shrubs. Although *E. granulatus* comprised more than 90% of the total truffle biomass in these unmanaged mature and old-growth stands, in managed-young stands, *E. granulatus* truffles were rare and total truffle biomass was low. In managed-young stands, organic layer depth and fine root density have been significantly reduced with the introduction of fire. Slash burning and soil scarification practices in these forests may have a strong affect on local food abundance and availability of the most common truffle for small mammal consumers. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: *Elaphomyces granulatus*; Hypogeous sporocarps; Pacific Northwest; *Rhizopogon parksii*; Ripley's K analysis; Soil organic layer; Truffles

1. Introduction

Truffles are an important food source for many forest animals (Fogel and Trappe, 1978; Maser et al., 1978; Claridge et al., 1996). Their abundance within a forest stand may influence local small mammal populations (Clarkson and Mills, 1994; Carey, 1995; North et al., 1997) as well as their predators, such as the spotted owl (*Strix occidentalis*) (Carey, 1995). Truffles make up more than 60% of the dietary biomass of several species of Geomyidae (pocket gophers), Microtidae (voles) and Sciuridae (chipmunks and squirrels) (Fogel and Trappe, 1978; Maser

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et al., 1978). In conifer forests, most truffles are the below-ground fruiting bodies of ectomycorrhizal fungi. The fungi mediate nutrient and water uptake for host trees and receive photosynthates (Fogel, 1980; Harley and Smith, 1983). While the linkage between conifer hosts, mycorrhizal fungi and animal consumers has been well-established, forest or soil conditions associated with truffle productivity are unknown for all but a few commercially valuable species. Although several studies in the western US have found truffles are more abundant in older, undisturbed forests than young-managed stands (Vogt et al., 1981; Amaranthus et al., 1994; North et al., 1997), the particular stand conditions associated with truffle productivity have not been identified. Changes in forest composition due to succession, disturbance or timber harvesting will affect truffle abundance and diversity because of the linkage between truffle producing mycorrhizal fungi and their tree hosts (Harley and Smith, 1983). Other ecosystem characteristics such as local edaphic conditions and the size and decay state of coarse woody debris may also influence truffle production (Amaranthus et al., 1994). Understanding which forest conditions influence truffle abundance would help foresters assess the impact of management on truffle biomass and evaluate the potential abundance of this food source for small mammals in different stands.

Factors that influence the production of above- and below-ground fungal sporocarps ('mushrooms' and 'truffles') have been suggested by field observations from several researchers but not systematically studied (Vogt et al., 1992). Environmental controls such as temperature and precipitation appear to influence timing and abundance of mushroom production (Laiho, 1970; Mehus, 1986; Wasterlund and Ingelog, 1981). However, for truffles the above-ground climate may not be as important as the temperature, moisture and nutrient availability within the soil (Hering, 1966; Peredo et al., 1983). Above- and below-ground sporocarp production is influenced by the species composition of the forest (Chu-Chou and Grace, 1982; Dighton and Mason, 1985; Dighton et al., 1986; Hilton et al., 1989; Jansen and Denie, 1988; Temorshuizen and Schaffers, 1989). Some studies suggest sporocarp biomass increases with stand age (Vogt et al., 1981; Amaranthus et al., 1994). Stand structures such as large pieces of woody debris or thick organic layers may also influence truffle production by providing a nutrient and moisture reservoir for the fungal mycelium. To improve manager's estimates of local truffle production, a spatially-explicit analysis of sporocarp locations and their association with forest structure or edaphic conditions is needed.

This study examines the distribution and stand characteristics associated with *Elaphomyces granulatus* (*E. granulatus*) and *Rhizopogon parksii* (*R. parksii*) sporocarps, possibly the two most common truffle species in western North America (Smith et al., 1981; J. Trappe personal communication). The spatial distribution of *E. granulatus* and *R. parksii* sporocarps and their association with forest conditions was analyzed by mapping organic layer depth, root density, forest and understory vegetation, and truffles in 12 square and six transect plots. To provide a range of vegetation and soil conditions, plots were located in young, mature and old-growth forests which had different disturbance histories. Mapped locations of *E. granulatus* and *R. parksii* truffles, soil conditions and stand structure were used to examine three questions: (1) are the truffles of these two species clustered, and if so, at what spatial scales?; (2) are *E. granulatus* and *R. parksii* sporocarp locations associated with the depth or root density of the organic layer?; and (3) are *E. granulatus* and *R. parksii* truffles associated with or 'repelled' by different species or decay states of trees, logs or understory vegetation?

2. Methods

Associations between truffles and forest stand conditions are difficult to identify because sporocarps are the sporadic fruiting bodies of more extensive mycelium networks. Furthermore, sporocarp clusters may be clones of the same genet rather than individuals (Dahlberg and Stenlid, 1995). Truffles provide a point location for a particular fungal species without providing information on the extent of the mycelium producing the fruiting body or whether different truffles come from one or more genets. Using a sample of epigeous sporocarps and testing for somatic incompatibility, some studies have found sporocarps from a single genet ranging from 1 to 27.5 m apart (Dahlberg and Stenlid, 1990; Baar et al., 1994; Dahlberg and Stenlid, 1995; Dahlberg, 1997). Therefore, factors effecting truffle fruiting may result from favorable

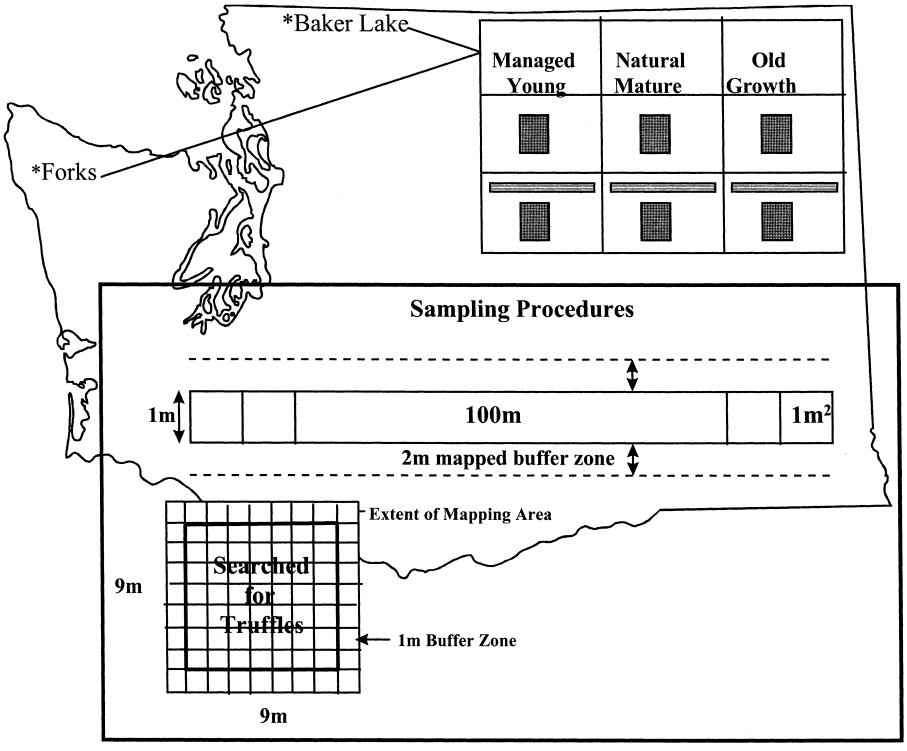

Fig. 1. Sampling methods used at two locations in Washington State. At Forks and Baker Lake, six sites were sampled in three stand types; managed young, natural mature and old growth. At all 12 sample sites, 81 m^2 plots (with a 49 m^2 truffle sample area) were established and at six of the sites, 1/100 m transects were established.

conditions near the truffle location or over the extent of the mycelium net.

In this study, our focus is on the production of truffles as a food source, and we do not attempt to identify mycelium size or genetic structure of different sporocarps. Truffles are treated as individuals although some are probably clonal sporocarps of the same mycelium. Our analysis does not attempt to identify whether forest conditions associated with truffles are influencing the location of particular truffles or the network of mycelium from which the truffle is fruiting.

2.1. Study areas

Truffle sampling was conducted in 12 stands at two areas in Washington State; near the town of Forks on the Olympic Peninsula and near Baker Lake in the foothills of the North Cascades (Fig. 1). Three stand types with different disturbance regimes were selected to provide a range of forest conditions which might influence truffle production; managed young, natural mature, and old growth. In both areas, stands were selected to minimize differences in conifer species composition between sample sites while varying the disturbance history. This was an effort to standardize the mycorrhizal hosts of the truffle community while varying disturbance treatments. Natural-mature and old-growth stands differed significantly from managed-young stands in organic layer depth, root density, and volume of coarse woody debris (Table 1) (North, 1993).

Six sample stands near Forks (47°58′N, 123°59′W) (two in each stand type) were located in the western hemlock/swordfern-oxalis (*Tsuga heterophylla/Polystichum munitum-Oxalis oregana*) association (Henderson et al., 1989) between 200 and 500 m elevation. Although typed as western hemlock, Douglas-fir and Pacific silver fir (*Abies amabilis*) were common cohorts (Table 1). The climate is moist with most

Table 1
Forest structure and edaphic conditions for 12 stands of three types in two areas. Values for the two replicate stands at each site have been combined

	Forks			Baker Lake		
	Managed young	Natural mature	Old growth	Managed young	Natural mature	Old growth
Tree basal area (m^2/ha)	68.3	74.2	70.7	65.1	54.6	69.6
Species composition (%)						
Tsuga heterophylla	75	78	70	61	69	63
Pseudotsuga menziesii	15	15	20	20	5	10
Abies amabilis	5	4	2	6	18	16
Mean dbh (cm)	43	45	83	39	43	104
Age of dominant trees (year)	60	71	>260	61	73	>345
Log volume (m^3/ha)	197	458[a]	402[a]	153	511[a]	347[a]
Shrub cover (%)						
Acer circinatum				10		
Gaultheria shallon	6					
Rubus spectabilis	3			2		
Vaccinium alaskaense		2	1		11	8
V. parvifolium		7	9		3	2
Root density[c]						
Low	93[b]	11[a]	6[a]	90[b]	5[a]	3[a]
Medium	7[b]	76[a]	64[a]	10[b]	85[a]	71[a]
High	0[b]	13[a]	30[a]	0[b]	10[a]	26[a]
Mean organic depth (cm)	3.0[b]	4.4[a]	4.0[a]	3.1[b]	5.0[a]	4.3[a]

[a,b]Values with different superscript letters are significantly different ($p<0.05$).
[c]Root density is the percentage of 1 m^2 sample grids with low, medium and high root density at each of the six sites ($n=198$ for each site).

of the annual 280 cm/year of precipitation falling as rain between October and May, and temperatures are mild year round. Soils are weakly-developed, well-drained spodosols with a metabasalt bedrock. Two managed-young stands were clearcut and burned in the early 1930s and now are fully stocked with western hemlock and Douglas-fir. Two natural-mature stands were disturbed by a severe windstorm in 1921 leaving on average 15 large, old-growth trees per hectare which survived the storm and a 70-year old cohort of western hemlock. Two sites adjacent to the natural-mature stands but on east-aspect slopes unaffected by the windstorm, were old-growth and without detectable signs of disturbance.

Six sample stands near Baker Lake (48°48′N, 121°29′W) were in the western hemlock/Alaska huckleberry (*Tsuga heterophylla/Vaccinium alaskaense*) association between 300 and 500 meters elevation. This area is typified by a mixture of western hemlock, Douglas-fir and Pacific silver fir (*Abies amabilis*) with a history of localized wind disturbances (Henderson and Peter, 1985). Most of the annual 210 cm/year of precipitation falls as rain and ephemeral snow between October and May. Soils are shallow, well-drained spodosols or inceptisols (Henderson and Peter, 1985). Two managed-young stands were clearcut and burned in the early 1930s and now have an even-age forest of western hemlock and Douglas-fir. Two natural-mature stands were moderately disturbed by a windstorm in 1917, have about 20 residual old-growth trees per hectare and a 75 year-old cohort of western hemlock. Two adjacent old-growth stands appear to be free of significant disturbance since stand initiation.

Managed-young and natural-mature stands were similar in the size, age and density of trees while significantly differing in organic layer conditions, log volume and understory vegetation (Table 1). Although natural-mature and old-growth stands differed in the age and size of overstory trees, understory composition was similar and organic depth and log volume was slightly higher in natural-mature stands. These differences were due to the stands' disturbance histories. In both the Baker Lake and Forks areas

pre-settlement disturbance was dominated by infrequent severe windstorms. Records of fire scars and soil charcoal are rare until the 1930s when clearcut logging and slash burning commenced (Henderson and Peter, 1985; Henderson et al., 1989). Natural-mature stands had a forest structure, edaphic condition and understory composition consistent with historical patterns, while harvest and slash burning altered these conditions in the young-managed stands.

2.2. Plot Design

Two types of mapped plots were used: 81 m^2 square grids and 1 by 100 m long transects (Fig. 1). The square plots were examined for neighborhood affects on *E. granulatus* and *R. parksii* distribution, and the long transects were designed to evaluate how the distribution of these truffles varies across a forest stand. Both plots were used to assess *E. granulatus* and *R. parksii* truffle clustering and spatial distribution. All sites were sampled in 1994 within an 8 week period in the fall when truffle productivity is high (Hunt and Trappe, 1987; Luoma et al., 1991).

For the square plots, an area in each of the 12 stands was selected at random. A square, 9 m×9 m was established and a grid pattern within the square was marked by connecting 1 m intervals on the opposite sides of the square with string. This established 81 1 m square grids. Using the strings as Cartesian coordinates, vegetation and stand structure was mapped before truffle excavation began (Fig. 2). Trees were identified to species, their diameter measured and their location within the grid mapped. Logs were identified to species, assigned a decay class (Harmon et al., 1986) and drawn to scale on the grid map. Four shrub species (*Acer circinateum*, *Gautheria shallon*, *Vaccinium alaskaense*, *V. parviflora*) and three fern species (*Blechnum spicant*, *Polystichum munitum*, *Pteridium aquifolia*) were found in the plots and all individuals were mapped. The area of tip-up mounds, created by windthrown trees, was mapped.

Organic layer depth and root density were assessed for each of the 81 squares. Organic layer depth was measured and 0–3 cm was classed as low, 3–6 cm as medium and >6 cm as high. Root density was assessed as a measure of the tearing strength of the organic layer. Soils in which the truffle fork could rake with little or no impediment were classed at low density. Medium density were soils in which raking tore many fine roots but the fork could be pulled through the soil with a full arm motion. High root density was a thick mat of roots in which short, strenuous raking ripped

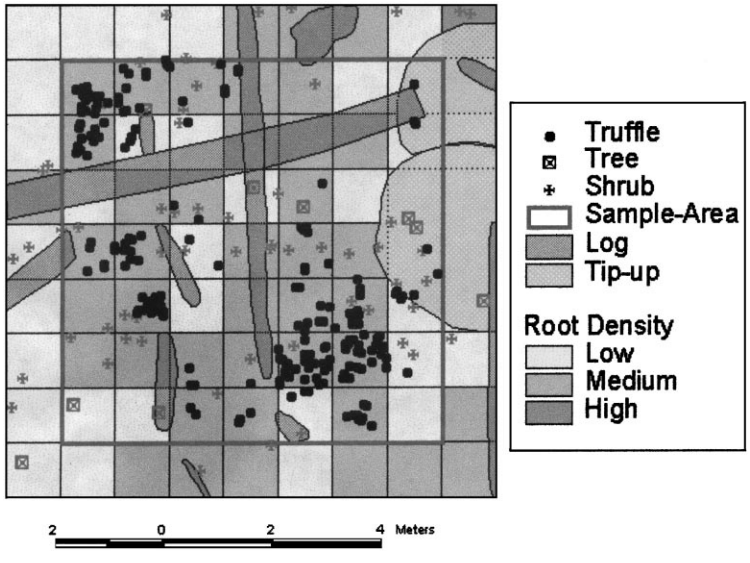

Fig. 2. Map of the types of data collected at each site. Truffles were only mapped inside the 7 m/7 m sample area. The area of tip-ups mounds was mapped. Truffles, trees and shrubs were identified to species. Logs were identified by decay class. Depth and root density (shown) of the organic layer were measured for each 1 m grid cell.

out a matted, cohesive block of soil. Field personnel were collectively shown examples of different root densities in an effort to standardize classifications.

Within the 9 m×9 m mapped grid, a central area 7 m×7 m was searched for truffles. In the 7 m×7 m grid, the organic layer was raked away to expose the mineral soil where most truffles fruit. Each sporocarp was identified to species and mapped using the string grids for reference. Sporocarps were placed in wax paper bags and identified by stand sample and grid square in which they were located. Sporocarps were cut in half, dried in a dehumidifier cabinet and weighed to the nearest 0.01 g.

Transects, 1 m wide/100 m long were also mapped in the sample stands. The same vegetative and stand structure features mapped in the square plots were recorded for the area within the transect and for 2 m on either side of the transect. Organic layer depth and root density were measured in 1 m blocks within the length of the transect. The locations of all truffles were mapped and each truffle was identified to species. Whenever a truffle was located, a 1 m^2 square area on each side of the transect was also searched to determine the size of each cluster encountered. The search of adjacent squares expanded to form a network of 1 m^2 squares until truffles were no longer found. Cluster size and the distance between clusters was calculated.

2.3. Analysis

All 81 m^2 plots were digitized from field maps using ARC/INFO software. Data for the stand structure, soil characteristics and truffle dry weights were entered into attribute tables associated with map locations. Although eight truffle species were found, only *E. granulatus* and *R. parksii* sporocarps were found in enough grids (>30 or 5% of total sample grids) to be analyzed.

Using the ARC/INFO files, maps of each 81 m^2 plot were made in ARC/VIEW assigning different symbols and colors to each truffle, shrub, fern, tree species, and log decay class. These maps were used as an initial evaluation of stand features which might be associated with truffle locations because different information layers could be added or deleted to clarify spatial patterns for sporocarp locations.

ARC/INFO was then used to calculate the distance from each *E. granulatus* and *R. parksii* truffle location to the nearest log segment. The relationship of truffle biomass with distance to logs of different decay classes was analyzed with regression.

Association between soil characteristics and truffle locations for *E. granulatus* and *R. parksii* was examined using hierarchical loglinear analysis in the 12 49 m^2 plots (n=588) and the six 100 m transects (n=600). The presence or absence of *E. granulatus* and *R. parksii* truffles in the 1188 1 m^2 squares was compared to the expected values given the proportion of each soil characteristic for all the plots.

To determine the distribution pattern of *E. granulatus* and *R. parksii* truffles, a univariate Ripley's K analysis was used (Moeur, 1993). Ripley's K compares distances between all location points in the same plane (Ripley, 1979; Diggle, 1983) using the reduced second moment measure or K function to examine spatial associations over a greater range of scales than immediate neighborhood (nearest neighbor) effects. The estimator of $K(d)$ is calculated as:

$$\hat{K}(d) = A \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{\delta_{ij}(d)}{n^2}, \text{ for } i \neq j$$

where A is the plot area with n truffles and δ_{ij} is the distance between truffle i and truffle j. We used a square root transformation $\hat{L}(d)$ which linearizes, $\hat{K}(d)$, stabilizes variance and has an expected value approximating zero (Moeur, 1993; Ripley, 1979).

Edge effects are eliminated with a toroidal edge correcting method which simulates wrapping each edge of the plot around to its opposite side using a three dimensional shift (Bailey and Gatrell, 1995). Confidence boundaries around $\hat{L}(d)$ were generated by measuring the departure of the observations from a Monte Carlo simulation based on a Poisson model (Moeur, 1993). One hundred random realizations were run to determine the 95% confidence boundaries for distances of 0–3.5 m at 0.1 m intervals. When $\hat{L}(d)$ values exceed the values of the Monte Carlo random realizations (P), the observed distribution is considered to be clustered and when $\hat{L}(d) < P$, the distribution is considered regular.

E. granulatus and *R. parksii* truffle distributions were also assessed with a Thiessen polygon analysis which provided a visual and quantitative comparison

to the Ripley's K univariate analysis. Thiessen polygons, also known as Voronoi polygons (Burrough, 1986), were created in ARC/INFO. Using each truffle as a center point, polygons were constructed by drawing perpendicular bisectors between the path of neighboring truffle locations. The resulting polygon around a truffle includes all points in a plane that are closer to that truffle than any other truffle. The size and distribution of Thiessen polygons have been used to evaluate how the growing space, density, and competition of adjacent plants change with succession (Mithen et al., 1984; Kenkel et al., 1989; Schuster et al., 1992). Using ARC/VIEW, patterns in the size and distribution of the Thiessen polygons were compared to significant cluster values from the Ripley's K analysis.

To assess truffle association with a site's vegetation, a bivariate Ripley's K analysis was used. The bivariate Ripley's K is similar to the univariate analysis except that pair-wise distances are between two different data sets. In bivariate analysis, points are either independent of, 'attracted', or 'repelled' by the other data set. The analysis indicates whether truffles are associated with or 'repelled' by different tree or shrub conditions. Spatial coordinates for the model were obtained from the ARC/INFO data, selecting a particular vegetative point set and discarding all buffer points outside the 7 m×7 m sample area. This created an identical extent for the truffle points and the other vegetation point locations.

Eight truffle species (including *R. parksii*), two shrubs and two ferns were not included in the bivariate analysis because of low sample sizes. Any measure with less than five locations in a plot produced erratic results using bivariate Ripley's K. All spatial analyses were critically interpreted because proximity or avoidance may result from many factors. For this reason the confidence envelopes from 100 Monte Carlo simulations in the univariate and bivariate Ripley's K were set at 5% and 95% to highlight only strongly significant departures from random distributions.

3. Results

Total truffle biomass and density were significantly greater ($p<0.05$) in natural-mature and old-growth stands compared to young-managed stands using combined samples from the transect and square plots (Table 2).

Table 2
Truffle biomass and density in three stand types for all nine species collected

Variable	Managed young	Natural mature	Old growth
Biomass (kg/ha)	1.27[b]	9.59[a]	7.20[a]
Density (#/ha)	1111[b]	6843[a]	9217[a]

[a,b]Values with different superscript letters are significantly different ($p<0.05$).
Values from Forks and Baker Lake were combined within stand type because there was no significant difference between the two areas.

Ripley's univariate analysis found *E. granulatus* truffles significantly clustered for distances of 1–3 m in all stand types (Fig. 3). Clusters varied from 5 to 63 truffles in size with an average density of 10.3 truffles/m^2 (s.d.=5.9, n=29). Using 4 truffles/m^2 (approximately the mean minus one s.d.) as a minimal definition of a cluster, 17 clusters were sampled along the six 100 m^2 transects. Distances between clusters varied widely from 4.1 to 75.6 m with a mean of 15.7 m (s.d.=19.3). No clusters were found along the sample transect in one managed-young stand. *R. parksii* truffle distribution was not significantly clustered or regular.

The hierarchical loglinear analysis did not show a significant association between *R. parksii* truffles and organic layer depth or root density. However, for *E. granulatus* truffles there was a significant association with organic layer depth, root density and the interaction term for medium organic layer depth×high root density (p=0.004). All standardized residuals were less than 1.96 in absolute value, indicating the final loglinear model was a good fit for the data. Because *E. granulatus* truffles were strongly clustered and grouped truffles may have been produced by a common mycelium, a second loglinear analysis was completed using a scale appropriate to *E. granulatus* cluster size. The square plots were re-analyzed using a 2 m×2 m grid and averaging the organic layer depth and root density values for each 4 m^2 unit (n=192). *E. granulatus* cluster units were significantly associated with medium organic layer depth and high root density (p=0.03).

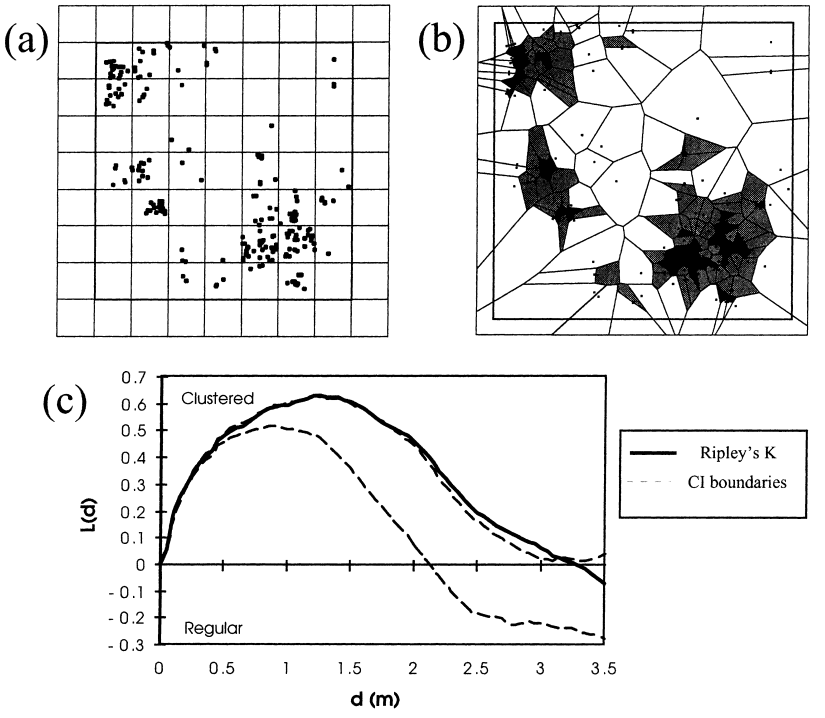

Fig. 3. Truffle data for site 1 (Forks) which was typical of the 12 sample sites. (a) Map of *Elaphomyces granulatus* truffles with 1 m sample grid. (b) Thiessen polygons for *E. granulatus* locations. The area of the white polygons is >1 standard deviation (s.d.) above the mean area size, the area of the gray polygons are within 1 s.d. of the mean, and the area of the black polygons are more than 1 s.d. smaller than the mean. Edge polygons were excluded from the analysis shading. (c) Ripley's K analysis of *E. granulatus* positions indicating a significant clustering pattern (above the 95% confidence boundary) at 1–3 m distances.

The Ripley's bivariate analysis indicates that *E. granulatus* truffle-tree locations were significantly repulsed at 1–2 m (Fig. 4(a)). No significant spatial interaction was detected for *E. granulatus* truffles and red huckleberry (*Vaccinium parviflorium*) (Fig. 4(b)) or deer fern (*Blechnum spicant*) (Fig. 4(c)). A bivariate analysis of *E. granulatus* and *R. parksii* truffle locations was possible at two of the sites which had sufficient sample sizes. The analysis did not find significant association between these two species (Fig. 4(d)).

E. granulatus truffle biomass was not correlated with distance from all logs (r^2=0.03, p=0.43) or logs by decay classes I–II (r^2=0.02, p=0.52), III (r^2=0.03, p=0.44), IV (r^2=0.13, p=0.26), or V (r^2=0.16, p=0.29). *R. parksii* truffles also were not correlated with the distance from all logs (r^2=0.13, p=0.26) or logs by decay classes I–II (r^2=0.05, p=0.46), III (r^2=0.07, p=0.48), IV (r^2=0.13, p=0.29), or V (r^2=0.18, p=0.21).

4. Discussion

While the importance of truffles as a staple food source for many forest small mammals was reported 20 years ago (Fogel and Trappe, 1978; Maser et al., 1978), the influence of forest composition, structure or soil conditions on truffle abundance has not been determined. Most truffle studies have focused on taxonomy and distribution of species because difficulty of sampling has limited the scope and scale of truffle collections. In turn, there have been few research studies at the ecosystem level because fundamental information on the autecology of different species is largely unknown, making it hard to model the composition, structure and function of the truffle community. The processes by which soil or forest conditions affect truffles can only be hypothesized because most of the ecosystem dynamics affecting fungal fruiting are unknown. This study assumes that habitat composition and structure may influence

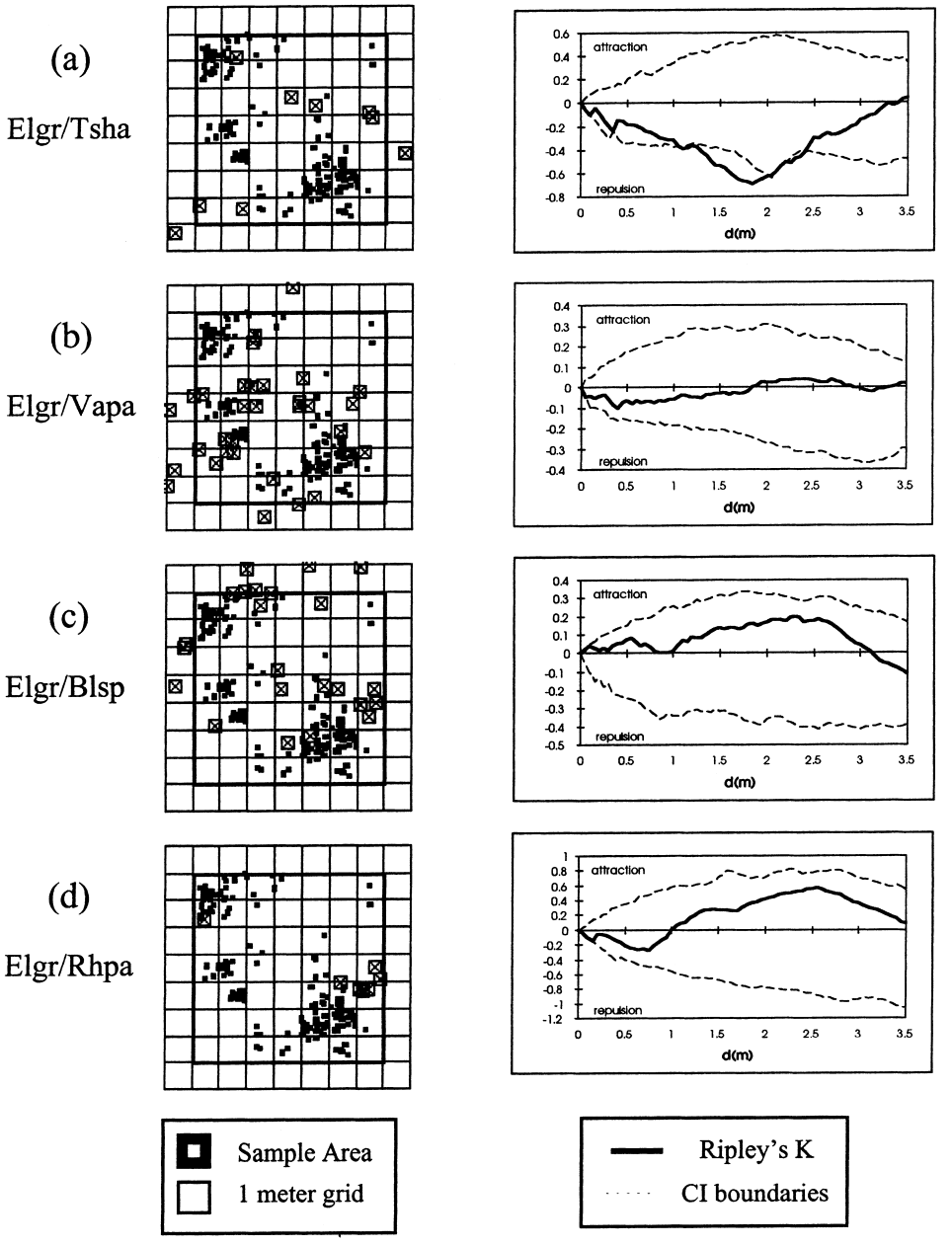

Fig. 4. Location maps and Ripley's bivariate analysis for four pairs of spatial locations at site 1 (Forks), which was typical of the 12 sample sites. On the Ripley's graphs is the solid line at 0, $\hat{L}(d)$ is the heavy solid line and the dashed lines are the 95% confidence envelope. (a) *E. granulatus* truffles and western hemlock, (b) *E. granulatus* truffles and red huckleberry, (c) *E. granulatus* truffles and deer fern, and (d) *Elaphomyces granulatus* and *Rhizopogon parksii* truffles.

sporocarp production, but it does not explicitly test this assumption. Our results, therefore, should be treated with caution because we examined only the spatial association between two species of truffles and selected forest conditions, not the mechanisms which trigger sporocarp formation. Correlation is not

causation, particularly when so little is known about the autecology of different truffle producing mycorrhizae. Research on these mechanistic questions may take several decades, and in the interim we hope this research can help managers understand how changes in vegetation and soil conditions may affect an important food source in forest ecosystems.

R. parksii truffles were not significantly associated with the measured forest variables or edaphic conditions. *R. parksii* truffles were distributed as widely scattered individuals rather than in clusters, making it difficult to identify a significant spatial association with particular stand or soil conditions. *R. parksii* is a mycorrhizal specialist associated with Douglas-fir. Only 5–20% of the basal area in the sample stands was Douglas-fir, possibly limiting the abundance of *R. parksii*.

The loglinear analysis indicates a significant association between *E. granulatus* truffles and thicker organic layers with a high root density. This association corresponded with the difference in *E. granulatus* truffle abundance between natural and managed stands. Generally young-managed stands lacked thick organic layers with a well-developed network of fine roots because slash had been burned after they were harvested. On the long transect plots two clusters of *E. granulatus* truffles were found in a managed-young stand but both were in surface depressions with seeps that had not burned. A 4 year long study in these stands (North et al., 1997) found abundant *E. granulatus* truffles in natural-mature and old-growth stands, but in managed-young stands *E. granulatus* truffles were only found in microsites which had not burned. In Pacific silver fir stands in Washington, Vogt et al. (1981) found high biomass *E. granulatus* truffle clusters in undisturbed old-growth but not in managed-young stands. In a 4-year study in central Oregon, Luoma et al. (1991) found only one large cluster of *E. granulatus* truffles whose biomass was an outlier compared to biomass collections of the other 46 truffle species collected. *Elaphomyces granulatus* becomes more common with increasing latitude (J. Trappe personal communication) where decomposition is slower due to a cooler, wetter climate (Harmon et al., 1986). In these conditions thick organic layers tend to develop because fire disturbance is rare. The burning of slash in these areas introduces a disturbance which was historically rare, producing thin organic layer conditions which are atypical. This change in the soil organic layer may be affecting *E. granulatus* truffle productivity and food abundance for mycophagists.

Spatial distributions of *E. granulatus* truffles were highly clustered in both the square plots and along the transects. The Ripley's univariate analysis of the square plots found *E. granulatus* truffles clustering from 1–3 m; a pattern which was verified in the Theissen polygon analysis of each site. Transect data indicates *E. granulatus* truffle clusters were sparsely and sporadically distributed across a stand. Other truffle studies have found the sporocarps of some species to be clustered (Fogel, 1976; Fogel, 1980; States, 1985; Hunt and Trappe, 1987). It is unknown whether these clusters are clonal because mycelium size and genetic structure for truffle producing fungi has not been studied. Analyzed as either individuals or clusters, *E. granulatus* truffles were significantly associated with thick organic layers with a high root density.

E. granulatus and *R. parksii* truffle locations and biomass were not associated with logs in our sample sites. A southern Oregon study, however, by Amaranthus et al. (1994) found a significant association between logs and truffles in young clearcut and old-growth stands. They concluded that logs may function as a moisture and nutrient reservoir during drought periods and thereby provide favorable microsites for truffles during the summer. Our study sites in Washington rarely dry out even during summer and therefore the seasonal need for a reservoir may not be as important as it is in the drier conditions of southern Oregon.

The Ripley's bivariate analysis revealed a significant repulsion between *E. granulatus* truffles and trees which peaked at 2.0 m. In his mapped plots, Fogel (1976) noted that truffles were generally located at the midpoint between tree locations which was about 2 m at his sample sites. The below-ground zone immediately around tree boles differs from the general stand both in microclimate and root structure. In this zone, through-fall precipitation is reduced and the fine roots associated with mycorrhizae may be less common than the large structural roots necessary for tree stability. Several studies suggest that as a tree grows, ectomycorrhizae succession can limit the distribution of some species to further from the tree bole (Mason et al., 1983; Fleming et al., 1986)

5. Conclusions

Hypotheses about the impacts of forest management practices on truffle productivity have focused on the changes in age and composition of the mycorrhizal tree hosts or the effects of reducing coarse woody material on the forest floor (Harvey et al., 1980a, b; Clarkson and Mills, 1994; Amaranthus et al., 1994). At our sample sites, however, the most significant impact on truffle abundance may be from changes in the organic layer due to slash burning. This response was seen in the common truffle *E. granulatus*, but it may not occur in other regions or with other truffle species. Sampling these sites and others, North et al. (1997) found *E. granulatus* constituted 93% of truffle biomass compared to only 40% in central Oregon (Luoma et al., 1991). The apparent domination of truffle production by *E. granulatus* in western hemlock dominated forests of Washington State suggests management practices which reduce its abundance may affect food availability for small mammals. Furthermore, *E. granulatus* truffles were not distributed as a homogenous population across the forest floor. Forest management practices, such as road building, skidding and burning which locally reduce organic layer depth or fine root density, could affect stand level abundance of *E. granulatus* truffles if disturbance occurs in an area where the truffles are clustered. Large-scale manipulation experiments are needed to follow the long-term effects of management practices on truffle abundance and diversity. In the interim, ecosystem management should consider how changes in stand conditions may affect an underground but important food source for forest animals.

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