Foundations of Biodiversity in Managed Douglas-fir Forests

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The controversy over old-growth Douglas-fir *(Pseudotsuga menziesii)* forests and late-seral species has resulted in substantial information about biodiversity (Carey 1989, 1995, Carey and Johnson 1995, Carey et al. 1990, 1992, Forsmann et al. 1984). Major compilations of old-growth related research and its management implications include Gutierrez and Carey (1985), Ruggiero et al. (1991), Thomas et al. (1990, 1993), and Thomas and Raphael (1993). The need to restore and create late-seral ecosystems in the future was recognized (Carey 1985, Thomas et al. 1990), and Thomas et al. (1990) called for experiments to determine if northern spotted owl *(Strix occidentalis)* habitat could be created silviculturally. Our study addresses the management of second-growth forests to develop late-seral "composition, structure, function, ecologic products, and economic products" (Carey 1994a).

Our Forest Ecosystem Study (PES) was designed to test whether late-seral forest attributes (specific targets include high architectural diversity, large diameter trees, high mycorrhizal and non-mycorrhizal fungal diversity, high vascular plant diversity, large prey base) can be developed from stem-exclusion phase (Oliver and Larson 1990) forests through silviculture, and whether providing dens (cavities or nestboxes) can increase the density of northern flying squirrels *(Glaucomys sabrinus)* in second-growth. A new silvicultural technique, variable-density thinning (Carey and Miller 1991, Carey 1994b) was devised to create spatial heterogeneity in composition and structure that mimics conditions found in old-growth forests.

We adopted a trophic pathway approach to the evaluation of our treatments. The basis for the forest ecosystem is the soil; forest soil foodwebs are characterized by a dominance of fungal activity over bacterial activity (Kromack et al. 1988). Mycorrhizal fungi assimilate large amounts of net primary productivity in Douglas-fir forests (Fogel and Hunt 1983) and enhance primary productivity by augmenting plant uptake of water and nutrients. Fungi are food for a diversity of consumers including arthropods, nematodes, and mammals (Perry et al.

1989). Fungal fruiting bodies are the primary food of northern flying squirrels which are the primary prey of the spotted owl (Carey et al. 1992, Carey 1995). Thus we evaluate the effects of thinning on soil foodwebs, production of truffles and mushrooms, abundance of vascular plants, and abundance of small mammals, including the flying squirrel.

This paper reports preliminary results of our research. Baseline data comparing biological and structural attributes of two forests with different management histories, and an overview of early effects of variable-density thinning and den augmentation are presented, along with sampling techniques, sample sizes and preliminary data.

STUDY AREA

The study area is located in 50-70 year old, Douglasfir forests in Thurston County, Washington. Terrain is flat to rolling and elevation is 100-140 meters. Annual precipitation is 800-900 mm with only 10-15 % of the annual precipitation falling during the peak growing months of June - September (Pringle 1990).

Soils are coarse-textured gravelly and gravelly-sandy loams (glacial till and glacial outwash) of the Tenino and Everett soil series (Pringle 1990). These excessively drained soils combine with low summer rainfall to create droughty conditions and an edaphic Douglas-fir climax (Franklin and Dyrness 1973).

The FES contains two forests with different management histories. The Farley/Hill (FM forest, comprised of the Farley and Hill blocks, was clear-cut in 1927, and following natural regeneration was lightly thinned in 1972 and 1989. During these commercial thinnings live, recently dead but salvageable, and fallen trees were routinely removed. FH is dominated by 55-65 cm dbh Douglas-fir (39-43 m tall) with small amounts (3-8% total stems) of black cottonwood *(Populus trichocarpa)* and red alder *(Alnus rubra)*. Trees in FH appear to have been open grown (i.e. with moderate stocking levels) since stand initiation; many trees had ample crowns and lateral branches to near ground level. The low understory was well developed and was dominated by salal *(Gaultheria shallon)*, California *hazel (Corylus cornuta* var. *californica)*, and swordfern *(Polystichum munitum)*. Other common Douglas-fir series associates (Henderson et al. 1989) such as servicebeny *(Amelanchier alnifolia)* , Western fescue *(Festuca occidentalis)*, baldhip rose *(Rosa gymnocarpa)*, and creeping snowberry *(Symphoricarpos mollis)* were common. The FH forest contained residual (previous stand) Douglas-fir (0.4 live trees/ha and 0.4 snags/ha) and had 1% cover of coarse woody debris.

The Star/Stellar (SS) forest, consisting of the Star and Stellar blocks, was clear-cut in 1937, and following natural regeneration had not been further manipulated. SS was a closed-canopy forest dominated by 30-45 cm dbh Douglas-fir (30-35 m tall), with a few western hemlocks *(Tsuga heterophylla)*, western redcedars *(Thuja plicata)*, and Pacific yews *(Taxus brevifolia)*. Trees killed by suppression and trees with small crowns were abundant, suggesting a very high stocking level since stand initiation. Understory vascular vegetation was sparse, with only small amounts of salal and Oregongrape *(Berberis nervosa)*. Douglas-fir series associates such as serviceberry, Western fescue, baldhip rose, and creeping snowberry were also found in this forest. The forest floor was typically dominated by mosses, particularly *Eurhynchium oreganum* and *Hylocomium splendens*. Exceptions to the high canopy closure and sparse understory were areas of laminated root rot *(Phellinus weirii)* infection, which comprised 7-15 % of the forest. -in these root-rot centers, understory shrubs, forbs, and ferns were well developed. The SS forest contained large (70-90 cm db) residual Douglas-fir (3 live trees/ha and 3.5 snags/ha) and had 4-6 % cover of coarse woody debris.

EXPERIMENTAL DESIGN

We used a complete randomized block design with 4 blocks (Star, Stellar, Farley, and Hill) of four treatments. The treatments included: no treatment (control=CT), variable-density thinning with three thinning intensities (subtreatments), den augmentation (cavities in live trees and nest boxes) and den augmentation and thinning. The three thinning subtreatments were: a light thin (LT) to 310 trees/ha, a heavy thin (HT) to 185 trees/ha and a rootrot thin (RT) that removed all low vigor trees from root-rot centers and 10-m buffers, while retaining apparently healthy trees (about 40 trees/ha). Each block was comprised of four 280 m x 280 m stands plus surrounding 40-m buffers. Thus the entire study area contained 16 stands (13 ha each), 8 of which were thinned experimentally. The study area, with buffers, encompassed 207 ha. The stands were surveyed into 8 x 8 grids of 0.16-ha cells (40 m x 40 m); it was to these cells that the thinnings (subtreatments) were applied. The RT thin was applied to approximately 15 % of the stands, either to actual pockets of infection where apparent (in SS), or to randomly selected cells where root-rot was not apparent (FH and SS). The LT and HT thinnings were randomly applied to the remaining cells in a 2:1 ratio. Thinning operations were performed in the

winter of 1992-93 and spring of 1993 using skidder removal from a limited number of skid roads.

The grids are also templates for trapping arboreal rodents and small mammals and for den augmentation. For arboreal rodents, 2 traps were placed at each of the 64 grid-cell comers (stations), 40 m apart in all 16 stands; small mammal traps (2 traps/ station) were placed at 100 stations spaced 20 m apart in the 8 unthinned stands. One-half of the thinned and half of the unthinned stands were augmented with 16 nestboxes and 16 cavities each, systematically located every 80 m at alternating trap stations. Details of nestbox and cavity design and construction follow Carey and Gill (1983).

This paper reports on the use of supplemental dens, but does not consider their effects on plant, fungal, or arboreal and small mammal species richness or abundance. Thus, control (CT) refers to unthinned stands with or without supplemental dens, and thinnings (RT, HT, and LT) refer to both den-augmented and non-augmented stands. Hereinafter, CT, RT, HT, and LT will be referred to as treatments.

SAMPLING METHODS

Plants, Epigeous Fungi and Soil Foodwebs

Vegetation was sampled prior to thinning with 15 randomly located plots per stand (60/block, 240 overall). One year after variable-density thinning (summer 1994), 192 permanent vegetation plots (6 per subtreatment per stand and 6 per control) were established at the centers of randomly selected grid cells. Vegetation composition, cover, and structure were measured using nested circular plots of 5.6-m radius (100 m^2) and 12.6-m radius (500 m^2). In fall 1994, species composition and biomass of epigeous fungi were recorded on a subset (n = 128) of the 100 m^2 permanent plots. Soil foodweb samples were taken in spring 1994 from a subset (n = 100) of 4 m^2 plots offset from permanent plot centers. The percent cover of recognizable mycorrhizal mat-types *(Piloderma* sp., *Hysterangium sp., Gautieria* sp.) was measured and mapped, and approximately 100 g of soil was collected from each plot. Soil was placed in plastic bags and stored in an insulated cooler during travel. Samples were then stored at 4° C and laboratory analyses of microbial activity were made within 5 days of collection. The following parameters were evaluated: (1) grams dry weight (gdw)/gram soil; (2) active and total bacterial and fungal biomass (gg/gdw); (3) total nematodes (#/gdw); (4) percent fungal-feeding, bacterial-feeding, plant-feeding and predatory nematodes. Active and total bacterial and fungal biomass (AB, AF, TB, TF) were determined as described by Babiuk and Paul (1970) and Ingham and Klein (1984), and were used to compute the ratios TF/TB and AF/AB. Nematodes were extracted as described by Anderson et al. (1978) and were separated into trophic groups based on morphological characteristics used in taxonomic classification (Bongers 1988).

Truffles

Truffles (fruiting bodies of hypogeous fungi of the sub-divisions Ascomycotina, Basidiomycotina, and Zygomycotina) were sampled every 5-7 weeks beginning in April 1993 (immediately after the thinnings). Truffles were collected from each of 10 circular 4.0-m^2 plots located systematically along randomly placed transects in each thinning subtreatment and in the non-thinned controls (160 plots/ period). At each plot, vegetation was removed, plots were raked to mineral soil depth (approximately 5 cm), and all fungal sporocarps were collected, identified to species, and dried for biomass determinations.

Forest Floor and Arboreal Mammals

Arboreal rodents were trapped twice a year (spring and fall, 1991-1995), and forest floor small mammals were trapped once per year (1992-1994) during the summer. Trapping data will be reported from fall 1991, and spring and fall, 1992 for the arboreal rodents, and for 1992 and 1993 for the forest floor small mammals. Forest floor mammal trapping effort was for a total of 6400 trap nights in each of 1992 and 1993. Small mammal abundance was calculated as captures per 100 corrected trap nights (CPUE) (Nelson and Clark 1973). Abundance was calculated for each of 4 trapped stands/forest/year, we report the mean CPUE ± SE for each forest in each year based on these 4 stand values.

We summed captures and counted individuals for the three arboreal species (flying squirrel, Townsend's chipmunk *[Tamias townsendii]* and Douglas' squirrel *[Tamiasciurus douglasii])* for 1991-1992. Chipmunks were not sampled in 1991. We estimated mean densities of flying squirrels (3 seasons) and chipmunks (2 seasons) per stand as recommended by Carey et al. (1991), combining the Chapman modification of the Lincoln-Petersen Index with grouping captures by week and estimating area sampled with site specific mean maximum distances moved. Forest means were calculated from stand means. All reported data is from pre-thinning sampling and does not consider the effects of supplemental dens.

Flying squirrels were radio-collared to document movement patterns and den use, but telemetry and

den site data are not included. Fecal pellets collected during trapping were placed in formalin and later analyzed for dietary components. The protocol for trapping is outlined in Carey et al. (1991); protocol for fecal pellet analysis follows McIntire and Carey (1989). Use of supplemental nestboxes and cavities was monitored on a yearly basis. In 1995, nestboxes and cavities were cleaned in March, and checked for use in July.

STATISTICS

We report descriptive statistics to compare groups for which analysis is in progress. For exploratory analyses, the Student's t-test was used to compare two independent means where assumptions (normal distribution, equal variance) were met and where sample sizes were not small (plant species richness, small mammal abundance). The Mann-Whitney U test was used (as in comparison of vegetative cover between forests) where there were violations of normality. Tukey's B post-hoc multiple comparison test was used for truffle standing crop data (natural log transformed) to test for differences between two or more homogenous subsets of data. Soil foodweb treatment variables were compared by ANOVA between treatment within each forest. Because of high variability among treatments and small sample size within some treatments, all treatments were also combined in each forest and a between forest comparison was made for each soil foodweb variable.

RESULTS

Vascular Plants

FH stands had more species of plants than SS stands in total, in controls, in each experimental treatment, and in all vertical strata (Table 1). The between-forest differences in species richness were statistically significant for each treatment *($P < 0.05$;* CT, $t = 2.79$; *LT,* $t = 4.79$; HT, $t = 4.69$; RT, $t = 6.61$). A total of 138 species were found in all treatments combined in FH (69 in CT only), 101 species were found in all treatments combined in SS (44 in CT only). Percent cover values in FH were significantly higher than in SS for all strata in all treatments except for stratum 2 (woody shrubs < 2.0 m high) in the RT treatment (Table 2). Differences were also biologically significant. Of 34 species unique to FH control plots (not found in SS controls), 12 were alien species (no graminoids), 4 were native graminoids, 8 were native woody understory or midstory species, and 10 were native forbs and ferns. All 9 species unique to SS controls were native forb, fern, or shade-tolerant tree species. Of the 44 species found only in FH (all treatments combined), 14 were aliens (4 graminoids), 7 were native graminoids, 7 were native woody understory or midstory species, and 12 were native forbs and ferns. No species were unique to SS (all treatments combined).

By summer 1994, species richness had increased by 17-53 species in all thinning treatments in both forests when compared to the controls (Table 1). The increase was most evident in stratum 1 (annual and perennial forbs and ferns), where approximately 40% of the new species in both forests (all treatments combined) were aliens. In both forests, the weed species were mostly composites (Asteraceae), grasses, and legumes. The weeds had low percent cover in both forests, except for occasional thick patches of wall lettuce *(Lactuca muralis),* bull thistle *(Cirsium vulgare),* and clovers *(Trifolium* sp.) that were confined to the RT treatments. FH had higher understory and midstory woody species richness and cover values than SS, where the lengthy stemexclusion phase had precluded understory development (Tables I and 2).

Epigeous Fungi

Preliminary results of epigeous fungi sampling (from one sampling period in fall 1994) indicated total species richness was higher in FH, but mycorrhizal species richness was higher in SS (Table 3). Epigeous fungal communities in both forests were dominated by the mycorrhizal genera *Russula, Cantharellus, Cortinarius, Inocybe, Laccaria, Lactarius, Boletus* and *Amanita,* and the saprophytic genera *Clitocybe, Collybia, Hypholoma, and Mycena.* The ratio of mycorrhizal to total species in control stands was higher in SS (49% of total species vs. 33% in FH). Mycorrhizal species richness diminished in both forests in direct proportion to the intensity of thinning, with both the absolute number of mycorrhizal species and the ratio of mycorrhizal species to non-mycorrhizal species decreasing more in FH thinnings than in SS. Total epigeous fungal standing crop was similar in both forests, with SS having more of its total standing crop being mycorrhizal than FH (Table 3). Two genera, *Cantharellus* and *Russula* (primarily C. *cibarius, C. subalbidus, R. brevipes, R. sororia, R. placita,* and R *xerampelina),* accounted for 75-85% of the epigeous mycorrhizal biomass in both forests.

Soil Foodwebs

Mycorrrhizal mat coverage was lower in FH than in SS, and was reduced in both forests in direct proportion to the degree of thinning (Table 4). Few within-forest, between-treatment foodweb parameters differed significantly. In SS, total bacterial biomass

was significantly higher ($P < 0.05$) in the RT treatment than in other treatments. The percentage of fungal feeding nematodes was significantly higher ($P < 0.05$) in the CT and LT treatments. The percentage of predatory nematodes was significantly higher ($P < 0.01$) in the HT treatment than in other treatments. In FH, total fungal biomass was significantly higher ($P < 0.10$) in the LT treatment than in other treatments. The percentage of predatory nematodes was significantly higher ($P < 0.05$) in the LT and RT treatments than in CT and HT. Other parameters did not differ significantly.

Control stands showed no significant difference between forests for any soil foodweb components ($P = 0.10$). When all treatments were combined in each forest, SS had significantly more active and total fungi ($P = 0.10$), significantly more active bacteria ($P = 0.01$), and significantly higher percentages of fungal feeding nematodes ($P = 0.05$) and predatory nematodes ($P = 0.10$) than FH. Soil dry weight in FH was significantly higher than in SS ($P = 0.01$). FH had a significantly higher percentage of bacteriafeeding nematodes ($P = 0.01$) than SS (Table 4). Other parameters were not significantly different.

Truffles: *In Situ* and in Fecal Pellets

Overall species richness and uniqueness were similar in each forest, with many species being exclusive to one forest or the other (Table 5). Species richness was similar for control, light thin, and heavy thin treatments, and less for root-rot treatments in both forests. All treatments in both forests had some unique species, comprising 16-36 % of total species. Of the approximately 50 identified species of hypogeous fungi, 4-6 were undescribed species, with one undescribed genus. In the first year of sampling (1993), mean truffle biomass was significantly less (natural log transform, Tukey's B post-hoc comparison, $P < 0.05$) in RT than in CT or LT; CT, LT, and HT did not differ significantly from one another. Graphical representation of biomass vs. thinning levels suggested that biomass decreases with increasing thinning intensity; statistical evaluation of this relationship is in progress. In the first year (1993), standing crop ranged from a maximum of 1318 g/ha (CT, April) to a minimum of 3.9 g/ha (RT, April) (Colgan et al. 1994). In the second year (1994), there were no statistically significant differences ($P < 0.05$) between any treatments in mean total biomass. In 1994, truffle standing crop ranged from 400 g/ha (HT, April) to 2 g/ha (HT, August). Between-forest comparisons have not yet been made for the first two sampling years separately. However, when standing crop from all sampling periods was summed to April 1995, mean total biomass did not differ significantly ($P < 0.05$) between FH and SS or between any of the individual sub-treatments. Average standing crop for both forests during this time was 440 (162 SE) g/ha (dry), ranging from 136 (t 61 SE) *g/ha* (FH, RT) to 689 (± 217 SE) g/ha (FH, CT). During the first two years of truffle sampling, one or more truffles were found on 17% (382 of 2240) of the truffle plots. The most frequently encountered truffle genera were *Rhizopogon, Melanogaster, Hysterangium, Endogone,* and *Leucogaster.*

Flying squirrel fecal pellets from 1991 through 1994 showed the truffle genera *Rhizopogon, Gautieria, Leucogaster,* and *Melanogaster* were the most common food items in both forests, with *Rhizopogon* sp. being the most frequently encountered spore type (198 of 200 sampled animals contained *Rhizopogon* spores). *Gautieria* sp. were more commonly consumed in the SS forest, and *Melanogaster* sp. were more commonly consumed in the FH forest. Fecal pellets from both forests also contained spores of 10 - 12 additional truffle genera, small amounts of amorphous plant material, and fungal spores of the mushroom genera *Russula* and *Peziza* and families Agaricaceae and Boletaceae. With the exception of the truffle genus *Weraroa,* which was observed only in fecal pellets from FH, all genera identified in fecal pellets were also collected during truffle sampling. Truffles were the primary food for flying squirrels throughout the year in this area, with marked seasonal variation in taxa consumed. Unlike in other portions of their range (Maser et al. 1985), flying squirrels did not use lichens as a food source, except incidentally.

Arboreal Rodents

Arboreal rodent communities in both forests were composed of the northern flying squirrel, Townsend's chipmunk and Douglas' squirrel. Northern flying squirrels were more abundant in SS than in FH, while the Townsend's chipmunk was more abundant in the FH (Table 6). The Douglas' squirrel was captured infrequently in both forests (Table 6).

Both nestboxes (75% of 64 total) and cavities (22% of 64 total) were used more heavily in FH than in SS (31% and 3%, respectively) in 1995. Three litters of flying squirrels were born in nestboxes in FH; 1 litter was born in a nestbox in SS. Nest material in both forests was predominantly moss *(Isothecium stoloniferum* and *Eurhynchium oreganum),* with some shredded cambium, bracken fern *(Pteridium aquilinum)* fronds, and fruticose lichen *(Usnea sp.).*

Forest Floor Small Mammals

Forest floor small mammal communities in both forests included 2 shrews *(Sorex trowbridgii, S. monticolus),* the deer mouse *(Peromyscus maniculatus),* the Oregon creeping vole *(Microtus oregoni),* the shrew-mole *(Neurotrichusgibbsii),* and the southern red backed vole *(Clethrionomys gapperi). Two* additional species, the Columbian deer mouse *(P. keeni = P. oreas)* and the vagrant shrew (S. *vagrans),* occurred occasionally in both forests. Other species that were caught infrequently included the Pacific jumping mouse *(Zapus trinotatus),* the coast mole *(Scapanus orarius),* and the Pacific water shrew *(Sorex benderii).* Although species richness was similar in both forests, overall abundance of forest floor small mammals was significantly higher in FH than in SS in 1992 *($t = 3.57$, $P < 0.05$)* and again in *1993 ($t = 2.18$, $P = 0.07$)* (Table *7).*

The deer mouse and Oregon vole accounted for most of the between-forest difference in overall small mammal abundance in both years (Table *7).* In *1992* deer mice and Oregon creeping voles were significantly more abundant in FH than in SS (deer mice, $t = 4.47$, $P < 0.01$; voles, $t = 3.38$, $P < 0.05$). In *1993,* both taxa were again significantly more abundant in FH than in SS (deer mice, $t = 3.57$, $P < 0.05$; voles, $t = 4.78$, $P < 0.01$). Other taxa were trapped consistently and frequently (e.g. *C. gapperi, S. trowbridgii, S. monticolus, N. gibbsii),* or infrequently (e.g. *P. keeni, S. vagrans)* in both forests in both years, and did not contribute greatly to differences in overall abundance between forests. *Sorex trowbridgii* and *S. monticolus* were numerically the most abundant forest floor small mammals in both forests in both years.

DISCUSSION

This study addresses how and to what extent the forest vertical and horizontal structure, and plant, animal and fungal species composition and structure differ between the FH and SS second-growth forests, and how the forests will respond to treatments designed to accelerate forest development Because the FH stands were thinned 20 years ago, they provide some insight into what the SS forests may look like 20 years hence. During the 20 years since thinning, FH has developed a richer vascular plant component and more vertical structure as well, with all vertical strata showing higher species richness and cover values than SS (except for stratum 2 in the RT cells where cover was greater in SS) (Tables 1 and 2), although some of the differences also might be attributable to the open-grown nature of the stand. Because SS rootrot treatments were applied to actual infected areas, the low-shrub layer (stratum 2), was more developed as a response to localized tree mortality. The rapid increase in species richness in both forests after experimental thinnings and as a function of thinning intensity, was not unexpected, despite lack of previous quantitative studies. The increases resulted from the growth of residual species coupled with species colonization. Colonizers were primarily weedy composites (family Asteraceae), grasses, legumes and infrequently encountered native forest floor species having the capacity to rapidly establish by runners, suckering, or germination from a soil seed bank. Extensive or long-term weed colonization does not appear to be a problem because of the intentionally small scale of the thinnings.

Concurrently, the small areas of RT treatment provide sites for ruderals, shade intolerant species, and other early- to mid-successional organisms, and so increase forest diversity. Seedlings of species that will contribute to the understory and midstory strata (e.g., willow, alder, maple, salal, huckleberry, hazelnut, cascara) were found in most thinned plots *(93%* of plots had one or more species; *65%* had three or more species). Thus, architectural complexity has the potential to develop rapidly on the thinned sites.

Salal was the dominant understory woody component in both forests; shrub cover in control stands was *>40%* in FH (60% of that salal), and *>25%* in SS *(80%* salal). Salal is one of a number of woody plants that may also form mycorrhizae with some of the same fungal symbionts as Douglas-fir (Largent et al. *1980,* Amaranthus and Perry *1994,* Smith et al. *1995). If* so, salal could facilitate the transition from thinned to re-stocked stands by stimulating rapid mycorrhizal recolonization and establishment on Douglas-fir (and other Pinaceae) in thinned areas where salal is present. The presence of salal and other potential mycorrhizal host-species (as well as coarse woody debris) (Amaranthus et al. *1994)* on thinned sites may also play important roles because non-mycorrhizal weeds and annuals (Trappe *1987)* may gain competitive advantage if mycorrhizal fungi and other essential rhizosphere species decline in abundance (Amaranthus and Perry *1994,* Perry et al. *1989),* making it difficult to re-establish the native plant community.

The small mammal communities in our study were composed of the same characteristic species, but had a different structure than those reported by Carey and Johnson *(1995)* in their analysis of managed and old-growth forests of the Olympic Peninsula. In particular, FH and SS communities were dominated by fewer species, showed a reversal of the relative abundances of Columbian mice and deer mice, and

contained fewer creeping voles (SS only) when compared to managed stands of the Olympic Peninsula.

Carey and Johnson (1995) found prevalence of herbaceous cover and shrub abundance (with coarse woody debris), respectively, to be the best predictors of creeping vole and deer mouse abundance in managed stands, with Columbian mice increasing with total understory vegetation in managed stands. Deer mice and creeping voles accounted for most of the differences in abundance between FH and SS (Table 7). Creeping voles are primarily foliage eaters, and deer mice are primarily seed and fruit eaters but will consume large quantities of insects; both are also known to consume truffles and mushrooms (Carraway and Verts 1985, Maser et al. 1978, Rhoades 1986, Van Home 1982). As such, both benefit from the increases in vascular plant species richness and cover observed in FH, and attributable to FH management history. Thus, we believe the greater abundance of deer mice and Oregon voles in FH to be a further validation of Carey and Johnson's (1995) predictors. These same species may be limited by the paucity of understory plant species richness and cover that characterizes SS and other closed canopy, stem-exclusion phase stands. The rarity of the Columbian mouse in SS and FH may be related to lack of tall understory development and the lack of tree species diversity. Thus, plant and small mammal biodiversity appear more likely to be preserved if understory vegetation enhancement and avoidance of stem-exclusion conditions are explicit goals in managed forests.

The arboreal rodent community, represented by the same three species in both forests, exhibits taxon-specific differences in abundance that we believe are attributable, in part, to past management practices. The northern flying squirrel is strictly nocturnal, and relies almost entirely on truffles for food in our study sites. We identified 16 truffle genera from squirrel fecal pellets out of the 21 genera identified during truffle sampling (these 16 genera contain 40 of the total 50-plus truffle species we have identified to date), validating the important role flying squirrels have in truffle dispersal. In SS with its larger component of residual trees and snags (potential den sites), and coarse woody debris, as well as an absence of thinning disturbances since stand origin, we found a greater abundance of flying squirrels than in FH (Table 6). Carey et al. (forthcoming), confirmed the significantly higher availability of potential natural den sites (large trees, snags) in SS than in FH, and a substantially greater use of supplemental den sites in FH, thus suggesting a need to proactively manage for such structures if maintenance of flying squirrel and other sciurid populations is desired.

In contrast, the Townsend's chipmunk is diurnal, and is more general in its diet and use of nest sites (Carey 1991, Maser et al. 1981). Townsend's chipmunks eat seeds and fruits as well as fungi (truffles and mushrooms) and insects (Maser et al. 1981). Food is thought to be the most limiting factor for Townsend's chipmunks, with annual differences in conifer seed and fungi production leading to large year to year variance in population density (Carey 1991). Their nest sites are widely variable, being found both underground in burrows, and in trees (Carey 1991). The greater abundance of Townsend's chipmunks in FH (Table 6) is primarily a response to the better developed and more diverse understory (Carey 1995) and thus the greater variety of fruits, nuts, and seeds, with nest site availability being less constraining for this species.

Past management or experimental treatments do not appear to have induced sufficient changes in soil microbial conditions to hinder establishment of shade-tolerant species or the growth of the current cohort of trees. Both forests have species-rich mycorrhizal floras (epigeous and hypogeous) (Tables 3 and 5), and fungal-dominated soils (Table 4). Observed between--forest differences in epigeous mycorrhizal communities may be explained by the spatial and temporal variation that is characteristic of epigeous sporocarp production (Vogt and Bloomfield 1992), by fungal community successional variation (Dighton et al. 1986, Mason et al. 1988) given the difference in age and management history between the two forests, and by differences in canopy closure (Jansen and Denie 1988). Succession is also known to occur with saprophytic fungi (Mason et al. 1988); the different management and coarse woody debris histories of the two forests may explain the observed differences in their saprophyte communities. However, the RT subtreatment, which was simply a very heavy thinning in FH (root-rot pockets were not apparent there), had fewer mycorrhizal species, lower TF/TB ratios, and more extensive weed populations, suggesting caution be used in prescribing extensive application of very heavy thinnings.

Mycorrhizal mats were reduced in FH relative to SS, and decreased father in direct proportion to increased thinning intensity in both forests (Table 4). However, other indicators of fungal abundance, such as total and active fungal biomass, total fungi/total bacteria, active fungi/active bacteria, and numbers of fungal feeding nematodes indicate that both forest's soils are fungal dominated, with SS soils being somewhat more so (Table 4). Although there is wide

variation in abundances of soil foodweb organisms, none approach the values seen in clear-cuts where tree establishment has failed (Ingham and Thies in press, Perry et al. 1989). The bacterial feeding nematode/fungal feeding nematode ratio is higher in FH than in SS, but we did not see a large shift in biomass ratios towards the greater bacterial dominance and concurrent loss of fungi that have been implicated in tree regeneration failure on the Olympic Peninsula (Ingham and Thies in press), and elsewhere (Perry et al. 1989). The retention of fungal-dominated soils and trophic pathways in both forests after thinning may be a result of the deliberately small-scale nature of the variable-density thinnings as well as the presence of salal and other woody shrubs in the understory. These plant species are hypothesized to "preserve ectomycorrhizal fungi during periods of rapidly changing aboveground community structure and that mycorrhizal links between hardwoods and conifers facilitate conifer establishment by providing a ready source of inoculum, nutrients, and water" (Amaranthus and Perry 1994). The ectomycorrhizal fungi comprise as much as 50-80% of the fungal community in forest soils (Allen and Allen 1992) and are fundamental to the many fungal-based trophic pathways (including those which support mycophagous protozoans, arthropods, nematodes, and mammals) found in these forest communities. These fungal-grazers (including flying squirrels and other sciurids, forest floor rodents, and numerous insects) are prey for other forest insectivores, raptors, and mammalian predators.

The data on hypogeous fungi also support the importance of maintaining salal and other native species in place during thinning operations (Carey et al. 1994b). The two forests are similar in patterns of truffle species richness and standing crop production; community structural differences have not yet been evaluated. The data suggest that FH management history has not brought about appreciable changes in truffle diversity and abundance compared to SS. In both forests, the effect of variable-density thinning on the productivity and biodiversity of truffles is limited temporally and spatially, with even the most aggressive treatments (RT) showing only short-term reduction in truffle standing crop. We believe this to be a result of the tempering effect of the deliberately small spatial scale of the variable-density thinnings. Such reductions might not be short-term if entire blocks had received RT or HT treatments or a mixture of both; heavier thinnings may also result in more widespread and persistent weed populations and could result in difficulty in tree regeneration due to soil microbial community alterations (Perry et al. 1989, Ingham and Thies in press). Truffle species richness was reduced somewhat in the RT cells (Table 5), but this reduction was minimal. The small size of our thinning subtreatments (0.16 ha), coupled with the root-grafting that is evident in such essentially monospecific Douglas-fir stands and the protective effect salal and other understory shrubs may have on mycorrhizal fungi (Largent et al. 1980, Perry et al. 1989, Smith et al. 1995), should temper and ameliorate soil microbial community disturbances. Thus, variable-density thinning should not produce the long-term alterations in soil structure and function known to be deleterious to tree establishment and which have occurred in some large clear-cuts that were burned or had herbicides applied prior to replanting (Perry et al. 1989, Ingham and Thies in press).

SUMMARY

The Forest Ecosystem Study seeks to document and understand linkages in forests not far removed temporally from pre-European-settlement conditions, and containing, by our estimates, much of their presettlement biodiversity. We have accumulated data on (1) the effects of two distinct management histories on biodiversity and productivity, and (2) the effects of contemporary variable-density thinning on this biodiversity and productivity. Our studies suggest that these forests contain much of the fungal, plant, and small mammal diversity found in later-successional stands (Carey 1989, 1995; Carey and Johnson 1995; Ruggiero et al. 1991; Thomas et al. 1993). Variable-density thinnings (Carey 1994b, Carey and Miller 1991) that aim to recreate the patchiness of late-seral forests when applied to stem exclusion phase forests (Oliver and Larson 1990), are an opportunity to manage for biodiversity, prevent stand stagnation, and accelerate forest development (Carey 1994a, Carey and Johnson 1995).

The similarity between the intensively managed FH forest and the unmanaged SS forest (with oldgrowth legacies), despite different site conditions and stand histories, suggests a high degree of resiliency in soil foodwebs, fungi, and capacity for vascular plant diversity. This resiliency suggests that late-seral communities could be restored with minimal intervention and with a high probability of success. Resiliency in these forest communities may be due to redundant functional connections and pathways among the plant, microbial, and small mammal communities. These include, but are not limited to: (1) control of and response to soil arthropod populations by the forest floor insectivores, (2) decay

and recycling of lignin, cellulose, chitin and other recalcitrant organic compounds by soil bacteria, fungi, protozoans and nematodes, (3) enhanced mineral and water uptake and utilization (and ultimately, carbon storage) by the overstory conifers and other woody plants, mediated by ubiquitous and extremely diverse mycorrhizal fungi and other rhizosphere organisms, (4) fungal-supported trophic pathways and mutualisms forming the base of many plant, nematode, arthropod and mammalian communities, (5) dispersal of bacterial, fungal, plant and lichen diaspores by sciurids, forest floor rodents and insectivores and arthropods, and (6) maintenance of a substantial mammalian prey base for mustelid, avian and large mammal predators. The physiological and genetic diversity of plant-fungal mutualisms (and their predators/consumers), and the redundancy in shared rhizosphere flora, should stabilize the plant-soil system (Perry et al. 1989). Retention of such spatial and temporal linkages between plants and their fungal mutualists (Amaranthus and Perry 1994) should be an explicit goal during any planned management disturbance. We believe these functions, relationships, and linkages can be maintained and enhanced in managed forests and that "many of these functions can be served simultaneously as well as sustainably" (Myers 1995) through proactive and innovative management approaches. By taking such approaches, we believe we can protect long-term site productivity, maintain plant, fungal, and small mammal and predator populations, avoid threatened species conflicts, hasten the development of late-seral forest and landscape conditions, and preserve future management options.

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Table 1. Total vascular plant species richness by forest by treatment by stratum, and mean species richness per 100 In^2 plot (n = 24) by treatment (with SE) in 1994, one year after thinning. Stratum 1 includes ferns, forbs and other vegetation less than 0.5 m in height. Stratum 2 includes woody shrubs less than 2.0 m in height. Stratum 3 includes sub-canopy woody shrubs and trees greater than 2.0 m in height Stratum 4 includes overstory trees. Treatments are defined in the text Bold numerals indicate significant difference between SS and FH for that treatment (t-test; $P < 0.05$).

Treatment	Number of species										
	Mean/plot (SE)	FH stratum					Mean/plot (SE)	SS stratum				
		All	1	2	3	4		All	1	2	3	4
All		138	128	35	17	6		101	95	23	12	5
Control	**18.5** (1.2)	69	50	23	11	3	14.8 (0.6)	44	35	14	6	1
Light thin	**27.5** (1.5)	94	86	19	9	4	18.0 (1.2)	61	56	9	6	2
Heavy thin	**32.6** (1.5)	94	83	21	8	4	24.0 (1.0)	76	71	14	6	3
Root-rot, thin	**43.6** (1.6)	122	109	28	11	3	30.6 (1.1)	84	81	14	5	2

Table 2. Mean percent cover of vascular plant sub-canopy layers by stratum by treatment for each forest type (with SE) in 1994, 1 year after thinning. N = 24 plots per treatment per forest type. Strata are defined in the Table 1 caption. Treatments are defined in the text. Bold numerals indicate significant difference between FH and SS for particular treatment and stratum (Mann-Whitney U test; $P < 0.05$).

Treatment	FH Stratum			SS Stratum		
	1	2	3	1	2	3
Control	**28.3** (4.9)	**48.3** (4.7)	**10.0** (2.0)	17.7 (4.6)	25.8 (4.1)	6.2 (1.9)
Light thin	**52.0** (4.0)	**32.9** (4.7)	**10.0** (1.9)	9.6 (2.7)	15.1 (2.9)	2.6 (0.6)
Heavy thin	**52.0** (3.2)	**29.5** (3.4)	**10.3** (1.8)	7.7 (1.4)	14.7 (2.1)	3.8 (1.5)
Root-rot, thin	**62.7** (1.3)	12.8 (1.8)	**5.6** (1.4)	25.6 (3.6)	17.6 (3.1)	1.4 (0.4)

Table 3. Epigeous fungi: total species richness, total mycorrhizal species richness, and total non-mycorrhizal species richness by treatment by forest type (n = 16, 100-m^2 plots/forest/ treatment); average total species richness, average mycorrhizal species richness, average nonmycorrhizal species richness per stand (each stand sampled with four 100-m^2 plots/treatment) by treatment by forest type; average total fungal biomass, average mycorrhizal biomass, average non-mycorrhizal biomass by treatment by forest type. "All" indicates all treatments combined. Sampling was conducted during October and November, 1994.

		Treatment				
Fungal element	Forest	All	CT	LT	HT	RT
Total no. species	FH	104	61	56	55	47
	SS	93	55	43	53	40
mycorrhizal	FH	29	20	13	19	7
	SS	39	27	19	21	16
non-mycorrhizal	FH	75	41	43	36	40
	SS	54	28	24	32	24
Average richness	FH	21.3	24	23.5	20.5	17.2
(no. species/stand)	SS	20.1	26.7	18.9	22.2	15.7
mycorrhizal	FH	4.7	7	5	5	2
	SS	8.2	10	7.2	9.7	5.5
non-mycorrhizal	FH	16.5	17	18.5	15.5	15.2
	SS	12.8	16.7	11.7	12.5	10.2
Average biomass	FH	5.6	4.6	7.4	4.3	5.9
(kg dry/ha)	SS	4.1	3.7	4.3	4.4	3.8
mycorrhizal	FH	0.6	0.6	1.1	0.7	0.2
	SS	1.5	0.9	2.1	2.0	1.1
non-mycorrhizal	FH	4.9	4.0	6.3	3.6	5.7
	SS	2.5	2.8	2.2	2.4	2.7

Table 4. Selected soil foodweb values by forest by treatment. "All" indicates all treatments combined. TF/TB = ratio of total fungal biomass/total bacterial biomass; AF/AB = ratio of active fungal biomass/active bacterial biomass; TF = total fungal biomass/gram dry soil weight (gdw) in *u*g/gdw x 100; nematodes are #/gdw; % mat = % of 4-m^2 plots covered by mycorrhizal mats. Values are means; sample size is indicated below sub-treatment captions, except as noted for % mat cover. Sampling was conducted in April 1994.

Foodweb parameter	Forest	Treatment				
		All	CT (n = 14)	LT (n = 7)	HT (n = 5)	RT (n = 3)
TF/TB	FH	104	101	100	125	93
	SS	130	123	156	146	77
AF/AB	FH	2.57	1.6	4.5	2.1	3.1
	SS	2.62	2.4	3.4	2.6	1.7
TF (x100)	FH	19.2	20.8	44	30.2	30.4
	SS	44.2	58.2	45.5	55.5	53.2
Fungal feeding nematodes	FH	13.5	20.0	5.2	9.3	12.9
	SS	21.1	18.0	24.7	18.5	29.7
Bacteria feeding nematodes	FH	13.3	15.9	4.5	12.2	19.9
	SS	11.1	11.1	12.8	6.8	20.5
Predatory nematodes	FH	2.53	2.5	1.4	1.2	4.4
	SS	5.14	2.0	4.9	11.5	6.7
% mat	FH		25.1 (n=10)	4.9 (n=10)	1.7 (n=10)	1.7 (n=10)
	SS		66.1 (n=10)	38.6 (n=10)	33.3 (n=10)	22.5 (n=10)

Table 5. Hypogeous fungal species richness by forest type by treatment, and number of species unique to a particular group. Numbers in parentheses are the number of species unique to that treatment of all the species in that particular forest type or combination. For example, of the 18 species found in the control treatment out of the total 35 species found in SS, 5 species were found only in the control treatment; or of the 37 species found in FH of the total 53 species found to date, 16 are unique to FH; or of the total 53 species found in both forest types, 28 are found in heavy thin treatments. Of these 28, six are found only in heavy thins. Data represents summary of all truffle samulina from April 1993 to April 1995.

Treatment	FH	SS	Both
	# species (# unique)	# species (# unique)	# species (# unique)
Total	37 (16)	35 (16)	53
Control	17 (6)	18 (5)	24 (6)
Light thin	15 (4)	16 (3)	26 (6)
Heavy thin	19 (3)	17 (4)	28 (6)
Root-rot, thin	11 (4)	14 (3)	16 (4)

Table 6. Total summed captures, total summed numbers of captured individuals, mean density (± SE), and range of density of northern flying squirrels and Townsend's chipmunks, and total summed captures and total summed numbers of captured individuals of Douglas' squirrels by forest. Data are summaries (captures, individuals) or means (density) of fall 1991, and spring and fall, 1992, sessions, and represent pre-manipulation conditions only.

	FH		SS	
Species	Total captures/ total individuals	Density (N/ha±SE)/ (range)	Total captures/ total individuals	Density (N/ha±SE)/ (range)
Flying squirrel	207/126	0.32±0.04/ 0.18-0.46	384/214	0.63±0.08/ 0.28-1.04
Townsend's chipmunk	641/312	0.71±0.09/ 0.29-1.43	100/34	0.11±0.02 0-0.28
Douglas' squirrel	29/20		21/20	

Table 7. Mean captures per 100 corrected trap nights (CPUE) ± SE for all forest floor small mammal species combined, and for selected species for 1992 and 1993 by forest. All FH captures are significantly greater than SS captures (*t* - test: * = $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.01$). Data are from unmanipulated (control) stands only.

	1992		1993	
Species	FH	SS	FH	SS
All species	13.95±1.12**	9.51±0.34	11.36±1.46*	7.83±0.70
Peromyscus maniculatus	2.54±0.39***	0.59±0.20	0.67±0.14**	0.15±0.03
Microtus oregoni	2.13±0.56**	0.19±0.12	1.83±0.37***	0.07±0.04