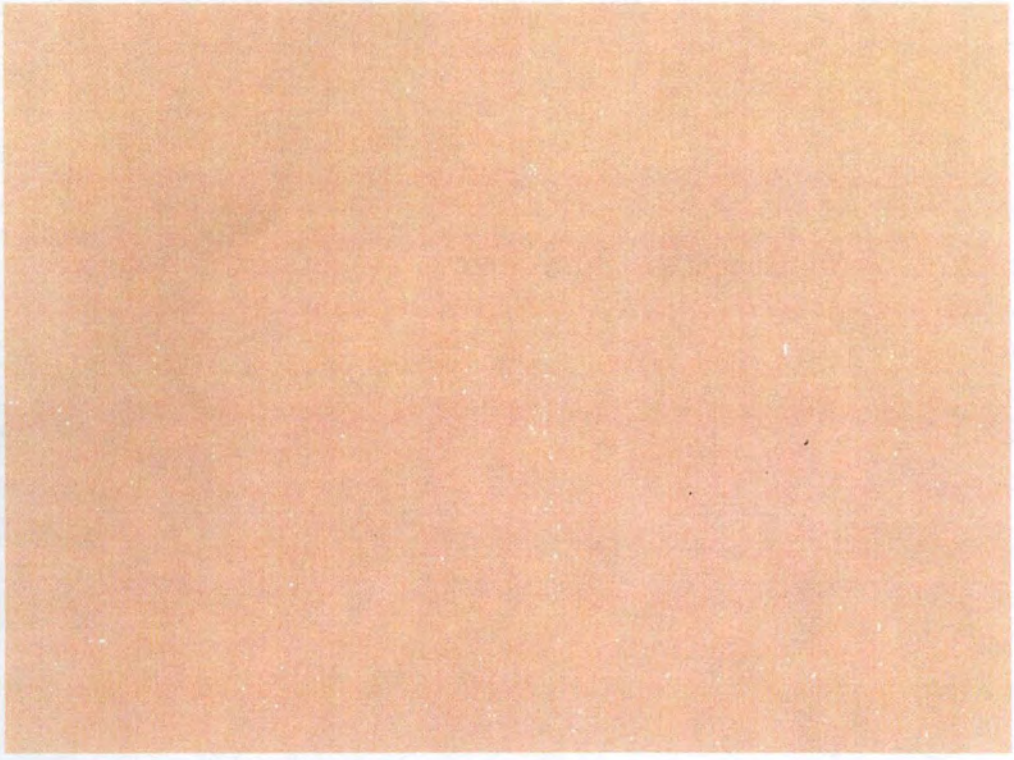

Long-term Effects of Mechanical Fuel Treatments, Manitou Experimental Forest, Colorado: First-year Results

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January, 2006

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Executive Summary

The purpose of this study is to assess the long-term ecological effects of mechanical fuel treatments in a mixed Ponderosa pine-Douglas fir forest following two different thinning strategies: (a) chip-harvesting with all biomass retained on-site, and (b) whole-tree harvesting with all thinned material removed from the site. Changes in forest community structure under each of the above treatments are being tracked and compared with unthinned control plots over a 10-year period by monitoring the following parameters: (1) soil chemical properties, including ammonia and nitrate-N pools, net mineralization, nitrification, and total C:N ratios, (2) understory plant composition, (3) small mammal population dynamics, and (4) insect emergence patterns.

Soil nitrogen levels and mineralization rates in our treatments are in line with values reported for a number of investigations in ponderosa and lodgepole forest types. Typical of other studies, soil NO3 concentrations in all treatments were low compared to NH4 concentrations. Net mineralization rates were significantly reduced in thinned treatments one year after harvest, but there were no differences between removal and chipped plots. This suggests to us that the effects of thinning *per se*, rather than disposition of harvested biomass, dominated below-ground response during the first year after treatment. Contrary to our expectations, the large mass of wood chips on the surface of the thinned/chipped plot did not effect soil C:N ratios in the first year. This may simply reflect the recalcitrant nature of the wood or it may indicate a functional separation between fungi in the wood chips and the soil beneath.

Biogeochemical processes provided some of the greatest challenges in our data interpretation and prompted considerable thought regarding future studies. Though we observed significant differences in first-year net mineralization rates between thinned plots and unthinned controls, the lack of belowground response to very different fuels reduction strategies (chipping vs. removal) begs several questions related to soil carbon and nitrogen cycling. We propose a 3-tiered approach to soil investigations for the coming field season: (1) a more targeted sampling protocol for C:N analysis; (2) continued monitoring of soil nitrification and mineralization rates; and (3) analysis of soil ergosterol levels as a proxy for determining fungal distribution. We believe these analyses will provide answers to important questions regarding the fate of carbon and its subsequent influence on nitrogen dynamics in thinned and chipped treatments.

Above-ground response to thinning was generally most pronounced in the chipped treatment. While there were no statistical differences in groundcover between

removal plots and controls, herbaceous vegetation in the chipped treatment was significantly lower. Grasses were reduced more than 60% and forbs were nearly eliminated. Juniper, the most common shrub in our study area, was unaffected by treatment differences, but the prostrate bearberry was entirely missing from our chipped plots. Douglas fir seedlings were most abundant in the removal plots where soil disturbance created suitable conditions for germination and seedlings were uninhibited by a layer of wood chips.

Two alien species, cheat grass (*Bromus tectorum*) and common mullein (*Verbascum thapsus*), appeared in both chipped and removal treatment areas – but not in control plots – late in the year following treatment. An unidentified thistle may constitute a third alien. While our initial groundcover survey recorded vegetation only by growth-form, in the coming field season the presence of invasive plants will be quantified by species.

Small mammal numbers were also dramatically lower in the chipped treatment compared to removal and control plots – a likely result of lower resource levels and the relative scarcity of protective cover in chipped plots. In all treatments only two species, the least chipmunk (*Tamias minimus*) and deer mouse (*Peromyscus maniculatus*), were captured in a session of 1800 trap nights. The combined population density of *P. maniculatus* and *T. minimus* was similar in control and removal plots, but *T. minimus* numbers in the removal treatment were considerably higher than expected, possibly reflecting displacement of animals from the neighboring chipped treatment.

In contrast to small mammals, insect emergence was significantly greater within the chipped treatment, compared to control plots. A smaller, but still significant increase in emergence occurred within the removal treatment. Fungivorous flies accounted for most of the effect in the chipped treatment, probably in response to a favorable environment for the growth of fungi beneath the wood chips, while an unexplained spike in the emergence of tiny parasitoid wasps accounted in large part for the higher numbers in the removal treatment.

Comparisons of insect community composition based on morphological species showed considerable differences between controls and the two thinning treatments, even though insect richness proved almost identical in all three treatments. These observations indicate that as some species disappeared from plots due to thinning, they were quickly replaced by others. This suggests important alterations in the ecology of the forest floor and raises several questions for future research, including the ecological implications of sudden large numbers of fungivores (that also feed on roots), the unexplained reduction in thinned plots of soil pupating moth species (many of which are important foliar feeders on pines), and the consequences of unusually large numbers of parasitoid wasps in our removal plots. It is our expectation that continued sampling will provide us with sufficient time-series analyses to factor out natural variation and clarify the effects of our treatments on insect community dynamics and the ponderosa ecosystem as a whole.

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Introduction

A century of landscape change in the montane regions of western North America has lead to widespread forest conditions now recognized as unnatural, unhealthy, and increasingly threatening to the values of our society. The quelling of indigenous fires with the westward incursion of Euro-americans, the widespread introduction of livestock to forested lands in the 1800's, and the pursuit of a judicious wildfire suppression policy since the early 1900's have contributed to artificially dense stocking, prolonged fire-return intervals, and wildfire behavior that is potentially damaging to ecosystems that evolved in concert with more frequent, but less severe fire regimes.

For land managers eager to restore forests to a more normal condition, mechanical thinning is rapidly becoming the tool of choice. Attempts to reintroduce fire as a natural ecosystem process without first restructuring forests to reduce stand densities and minimize ladder fuels has proven difficult and often dangerous. Yet mechanical thinning carries some unknowns, too. Our knowledge of forest community dynamics is incomplete at best and the many landscape changes that have occurred in the west over the last century, including the spread of aggressive, non-native plant and animal species, present new ecological challenges of largely unknown dimension.

Changes in the structure of a forest canopy, whether initiated by natural processes or purposeful manipulation, set into motion a series of reactions that may profoundly affect the entire forest community. In the simplest case, opening the forest canopy admits more sunlight to the forest floor, resulting in warmer soil temperatures. Warmer soil accelerates microbial activity and subsequent mineralization of organic matter. Increased nutrient availability (plus sunlight) then stimulates more understory growth, raising the level of resources available to consumers (herbivores and their predators) at all trophic levels. Energy flow is increased and nutrient cycling is accelerated. But there are potential complications with this simple scenario: Nitrogen may be immobilized through large additions of carbon to the soil from logging residue or death of tree roots; nutrients may be leached from soils and lost before new groundcover is established; tree regeneration, stimulated by release from overhead competition, may quickly sequester nutrients into long-lived tissues. The effects of opening the understory to more light are further confounded by the potential negative feedback (particularly on nutrient cycles) of increasing evapotranspiration and reducing soil moisture. Acting in concert, these changes may shift competitive balances, possibly in favor of alien species that could have a lasting impact on native plant and animal communities.

While a return of our forests to more natural conditions may be desirable, the simplified scheme presented above highlights just a few of the unknowns that can plague well-intentioned management plans. Given our present understanding of complex montane forest ecosystems, we cannot be sure that the outcome of wide-scale forest thinning will be exactly as we anticipate.

The purpose of this study is to assess the long-term ecological effects of mechanical fuel treatments in a mixed Ponderosa pine-Douglas fir forest following two different thinning strategies: (a) chip-harvesting with all biomass retained on-site, and (b) whole-tree harvesting with all thinned material removed from the site. Changes in forest community structure under each of the above treatment regimes are being tracked and compared with unthinned control plots over a 10-year period by monitoring the following parameters: (1) soil chemical properties, including ammonia and nitrate-N pools, net mineralization, nitrification, and total C:N ratios, (2) understory plant composition, (3) small mammal population dynamics, and (4) insect emergence patterns.

Methods

Study area

This study is being conducted at the Manitou Experimental Forest, located 15 miles north of Woodland Park, CO in the Trout Creek watershed, a tributary drainage of the South Platte River. The experimental forest lies between 2300 and 2800 m on the western slopes of the Rampart Range, a topographically diverse area characterized by steep gulches as well as gently sloping valley bottoms. At lower elevations Ponderosa pine is the dominant tree species, with aspen and Douglas-fir increasing in importance wherever soil moisture permits. Steeper, north-facing slopes and higher elevations support mixed Engelmann spruce-Douglas fir-aspen stands, with lodgepole pine appearing on the higher ridges in the northeastern part of the forest.

Fire mitigation treatments used in the present study involved two different mechanical thinning techniques in a mixed Ponderosa-Douglas fir stand (aspen a minor component) of approximately 25.5 m2 basal area per hectare. In one case, where private residences were located close to the treatment boundary, whole-tree removal was employed to reduce stand density by approximately 45%. Trees were skidded intact to a landing site outside the treatment area, with a minimum of logging debris left on site. In the second case, a whole-tree harvester with chipper was employed to fell and chip trees in place, spreading the entire biomass of the trees over the forest floor to an average depth of 2.0 cm (range 0-6.5 cm). Basal area of this stand was also reduced by approximately 45%. A third mastication treatment was not included in the present study. Thinning was completed by mid-July, 2004, and field work was started in early August.

Sample-site selection

The relatively small size of treatments (<4 ha) and considerable topographic heterogeneity of our experimental plots mandated a non-random selection of sample sites for cross-treatment comparisons, based on similarity of slope and exposure. Accordingly, we employed a nested-plot sampling scheme within relatively homogenous treatment areas (fig 1.), adopting a conservative statistical approach to our analyses (see below).

Within each of the thinned and unthinned treatments we established a grid system consisting of 3 quarter-hectare blocks, 50m on a side, divided into a 5 x 5 array. We then assigned unique numbers to every 10m x 10m square within the treatment blocks and used a random number generator (www.random.org/cgi-bin/randseq) to select specific subplots for sampling within each block. Thus, 9 sets of random numbers were created (3 blocks x 3 treatments), designating a maximum of 8 separate subplots or 32% of the area of each block for data collection. The number of subplots actually used depended on the parameter being measured – e.g. all 8 for soil samples, but only 3 for insect collections. Groundcover and small mammal surveys were sampled over the entire grid, using all 25 of the sub-plots.

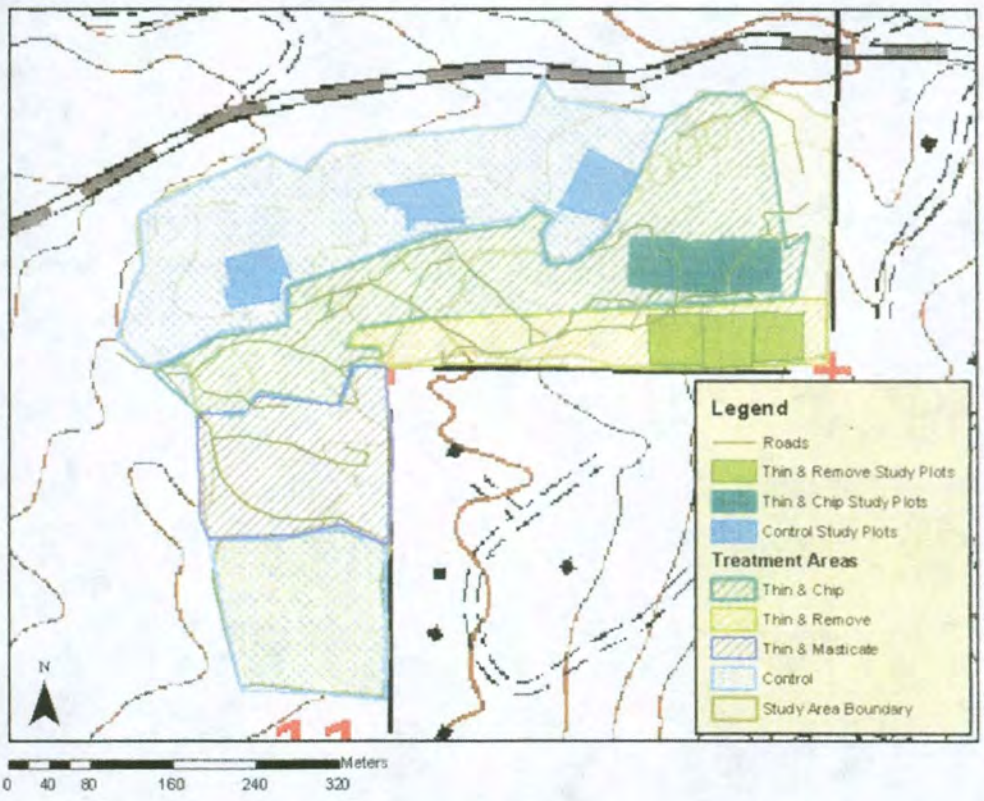

Figure 1. Location of study plots within the experimental treatment area.

Soil analyses

Soil chemical analyses were initiated in mid-October with the installation of *in situ* incubation chambers and resin bags and the collection of bulk samples for initial ammonium, nitrate, and C:N analyses. For net mineralization and nitrification determinations we followed the recommendations of D. Binkley (pers. comm.), driving 15 cm lengths of PVC pipe (3.8 cm diameter) into the ground to isolate soil samples for incubation, rather than coring soils and transferring them to gas-permeable plastic bags for subsequent burial. Exposed tops of pipe sections were covered with duct tape to prevent rainwater from leaching ammonium and nitrate from the soil core, but open bottoms still allowed for gas exchange within the samples. In addition to the PVC incubation chambers, we constructed and buried 5cm x 5cm nylon mesh bags containing ion exchange resins, enabling us to measure net sorption of ammonium and nitrate-N *in situ* over time (D. Binkley, pers. comm.).

Incubation chambers and resin bags were first placed in the field on October 17, 2004. Soil cores, 7 cm diameter x 15 cm depth from the O-horizon surface, were collected at that time for initial ammonium, nitrate-N, and C:N analyses. Samples were processed from 8 subplots in each of the 3 replicate blocks for each treatment, giving us a total of 24 chemical analyses per treatment. On November 17, all resin bags and one set of incubation chambers (n = 72 for each) were pulled for time-dependent N analyses, from which initial net N-mineralization rates were determined. A second set of incubation chambers were left in the ground for subsequent analysis in the spring of 2005. In July, 2005, this sampling protocol was repeated (except that no additional resin bags were buried), with incubation tubes removed for analysis 1 month later.

In the laboratory, fresh soil samples were dried at 70° C overnight and sieved through a 2 mm screen to remove coarse material. For determination of ammonium and nitrate-N, 10g subsamples were weighed into a specimen cup, 50 ml 2M KCL added, and the slurry shaken vigorously for 1 minute. After sitting undisturbed for 18-36 hours, the KCL extractions were filtered through pre-leached Whatman #1 paper into duplicate Lachat tubes and processed in a Lachat QuickChem (Hach) 8000 flow injection analyzer. Gravimetric soil moisture content was determined for a subsample by drying to a constant mass at 70° C.

Additional subsamples of dried and sieved soil were ground in a jar mill for C:N analyses. Approximately 25mg of the powdered soils were transferred into small tin capsules, wrapped carefully using forceps, reweighed, and placed in a microtiter plate. Every 10^{th} soil sample was followed by an atropine standard similarly weighed and wrapped, and batches were then combusted in a ThermoQuest NC2100 elemental analyzer for determination of total organic carbon and total organic nitrogen.

Groundcover survey

Herbaceous and woody groundcover was sampled by a point-quadrat technique, utilizing a square grid-frame strung with nylon cord at 7.5 cm intervals on a side to

provide 49 line intersections (7 x 7 grid) within the frame. The grid-frame, elevated on 10 cm legs, was placed at the corner of each subplot (n=75 per treatment) and plant cover was recorded as present or absent for each of the 49 line intersections on the grid, depending on whether or not a vertical projection from the intersection contacted live plant material. Plants were differentiated only as grass, forbs, lichen, bearberry (*Arctostaphylis, uva-ursi*), common juniper (*Juniperus communis*), or "other". The latter category included germinating tree seedlings as well as other shrub species infrequently encountered. Rock and coarse woody debris (>5 cm in width) were also recorded as an indicator of habitat value for small mammals. The survey was conducted in late-July, one year after thinning was completed.

Small mammal census

Small mammal populations were surveyed in late May, 2005, before reproduction and juvenile dispersal masked the territorial patterns of established animals. This gave us a clearer picture of how adults that had successfully overwintered were distributed within thinned and unthinned treatments (i.e. where the 'safe sites' were). At each study site, Sherman live-traps baited with sunflower seeds were set out in 4 lines of 15 traps each, spaced 10 m apart, for a total of 60 traps per treatment. Two different sizes of traps (16.5 x 5 x 6.3cm and 25.5 x 7.6 x 7.6cm) were alternated to maximize the possibility of catching all species. Captured animals were recorded by trap location, weighed, sexed, and marked on the ears with white correction fluid in various combinations (right, left, inside, outside) to identify individuals for the duration of the trapping period. A total of 1800 trap-nights, 600 per treatment, were accumulated during the last two weeks of May.

Insect emergence

In August, 2004, we constructed and field-tested a new design for insect emergence traps consisting of pyramidal, mesh enclosures of black nylon netting affixed to PVC pipe (fig. 2). Insects pupating in the soil beneath the traps, upon emergence, climb the dark sides of the pyramid toward light, a clear glass collection jar at the trap apex. Short lengths of vapona "No Pest Strips" (Shell Corp.) placed in the collection jars kill the insects as they enter. Traps stand 1 m tall and cover 0.7 m2 of ground surface, but allow free air circulation and permit rainfall and some sunlight to reach the trap footprint. Emergence trapping has been used successfully elsewhere to evaluate the effects of changes in litter on habitat partitioning among insects (e.g. Hartman, et al. 1995; Howard and Oropeze, 1998) and we felt this approach would best serve our needs.

In May, 2005, twenty-seven traps were set out in randomly chosen subplots, nine per treatment. Insects were collected from these traps at one-week intervals from 15 May through 31 August and were preserved in 80% propanol until they could be processed. In the lab, samples were combined into two-week collections for ease of storage and analysis. Insects were keyed to family level using many literature sources including Borror and DeLong (1964), Arnett (2000), White (1983), Cole (1969), and on-line sources specific to parasitic wasps of the superfamilies Ichneumonoidea, Cynipoidea, and Chalcidoidea.

Emergence traps were moved to a new footprint within sample subplots on the first of July in order to minimize restriction of normal insect activity on the ground.

Figure 2. Insect emergence trap in a thinned/chipped plot. See text for details.

Statistical analysis

For soil analyses we calculated means, standard deviations, normality, power and p-values for two-way ANOVA and pair-wise comparisons using a nested design described by the equation

$$Y = \mu + T_i + P_{(i)j} + e_{(ij)k} \qquad (1)$$

where: i = 1..3 (number of treatments)
j = 1..3 (number of plots per treatment)
k = 1..8 (number of samples per plot)
T represents the treatment
P represents the plot nested within the treatment
e is an error term representing residual variance.

In this design the random variance is distributed between the error and plot terms. Thus, the following was used for all nested analyses:

Source	df	EMS	F
T	2	$s_e^2+8s_p^2+\theta_T$	MST/MSP
P	6	$s_e^2+8s_p^2$	MSP/MSE
Error	63	s_e^2	
Total	71		

Statistical analyses were performed on SPSS 11 for Mac. When analysis by Levene's method indicated that data were not normal, we used Tamhane's measure of multiple comparisons to test for two-way interactions. When the data were normal, we used Bonferroni's pair-wise test for assessing two-way interactions, this being the most conservative approach when a small number of means are tested. Groundcover data were subjected to two-way analysis of variance and the small mammal census to chi-square analysis.

For insects we used a number of descriptive statistics. Collections sorted into families and pooled from each trap were used to characterize the insect community in each treatment utilizing Jaccard's Index of Community Similarity and the Percent Similarity Index. Differences among treatments were compared and tested for statistical significance using Wilcoxon's Rank Sum Test. Gotelli and Coldwell (2001) note that comparing species or higher taxon richness without reference to accumulation curves is problematic; therefore we also included species accumulation curves for all three treatments.

Our family sorting is not perfect. Chalcidoid wasps and acalypterate flies are difficult to key, even to the family level. For the Chalcidoidea, we are confident of the larger Torymids, Eulophids, Encyrtids, Eupelmids, Mymarids, and Pteromalids, but many minute black Chalcidoids (small enough to require slide mounts), if possessing a grooved mesopleuron, are lumped with the Pteromalidae. In the acalypterates, such problematic species are lumped in the Chloropidae, to which they key most closely.

Given the coarseness of the family-level analysis, a more detailed assessment of species richness, dominance, and community similarity was made based on 250 "morphological species" from insect groups with the most easily observed apparent species. These included 11 families of flies, 5 families of wasps, 4 families of bugs, and the Cicadellid leafhoppers. Morphological species assemblages were analyzed to compare biodiversity using Simpson's (1949), Shannon's (Shannon and Weaver, 1949), and Fisher's alpha (Fisher et al. 1943) indices.

The experimental design produced samples that are comparable without rarefaction, so that species richness data from the Shannon and Fisher statistics are credible. Nevertheless, in the Cicadellidae, where sample sizes were radically different, the larger sample was rarefied and compared with others to further inform our observations.

Results and Discussion

Soil analyses

With one exception, initial changes in soil characteristics appear related primarily to the effects of thinning *per se*, rather than to differences in disposition of harvested biomass. The exception was a significant ($p = .01$-$.03$) increase in soil moisture in the chipped treatment compared to both removal plots and controls (fig. 3).

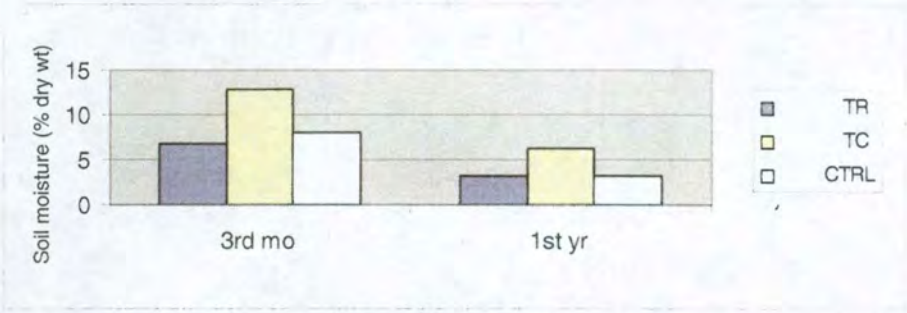

Figure 3. Soil moisture 3 months and 1 year after thinning treatments. Lower moisture contents for all treatments at year 1 coincided with a relatively dry period. The chipped treatment differs from others at $p < .03$.

The large mass of wood chips on the surface of the thinned/chipped plot, estimated at 117 mT/ha dry wt., had not, however, effected soil C:N ratios one year after treatment (fig. 4). In spite of higher soil moisture levels and apparent rapid colonization of the chips by fungi, as indicated by an average 4-fold increase in capture of fungivorous insects in the chipped treatment (see 'Insect emergence' below), C:N ratios remained level across all sites. The lack of change in C:N ratio under the wood chips during the first year may simply reflect the recalcitrant nature of the wood, or it may indicate a functional disconnect (e.g. spatial separation) between fungi in the wood chips and the soil beneath. The original litter layer under the chips might serve essentially as an air gap, preventing fungal hyphae from penetrating the mineral soil (Binkley, pers. comm.). In this case, carbon may be lost from the system primarily as respired CO2, rather than entering the soil via fungal food webs.

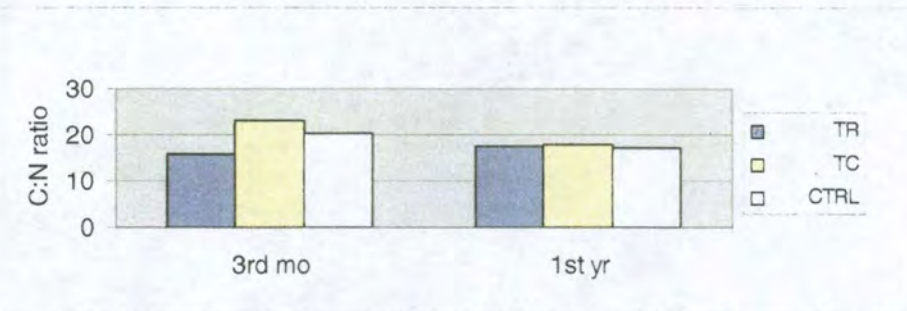

Figure 4. Ratio of carbon to nitrogen in soils 3 months and 1 year after treatment.

Soil nitrogen levels and mineralization rates in our treatments are in line with values reported for a number of investigations in ponderosa and lodgepole forest types (table 1). Typical of other studies, soil NO3 concentrations in all treatments were low compared to NH4 concentrations (fig. 5a), even though ion adsorption in our resin bags indicated greater availability of nitrate-N, relative to NH4, in the soil solution (fig. 5b).

Table 1. Soil N characteristics for ponderosa and lodgepole pine ecosystems. Units are ug/g dry wt for NO3 and NH4 and ug/g/31d for net nitrification and net mineralization.

Authors	C:N	NO3	NH4	Net Nitrification	Net Mineralization
MacKenzie et al., in press	16-29	0.04-.18	1.3-2.8	1.4-4.3	
Smithwick et al., 2005					2.4-5.4
Gundale et al., 2005	20-30	0.0-.83	0.2-1.1	0.0-1.1	2.3-5.7
DeLuca and Zouhar, 2000		0.2-1.8	1.2-3.3		
This study	16-23	0.02-.37	1.8-4.8	0 .28-.59	1.7-5.5

Assuming that resin adsorption provides an accurate measure of N-availability – the premise here being that nitrogen in solution adsorbs tightly to resin surfaces, making it no longer available for uptake or loss (MacKenzie et al., in press; Binkley and Matson, 1983) – the discrepancy between relative concentrations in soil and resin bags seen here suggests either (1) a preferential uptake of NO3 by vegetation, or (2) a loss of NO3 from the system through leaching, immobilization, or denitrification. Alternatively (3) the ion exchange resins may differentially adsorb NO3 and NH4 over time.

Regarding hypothesis (1), there is ample evidence that plants uptake a wide range of N compounds, but a recent field study by Persson et al. (2003) suggests that spruce seedlings preferentially absorb NH4 over NO3, in contradiction to our interpretation of figure 5. Whether this holds for mature trees and other species is unknown. Regarding hypothesis (2), climatic conditions at our site are such that neither leaching losses of NO3 nor denitrification are likely to be important, but immobilization is a possibility (see also hypothesis II below), though questionable given the rather low C:N ratios of our soils (fig. 4; table 2).

Hypothesis (3) is also equivocal. Binkley (1984) has shown NO3 mobility in the soil to exceed that of NH4 by 30-fold and yet Kjønaas (1999) found better correlations for NO3 than for NH4 between resin bags and soil lysimeter samples, especially during the dormant season. Kjønaas concluded that ion exchange resins quite accurately reflect NO3 changes in the percolating soil solution.

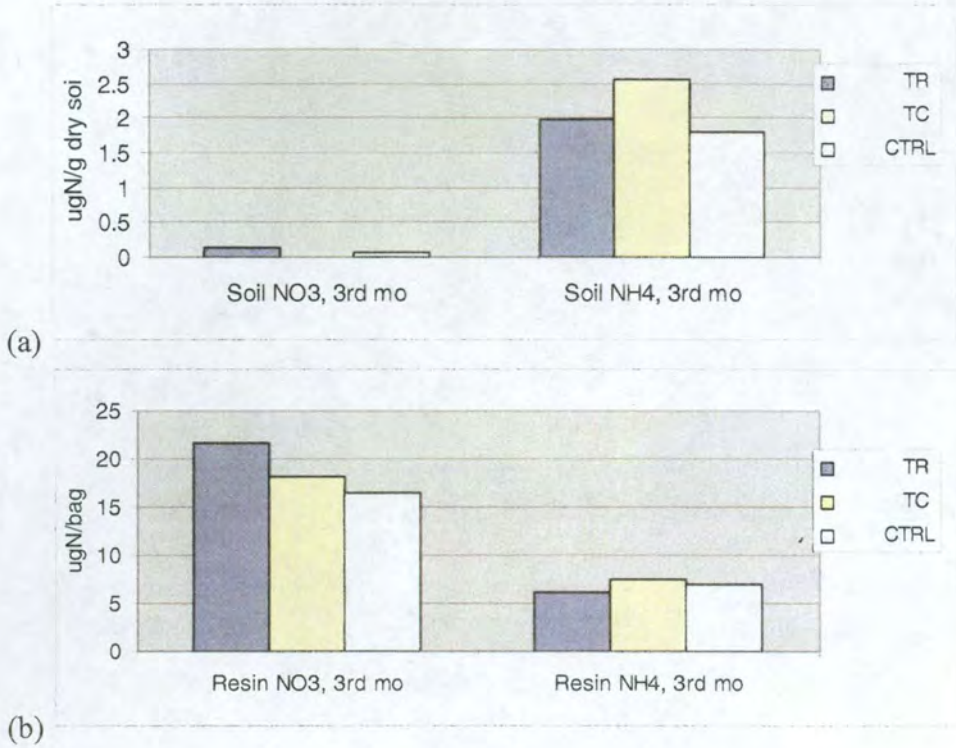

Figure 5. Nitrogen concentrations in bulk soil samples (a) and resin bags (b).

While in our view the weight of evidence here favors hypothesis (1), further investigation is clearly needed to reconcile the disparity between NO3 and NH4 concentrations in exchange resins and bulk soil samples.

Differences in net nitrification and net mineralization between treatments and control plots suggest to us that the effects of thinning, rather than disposition of harvested biomass, dominate below-ground response during the first year after treatment. 31-day net mineralization rates were significantly reduced ($p = .01$) in thinned plots one year after treatment, with no differences between removal and chipped plots (fig. 6). This might be explained by one of two opposing hypotheses related to reduction of standing crop in the thinned plots:

(I) Thinning results in a relatively rapid and substantial (albeit temporary) increase in below-ground carbon supply through the death of fine roots, accompanied by a more gradual decline in labile carbon exudates as larger roots release stored reserves. This influx of carbon leads to immobilization of NO3 by microbes previously carbon-limited, resulting in the lower net mineralization rates observed in both thinned plots (fig. 6). While under many circumstances this is a plausible scenario, we feel that the relatively low C:N ratios (below the critical threshold of 25) in our study plots 1 year after thinning argues against this hypothesis.

(II) Thinning substantially reduces the supply of labile carbon to the rhizosphere via root exudates, significantly reducing net ammonification (evident by subtracting nitrification from mineralization in fig. 6). In spite of lower ammonification rates, however, reduced plant demand for N (as a result of thinning) could be expected to give nitrifying bacteria greater access to NH4, and this, coupled with a low C:N ratio, should result in higher nitrification. In our study, net nitrification as a percentage of net ammonification shows an upward trend in both removal and chipped plots (20% and 47% respectively, compared to 11% in controls). The slight (non-significant) increase in NO3+NH4 pools in the two thinned plots (fig. 6) may be early evidence of increased nitrification combined with reduced plant uptake (see pp.21-22 for further discussion).

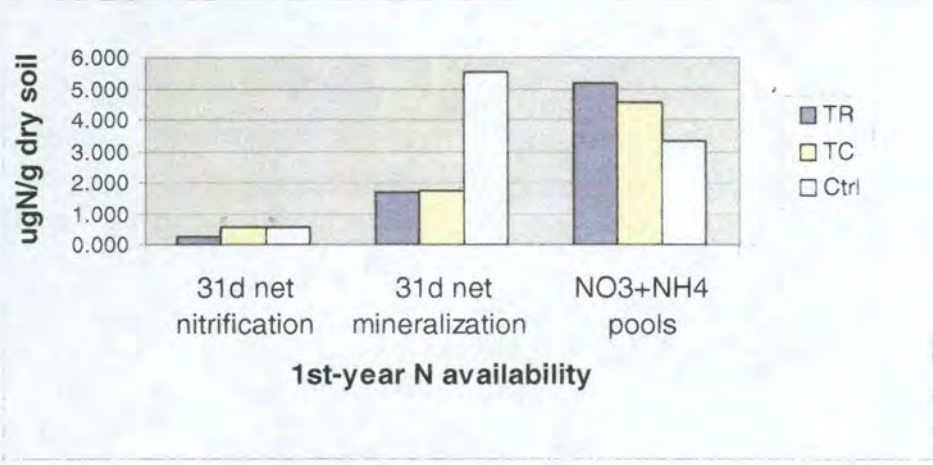

Figure 6. Net nitrification, mineralization, and inorganic N pools in thinned and control plots, one year after treatment.

Vegetation and small mammals

Understory sampling revealed little difference in total plant cover or relative frequency of grasses, forbs, and shrubs in control and removal treatments, but total ground cover was significantly lower in the chipped plots ($p = .003$, fig. 7a). Herbaceous cover was most affected by the chipped treatment, with grasses reduced more than 60% and forbs dramatically underrepresented in chipped plots (fig. 7a). Individual plant size is not recorded in our survey protocol, but the frequency with which grasses and forbs were encountered in our samples (number of grid-frames in which a grass or forb scored at least one hit) was considerably lower in the chipped plots compared to removal and control plots (fig. 7b). Common juniper (*Juniperus communis*), the most abundant shrub throughout our study area, differed little in cover value between treatments, but the more prostrate bearberry (*Arctostaphylos uva-ursi*) was completely absent from our ground cover sample in the chipped treatment (fig. 7b). Seedlings, mostly of Douglas fir, comprised less than 0.5 percent of ground cover in any plot, but occurred with greatest

frequency in the removal treatment (fig. 7b). Two invasive species, cheat grass (*Bromus tectorum*) and common mullein (*Verbascum thapsus*), were sighted in both chipped and removal treatment areas (but not in controls), though neither species fell within our sample grids.

Total plant cover varied inversely with rock and coarse woody debris, the latter two showing highest cover values in the chipped treatment and lowest values in the control plots (fig. 7c). The higher rock cover in chipped and removal treatments reflects in part the occurrence of outcrops in these two areas (see fig. 2). Though plant cover might reasonably be expected to co-vary with rock and coarse woody debris, we do not propose a cause and effect relationship here because overall groundcover values are quite low.

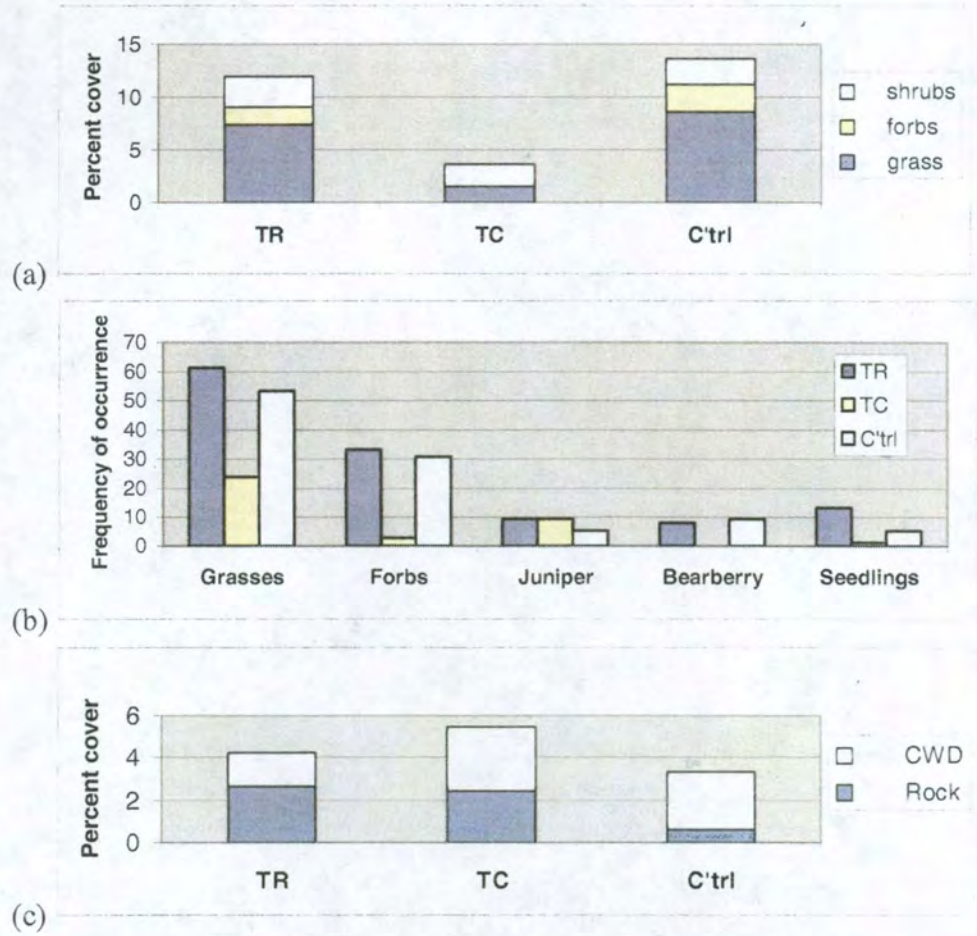

Figure 7. Total plant cover (a), frequency of occurrence by growth form (b), and amount of coarse woody debris and rock in treatment and control plots (c).

Small mammal numbers were also significantly lower ($p = .001$) in the chipped treatment compared to removal and control plots (fig. 8). Only two species, the least

chipmunk (*Tamias minimus*) and deer mouse (*Peromyscus maniculatus*), were captured over all sites in a session of 1800 trap nights. Absent from our trap sample, but listed as common on an earlier check list of mammals for the Manitou Experimental Forest (Morris et al., 1977), were the red-backed vole (*Clethrionomys gapperi*), meadow vole (*Microtus pennsylvanicus*), and long-tailed vole (*M. longicaudus*). These species, however, are less likely to be found in the Ponderosa-dominated habitats of our study area than in wetter sites with greater plant cover.

The combined population density of *P. maniculatus* and *T. minimus* was similar in control and removal plots (24 and 22.6 animals per ha, respectively, fig. 8). However, *T. minimus* numbers in the removal treatment were considerably higher than expected based on experience elsewhere (Marchand, unpublished data), extrapolating to a density of 9.3 per hectare. The highest population density of *T. minimus* known to Morris et al. (1977) was 5 per ha in "ungrazed open ponderosa pine." The high density observed presently may reflect displacement of animals from the neighboring chipped treatment. *T. minimus* favors sites with scattered boulders or rock outcrop that allow for escape from predators (Winterrowd and Davenport, 2004) and both our chipped and removal areas provide such habitat. Predator avoidance must be balanced with energy procurement, however, and the lack of ground vegetation in the chipped treatment may represent a case of double jeopardy. The necessity for increased vigilance in the sparsely covered plots may further reduce the efficiency of energy harvest in an already low-resource area (Winterrowd and Davenport, 2004). Thus, inadequate ground cover, rather than physical habitat (e.g. rock and coarse woody debris), may be driving the population differences seen here.

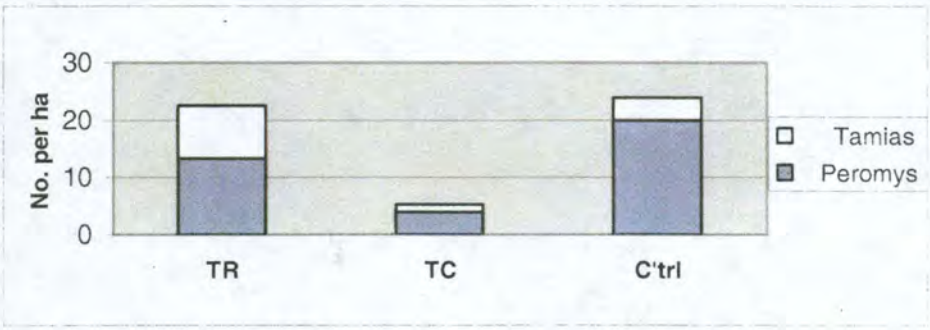

Figure 8. Population density of least chipmunks (*T. minimus*) and deer mice (*P. maniculatus*) in treatment and control plots.

Insect emergence

Insect sample sizes across treatments are presented in figure 9. We found a very large increase in total captures within the chipped treatment, compared to control plots ($p = 0.004$), and a smaller but still significant increase in numbers within the removal treatment ($p = 0.003$). The chipped and removal treatments differed from each other in total captures at $p = 0.056$. Extrapolating from average catches, our unthinned control

would produce about 17.9 million insects/ha in a 16-week summer; thinning and removal of harvested biomass would produce about 36.5 million insects/ha; and the thinned and chipped treatment would produce about 74 million insects/ha. The most productive trap (chipped treatment) captured a total of 6236 insects in the first eight weeks, extrapolating to over 178 million insects per hectare in a 16-week summer, while the least productive trap (control plot) yielded about 1/18th as many, extrapolating to 9.9 million insects/ha.

Over 72,000 insects were collected between May 15 and Aug 31 and sorted to the family level. At least 109 families from 13 orders were represented. The entire collection of Homopterans, fungivorous flies, and parasitic wasps smaller than the Ichneumonoidea, were analyzed separately for this report.

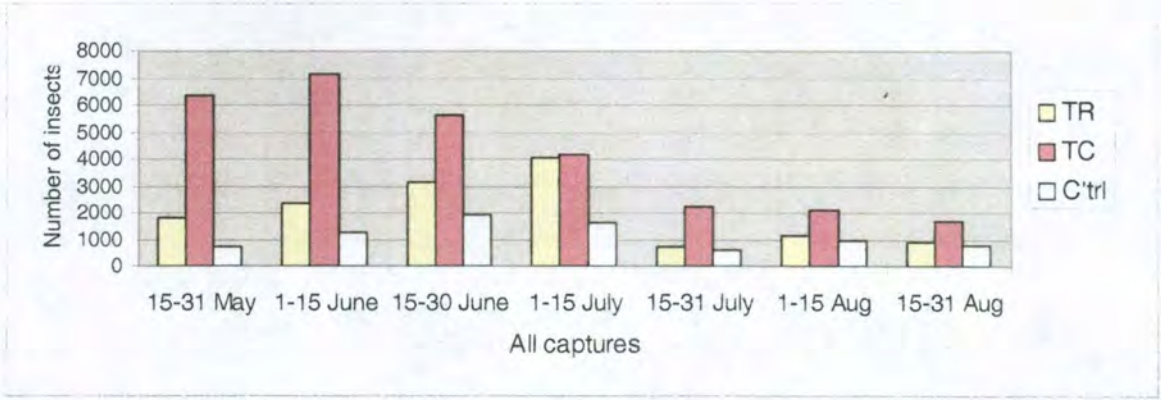

Figure 9. Total yield from insect emergence traps, May 15-Aug 31, 2005, one year after thinning treatment.

Comparing trap counts at the family level, fungivorous flies (mainly Sciaridae, Chironomidae, Cecidomyiidae, and Phoridae) accounted for most of the effect in the chipped treatment (fig. 10). This is probably in response to a favorable environment for the growth of fungi beneath the wood chips, although many of these flies also feed on living tissue such as tertiary roots and root hairs (Lyon 2000), and population explosions of these species may deleteriously affect the living trees remaining in these plots. Emergence patterns were asynchronous among the families dominating the fungivores, with Chironomidae peaking in late May, Sciaridae in June, and Cecidomyiidae in July. Phoridae showed a strongly bi-modal emergence pattern with peaks in mid-June and early-August.

The enormous explosion of Sciarid and Chironomid flies in the chipped treatment accounts for a substantially lowered Percent Similarity Index (51%) when this community is compared to either of the others (Table 2). In the removal treatment the general increase in numbers did not greatly affect the species composition of the samples. Thus, the removal treatment community is 83% similar to the control. At the family level the three community comparisons yielded similarly high Jaccard Indices, ranging

between 70% and 75% (Table 2). The Jaccard Index, however, does not account for percent composition by family, but only for presence or absence.

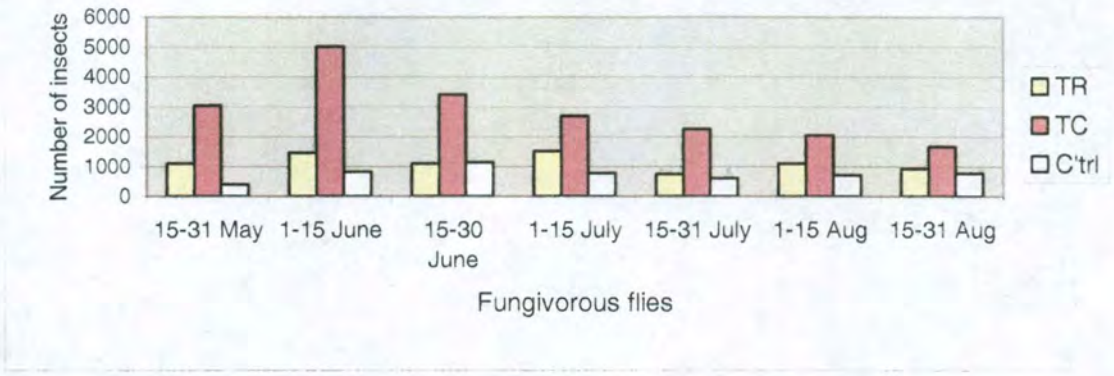

Figure 10. Emergence of fungivorous flies one year after thinning treatment.

Table 2. Similarity indices for insect communities based on family-level classifications.

Treatment	Jaccard Index	%Similarity
C v TC	0.75	0.51
C v TR	0.70	0.83
TC v TR	0.74	0.51

Statistically significant differences from the controls were found when comparing families of every common order except Lepidoptera. Wilcoxon's Rank Sum Test found differences in Diptera, Hymenoptera, Coleoptera, Homoptera, and Hemiptera, but the latter only showed differences between the control and the chipped treatment. The only family that proved significantly different between the two thinning treatments was the Hymenoptera ($p = 0.04$). This reflects a much larger number of parasitoid wasps in the removal treatment.

In treatment comparisons based on morphological species, Jaccard indices were substantially lower than for family-level comparisons (table 3), indicating considerable differences in morphological species composition between controls and either of the two thinning treatments. The Percent Similarity measure, which takes into account not only presence or absence but also the relative abundance of species, shows somewhat higher levels of similarity in all comparisons (table 3). This suggests that the rarer species are the ones most likely to be excluded by thinning (though rarer species are more likely to be missed by sampling as well).

Table 3. Similarity indices for insect communities based on 'morphological species'.

Treatment	Jaccard Index	% Similarity
C v TC	0.35	58.4
C v TR	0.28	59.2
TC v TR	0.50	61.9

Low community similarity indices based on morphological species indicate that as species have disappeared from a plot due to thinning, they are replaced by different species in each treatment. This suggests important alterations in the ecology of the forest floor in the different treatments.

Interestingly, insect richness based on total captures proved almost identical in all three treatments, by three different measures. The Shannon Index ranged between 0.58 and 0.63 while the Simpson Index of dominance placed all treatments between 0.91 and 0.96. Fisher's alpha values are extremely close as well, ranging between 33.2 and 34.8 (fig. 11).

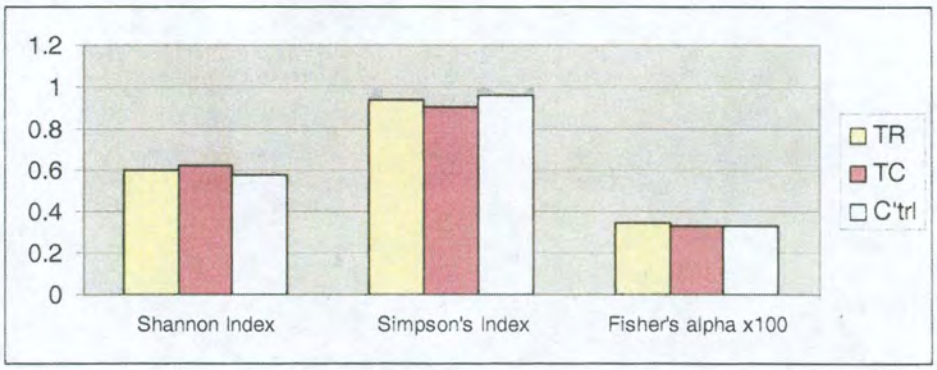

Figure 11. Insect richness/biodiversity indices at the family level.

Certain groups, however, did show changes in representation between the three treatments. Hemiptera, for example, demonstrate a significant biodiversity loss due to thinning and removal (8 species vs. 14 in control plots), but are represented in our samples by few species and a small number of specimens (total N = 114). Acalypterate flies experience a significant increase in species richness due to thinning by either means, with the chipped treatment showing the greater gain. Other groups that either increased or decreased in response to thinning treatments are summarized in tables 4a and 4b.

Table 4a. Ten leading 'increaser' and 'decreaser' families and the amount of change (numbers of insects) in the chipped treatment vs. control plots.

Family	Order	Increase
Sciaridae	Diptera	8644
Chironomidae	Diptera	5737
Phoridae	Diptera	1473
Cecidomyiidae	Diptera	782
Empididae	Diptera	201
Mycetophilidae	Diptera	165
Cicadellidae	Homoptera	160
Muscidae	Diptera	112
Ichneumonidae	Hymenoptera	71
Diapriidae	Hymenoptera	61

Family	Order	Decrease
Chloropidae	Diptera	- 49
Dolichopodidae	Diptera	- 20
Eulophidae	Hymenoptera	- 18
Mymaridae	Hymenoptera	- 13
Pipunculidae	Diptera	- 13
Formicidae	Hymenoptera	- 8
Gelechiidae	Lepidoptera	- 8
Braconidae	Hymenoptera	- 7
Torymidae	Hymenoptera	- 4
Blastobasidae	Lepidoptera	- 4

Table 4b. Ten leading 'increaser' and 'decreaser' families and the amount of change (numbers of insects) in the removal treatment vs. control plots.

Family	Order	Increase
Phoridae	Diptera	1163
Sciaridae	Diptera	597
Encyrtidae	Hymenoptera	408
Chironomidae	Diptera	379
Cicadellidae	Homoptera	371
Pteromalidae	Hymenoptera	364
Cecidomyiidae	Diptera	327
Dolichopodidae	Diptera	269
Chloropidae	Diptera	258
Empididae	Diptera	191

Family	Order	Decrease
Mycetophilidae	Diptera	- 41
Blastobasidae	Lepidoptera	- 6
Vespidae	Hymenoptera	- 4
Torymidae	Hymenoptera	- 3
Sphaeroceridae	Diptera	- 3
Sarcophagidae	Diptera	- 2
Ceraphronidae	Hymenoptera	- 2
Oecophoridae	Lepidoptera	- 2
Raphididae	Neuroptera	- 2
Tipulidae	Diptera	- 1

Ichneumonid wasps were considerably more abundant in chipped and removal plots, compared to controls, but showed a 21-24% loss in species richness in the thinned treatments. Ichneumonids parasitize many soft-bodied insects, and are important parasitoids of moth larvae. Both Lepidopterans and Ichneumonids were taken in reasonable numbers, but showed very high specimen-to-species ratios (thus low alpha values) in the chipped stand. Based on Fisher's alpha values, the predicted species of Ichneumonids in the chipped stand is about half that predicted for the control (68 versus 125); moths show the same trend with predicted values for total species being 19 in the chipped treatment versus 47 in the control.

While many moth species are predacious on pines, our emergence traps collected relatively few such species. Most of those taken were polyphagous herb-feeders, and only two species, both cutworms, were found in large numbers. Much more work will be required to clarify the response of moths to thinning, but in the first year, from emergence trap data alone, there appears to be a substantial reduction in soil-pupating moth species in the chipped treatment. This may be because the microenvironment in which pupation occurs was so radically altered that some species may not have been able to break diapause, and it is possible that they will survive an additional year before emergence.

Tiny parasitoid wasps of groups smaller than the Ichneumonoidea were present in larger numbers in thinned treatments than in the controls throughout the summer, but one surprising result was a huge spike in July in the removal treatment traps (fig. 12). It was postulated that such a spike might occur in the chipped treatment as a result of the huge numbers of small flies that might serve as hosts of these tiny parasitoids, but there is no clear explanation for the appearance of such large numbers in the removal treatment. This was not due to a swarm in any single trap, but rather to a general increase in almost all of the traps in the removal plots. This presents a perplexing puzzle that might form the subject of future research.

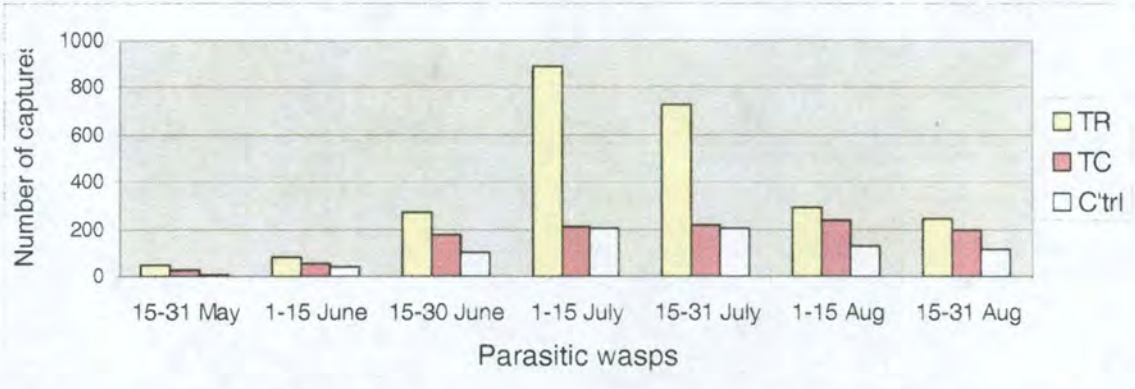

Figure 12. Emergence of parasitic wasps one year after thinning.

The Ciccadellidae (Homoptera), treated separately, best mirror overall community composition and may be the best index family for future sampling. The family shows insignificant differences in Fisher alpha values among the treatments, indicating no gain

or loss of species richness within this group. Jaccard comparisons also reflect the larger community picture based on morphological species – i.e. control vs. thinning treatments are very low in similarity while the two thinning treatments are more like each other (table 5). The three most abundant species in this family amounted to 62% of the control sample, 81% of the removal sample, and 90% of the chipped sample. This is suggestive of the paradox of enrichment, in which a large resource is exploited by the best competitors and species richness collapses. In this case, however, the richness differences are not statistically significant. This group presents a prime opportunity for further study. As pointed out by Danks (1996) in the Biological Survey of Canada, analysis of good indicator subsets may greatly reduce sorting time and save future costs.

Table 5. Comparison of community similarity (Jaccard index) based on different groupings of insects

	C v TC	C v TR	TC v TR
All insect families	0.75	0.70	0.74
Morphological species	0.35	0.28	0.50
Ciccadellid leafhoppers	0.25	0.26	0.50

Species accumulation curves for all three treatments are shown in Fig. 13. These further inform species richness measures, indicating that even though Shannon and Fisher indices show little difference between treatments, thinning tends to positively affect both the total numbers and the insect biodiversity of the plots. Accumulation curves for insect families as well as for species within representative groups (e.g. Homoptera) parallel the trends in figure 13. The lack of asymptote also indicates that 9 emergence traps per treatment may be a minimum number for adequately characterizing insect communities.

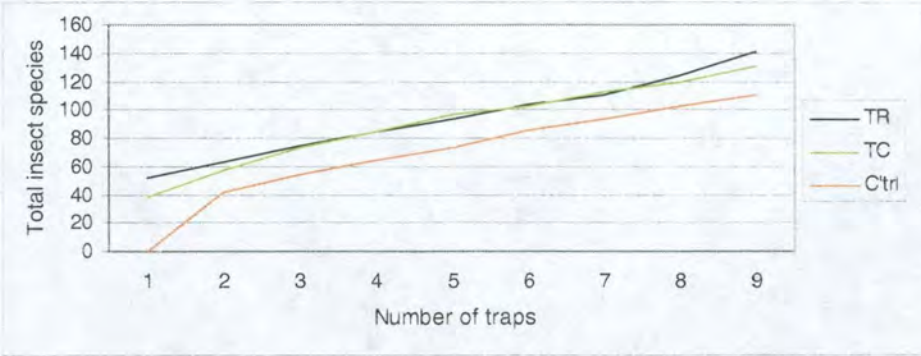

Figure 13. Insect species accumulation with increasing numbers of traps.

In sum, thinning by either chipping or removal of biomass significantly altered the insect community in the short term, causing population explosions, enriching some groups, and diminishing others; but neither treatment created an overall loss of insect biodiversity in the groups studied. In this first-year analysis, responses of coevolved groups cannot be known. It is entirely possible that present trends may change or disappear with further sampling, partly because rare species, which turn up in singles here and there, and which drive the differences between plots, may be encountered in the future in all plots; and because species extirpated by the thinning process itself may re-establish when the immediate trauma has passed. Rotting of wood chips, recovery of ground vegetation, and canopy enhancement may reconstitute some niches in time.

Future directions

While some of the most dramatic responses to thinning treatments occurred in above-ground compartments of this ecosystem – small mammal and insect population changes being the outstanding examples – biogeochemical processes provide some of the greatest challenges in interpretation and prompt considerable thought regarding future studies. Though we observed significant differences in first-year net mineralization rates between thinned plots and unthinned controls, the lack of belowground response to very different fuels reduction strategies (chipping vs. removal) begs two overarching questions: (1) What is the dominant effect of tree removal with respect to changes in the soil carbon budget, and (2) can we really expect wood chips from the thinned/chipped treatment to alter carbon levels and subsequent N-mineralization rates as originally hypothesized, or will most of the carbon from decomposing wood chips be lost to the atmosphere as respired CO2?

Differences in relative concentrations of NO3 and NH4 in ion-exchange resins and bulk soil samples (fig.5) and differences in net nitrification, mineralization, and available N pools between thinned and unthinned plots (fig. 6) suggest that nitrogen may have been immobilized in the thinned plots following a substantial increase in carbon supply to soil microbes. The increased carbon supply in this case would likely be related to the large-scale death of roots rather than to the chipping of above-ground biomass, since differences appear only between thinned and unthinned treatments and not between chipped and removal treatments (hypothesis I, p.11). There is an alternate interpretation of these data, however, in which it can be argued that thinning has substantially *reduced* the supply of labile carbon compounds to soil microorganisms in the rhizosphere and that nitrification, when expressed as a function of ammonification, is actually showing early signs of increasing (hypothesis II, p.12). This interpretation is in line with the root trenching effects observed in other investigations (e.g. Ross et al. 2001) where experimental elimination of living roots and their carbon exudates has resulted in higher nitrification rates (see also Hart and Sollins, 1998, and Fisher and Gosz, 1986).

Both arguments have merit, but determining which is the dominant process is not possible with the data presently available. In Douglas-fir ecosystems the death and

decomposition of fine roots under normal turnover rates may release to the soil 40% or more of the total carbon translocated to roots annually (Santantonio, 1982). If this holds for ponderosa pine as well, tree removal and subsequent death of large root systems in our thinned plots might indeed represent a substantial – albeit temporary – belowground pulse of carbon. On the other hand, the supply of labile carbon from living roots is a continuous process and a growing body of evidence indicates that such exudates account for a substantial portion of the carbon available to soil microbes. In experiments conducted by Norton et al. (1990), more than 30% of the labeled CO2 assimilated through photosynthesis by ponderosa seedlings was recovered in non-rhizosphere soil (i.e. soil <5 mm from roots). Estimates for the transfer of assimilated carbon to roots and mycorrhizae in other species range from 22% of gross primary productivity in *Pinus radiata* (Waring and Running, 1998) to 40% in *Liriodendron tulipefera*, 60% in *Pinus sylvestris*, and as much as 73% in *Pseudotsuga menziesii* (see Grayston et al. 1996 for numerous citations). Thus, reduction of root exudates through thinning would just as likely alter microbial access to carbon, but in the opposite direction.

Bulk soil sampling for C:N ratios is apparently not sensitive enough to differentiate between these short-term changes within the critical rhizosphere. Sanchez and Bursey (2002) instead used a small diameter (8 mm) coring tool and a freon-22 extraction procedure to measure significant carbon accumulations in the soil adjacent to first-, second, and third-order roots. Short of employing Freon-22 extraction, we feel that similar small-volume sampling of soils adjacent to roots of living trees and stumps of trees cut in 2004 should reveal differences in C:N ratios by traditional elemental analyzer procedures. Given the somewhat ephemeral nature of both carbon sources (dead fine-root tissue and labile exudates from living roots), we believe enough time will have elapsed by summer of 2006 to clarify the two possibilities: either we will see higher C:N ratios in soils adjacent to roots of cut stumps in thinned treatments, compared to controls (hypothesis I), or we will see lower ratios (hypothesis II).

Separating the two potential outcomes described above should also be possible with continued monitoring of soil nitrification and mineralization rates. If the 'carbon pulse' hypothesis (I) is correct, we should see clear evidence of N-immobilization (net mineralization significantly lower in thinned plots compared to unthinned controls) until the new supply of carbon from dead roots is exhausted. If the 'carbon famine' hypothesis (II) is correct, we would expect to see a gradual increase in net nitrification – especially relative to net ammonification – with a concomitant increase in NO3 + NH4 pools due to a reduction in root uptake.

It is possible that the relationships outlined above will become somewhat obscured in the chipped plot where carbon from decomposing wood on the ground may enter the soil via fungal hyphae and detritivore food webs. This, however, leads us directly into the next question; will the chipped treatment, as we originally hypothesized, raise C:N ratios significantly, thus immobilizing N, or might there indeed be a functional disconnect between the layer of wood chips and the mineral soil beneath, effectively preventing entrance of carbon into the soil (see p.9)? While the explosion of fungivorous insects in the chipped plot would indicate an abundance of saprophytes, the question

remains as to whether or not fungal hyphae are able to reach the mineral horizon. If not, then decomposition may be severely restricted by low N availability in the wood chips, with carbon transfers limited primarily to loss of respired CO2 to the atmosphere.

Perhaps the most effective way to determine whether or not saprophytic fungi in the wood chips are accessing nitrogen in the mineral soil is to assay the A horizon for ergosterol, a specific marker for the presence of fungal hyphae. Ergosterol is synthesized in cell membranes by fungi and certain microalgae and has been used as an indicator of living fungal biomass in soils because of its rapid turnover in dead cells and because soils and plant residues do not favor the growth of microalgae (Grant and West, 1986). Conversion of soil ergosterol concentrations to fungal biomass can be problematic because the ergosterol content of fungal tissue can vary with species and physiological state of the fungus (Olsson et al. 2003; Tunlid and White 1992); nonetheless the technique has proven useful in several cases. Stahl and Parkin (1996) measured both living and non-living hyphal length in soil samples from 8 different sites and found highly significant positive correlations between soil ergosterol content and both measures of hyphal length, and developed a regression equation that predicted living fungal biomass with a correlation coefficient of 0.999. Likewise, Montgomery et al. (2000) found a strong correlation between soil ergosterol concentration and fungal biomass ($r^2=0.95$) and showed that a conversion factor of 250 ug dry fungal biomass per ug of ergosterol provided consistent results for 6 fungal species across soils that differed in pedogenesis and physical properties.

Though not without analytical difficulties, the quantification of fungal biomass by soil ergosterol determination provides a relatively simple and accurate method compared with alternatives such as glucosamine analysis (Grant and West, 1986), soil respiration and fumigation (Lin and Brookes, 1999) and counting of fluorescent-stained hyphae by microscopy (West et al., 1987; Stahl and Parkin, 1996). Montgomery et al. (2000) and Young (1995) describe an extraction technique using microwave-assisted saponification. Drossman (pers. comm.) has adapted this procedure and finds low analytical variance and good recoveries in mineral soils but variable recoveries in organic layers. To alleviate some of the recovery problems, Drossman is currently comparing the efficiency of a sonication extraction method (Ruzicka, 1995) with the microwave extraction protocol. He is also evaluating the use of internal standards and solid phase extraction to replace pentane extraction, in order to improve the precision and speed of the assay.

While there is still some debate as to whether ergosterol in soils reflects the presence of living fungi exclusively (Zhao et al. 2005), the consensus seems to be that this approach yields the best estimate of fungal biomass currently available. Recent studies in chronically fertilized soils on Cape Cod (Drossman, unpublished) showed ergosterol to provide consistent relative quantification of fungal biomass in similar soils within a given geographical area. We believe that analysis of ergosterol distribution in the A horizon of our soils will best answer our questions regarding the fate of carbon in chipped treatments.

Our insect emergence data also raise several interesting questions. The explosion of fungivores in the chipped treatment, for example, is perhaps not surprising given the abundance of material available for fungi. However, with many of these insects also known to feed on living tissues of fine roots, questions arise regarding the implications of their sudden large numbers to living trees. Similarly, the unexplained reduction in thinned plots of soil pupating moth species, many of which are important foliar feeders on pines, may have ecological implications. Equally puzzling are the unusually large numbers of parasitic wasps that emerged from our removal plots.

Morphological species replacements and low insect community similarities observed here indicate substantial changes in the ecology of the forest floor under the different treatments employed in this study. It is our expectation that continued sampling will provide us with sufficient time-series analyses to factor out natural variation, perhaps based on the methodology of Diserud and Aagaard (2002), and clarify the effects of mechanical fuels treatments on insect community dynamics and the ponderosa ecosystem as a whole.

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