

AN ABSTRACT OF THE THESIS OF

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Jeffrey C. Miller

The effects of forest cutting on forested systems and the biotic components of those systems has been at the forefront of scientific research. The inventory and monitoring of biodiversity is one technique used for measuring the effects of forest management. Because bioinventory studies are expensive, indicator species are often sought to serve as surrogates for the entire biotic community. Insects may be useful as indicator species. The purpose of this study was to perform an inventory of the ground dwelling beetles of the H.J. Andrews Experimental Forest, and then use that inventory to assess the impact of forest management. Beetle communities were compared over time (17 years) and across variously aged stands and associated floral communities to determine the effects of clear-cut management. Pitfall traps were used at 37 sites to collect ground dwelling Coleoptera over a three week period in 1982, 1983, and 1999. A total of 11,191 individuals of 224 species were collected.

The resultant catch was analyzed using univariate and multivariate statistical techniques. Results showed significantly different beetle communities among the four seral stages sampled. Beetles were more abundant in old growth sites. Species diversity was highest in clear-cut sites. Vegetation association was shown to significantly affect beetle communities, but was dependent on level of definition.

Time also significantly affected beetle communities, with the beetle assemblages following a predictable trajectory parallel to vegetation succession. Functional group composition was found to change significantly over time, but was inconsistent between years.

Ground Dwelling Beetles in Early and Late Successional Forests in the Western
Cascades of Oregon

by

William H. Heyborne

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APPROVED:

Redacted for privacy

~~Major Professor~~, representing Entomology

Redacted for privacy

Chair of Department of Entomology

Redacted for privacy

Dean of Graduate School

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Ground Dwelling Beetles in Early and Late Successional Forests in the Western Cascades of Oregon

INTRODUCTION

At the landscape scale, the forests of the Pacific Northwest of the United States, like other forested ecosystems (Niemelä et al. 1993), may appear to be uniform and composed of only a few coniferous evergreen species. In fact, these forests contain considerable habitat diversity (Niemelä et al. 1993; Dyrness et al. 1974). Historically, wind, fire, insects, and disease, among other factors, have created and maintained habitat heterogeneity in forests (Attiwill 1994; Niemelä et al. 1993; Waring and Running 1998). However, natural disturbance, particularly fire, has been seen as incompatible with modern intensive forestry management techniques (Kimmins 1997, p. 312). Anthropogenic disturbance is now largely responsible for forest heterogeneity (Hansen et al. 1991; Niemelä et al. 1993).

Forest cutting is one of the primary sources of disturbance leading to the creation of young stands (Hansen et al. 1991; Franklin and Forman 1987; Niemelä et al. 1993). Franklin et al. (1986, p. 378) describe the use of the "staggered-setting system" of forest cutting. Using this management procedure, 25 – 40 acre patches of clear-cut forest are interspersed with uncut forest stands. After many decades of cutting the coniferous forests of the Pacific Northwest, and elsewhere, have been broken into a patchwork of "young plantations, mature forests and nonforest" sites (Spies et al. 1994, p. 555). The system was originally thought to mimic natural disturbance patterns, but has been shown to be inadequate in some regards (Franklin et

al. 1986; Franklin and Forman 1987). It is now being reexamined (e.g. Hansen et al. 1995), and the resulting fragmentation is currently on the forefront of scientific research (Lubchenco et al. 1991). Attiwill (1994) describes the recent reevaluation of our management techniques and the increased effort to manage such that the effects of that management will more closely match those from various natural disturbance regimes.

One way to quantify the effects of differing management strategies, is to monitor the secondary succession of variously managed and unmanaged stands (e.g. Schoonmaker and McKee 1988). Comparisons may then be made between managed and unmanaged stands, in order to determine if the management technique mimics the natural system or not. The practical importance of secondary succession has been noted by scientists and managers, and secondary successional sequences have been documented for many forested ecosystems (Schoonmaker and McKee 1988).

Another technique for measuring the effects of forest management, fragmentation and subsequent regeneration, is the inventory and monitoring of biodiversity and resource managers are including biodiversity measures in their management plans with increasing frequency (Spence et al. 1999). Currently, forest stands with biodiversity measures within the range of "natural variation" are assumed to be "healthy" stands (Spence et al. 1999, p. 81). The range of natural variation is generally established by monitoring undisturbed areas of comparable habitat type (Spence et al. 1999), similar to the monitoring of plant succession. The problem with this approach is the lack of baseline studies, particularly with species which are small

in size, uncharismatic, or are apparently economically unimportant (Spence et al. 1999).

Intensive forestry management has already been shown to have a significant effect on biodiversity (Harris 1984; Schoonmaker and McKee 1988). Perhaps the most widely publicized example of the effects of forest management on an animal population is the northern spotted owl (Gutierrez and Carey 1985). However, management has been shown to cause changes at the scale of forest invertebrate communities as well (e.g. Jennings et al. 1986; McIver et al. 1992; Parsons unpublished; Schowalter 1989, 1995; Niemelä et al. 1993; Work 2000). Schowalter (1989, 1995) found more species and more functional groups in the canopies of old, uncut forests than in regenerating Douglas-fir stands. Functional group analysis is important because as the plant community changes, due to vegetation dynamics or disturbance, so do the resources available to other organisms (Price 1975). In contrast to the Schowalter studies, Niemelä et al. (1993) found that the abundance and species richness of ground beetles was higher in regenerating sites than in mature forest sites. However, they did find that several forest specialists were absent from even the oldest regenerating stands. Spence et al. (1999) note that recolonization of clear-cut forest stands, by both plants and animals, is dependant upon appropriate spatial and temporal scales for the organisms of interest, and that invertebrates, in particular, may be unable to bridge the gaps between appropriate habitat types in highly fragmented landscapes.

The results of the studies cited above, and other related work, make it clear that the effects of forest management on biodiversity is a complex issue, and one worthy of

further examination. But, due to time and monetary constraints, inventory and monitoring of biodiversity can not be exhaustive (Kremen et al. 1993). We must look for indicator species, or indicator species assemblages “that respond readily to environmental change in ways that are easily measured or observed” (Kremen et al. 1993, p.797; see also Noss 1990; Pearson and Cassola 1992). Consequently, studies looking at the effects of forest management, and subsequent stand regeneration, on animal communities are of great interest (e.g. Harris and Silva-Lopez 1992). Insects may prove to be very useful in these studies.

Insects are very abundant. Of the approximately 1.4 million described animal species, over 750,000 of those are insects (Wilson 1992, p. 133). Kremen et al. (1993, p. 799) state that in situations where conservation of biodiversity is the goal, “using the most diverse biotic elements as indicators” is most logical. In addition to high diversity, insects possess several other characteristics which make them particularly suitable for use in environmental monitoring, including their small size and acute sensitivity to environmental change (Weaver 1995). This sensitivity is largely due to their “rapid population growth rates, and short generation times” (Kremen et al. 1993, p. 801). Longer lived vertebrates, which are commonly used as indicators of habitat alteration, are less likely to show immediate changes in community structure. Furthermore, insects may serve as indicators of fragmentation in highly disturbed areas, which no longer support vertebrate indicator species (Kremen et al. 1993).

Among the insect groups available as indicator taxa, some may prove more useful than others. Beetles may be particularly suited for this type of work. Niemela

et al. (1993) suggested that beetles are: 1) particularly abundant, with nearly 300,000 described species (Wilson 1992, p. 136), 2) relatively well known taxonomically, and 3) particularly sensitive to disturbance. Additionally, as Rykken et al. (1997) observe, beetles may be collected using standardized methods. Furthermore, distribution of some beetle groups has been shown to be closely tied to larval habitat requirements, particularly soil moisture levels (Lövei and Sunderland 1996; Niemelä et al. 1992), and soil moisture in a particular stand may change due to vegetation succession or habitat alteration. All of the above stated factors support the use of beetles as adequate indicators of habitat dynamics. Lövei and Sunderland (1996, p. 249) noted that beetles (specifically carabids) have already “been used as indicator organisms for assessments of environmental pollution” and “habitat classification for nature protection.” Additionally, beetles have been used for biodiversity and conservation studies (Pearson and Cassola 1992), and studying the effects of forest management (e.g. Niemelä et al. 1993; Work 2000).

Forest management studies using beetles have covered a range of habitats and management situations. Martin (1965) examined red pine plantations in order to identify insect indicators of stand age. Lenski (1982) looked at the impacts of forest management on ground beetle diversity in the Appalachians. Niemelä et al. (1988) looked at beetle communities in adjacent managed and unmanaged coniferous forest stands in Europe. Niemelä et al. (1993) looked at clear-cut harvesting, and the effects on ground beetle assemblages in Canada. Work (2000) studied edge effects on beetle

communities associated with stand manipulation, due to harvesting, on the H.J. Andrews Experimental Forest.

The H.J. Andrews Experimental Forest is located approximately 80 km (50 mi) east of Eugene, Oregon, in the Cascade Range of Western Oregon. The 6,400 ha site encompasses the entire basin of Lookout Creek, and is cooperatively administered by the USDA Forest Service Pacific Northwest Research Station, Oregon State University, and the Willamette National Forest (McKee 1998). The site was designated a Biosphere Reserve as part of the United Nation's Man and Biosphere Program in 1976, and four years later, became part of the National Science Foundation's Long Term Ecological Research (LTER) Program (McKee and Druliner, 1998).

With elevations ranging from roughly 410 m (1350 feet) to 1630 m (5340 feet), the H.J. Andrews Forest is representative of the mountain landscapes prevalent in the west slope of the Cascade Mountains of the Pacific Northwest (McKee 1998). Dyrness et al. (1974) described 23 vegetation associations from the Western Cascades, including the H.J. Andrews Forest. The plant associations fall into two major zones within the H.J. Andrews Forest. The two zones are: the Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco)/western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone generally below 1050 m (3400 feet) in elevation, and the Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) zone above 1050 m in elevation. The two zones may then be divided into distinct plant associations. The location of the two zones is a function of temperature (elevation), while the distribution of the associations within the zone

are controlled mainly by moisture availability. Moisture availability is affected by slope, aspect and other environmental variables (Dyrness et al. 1974).

The diversity of the stands within the H.J. Andrews Forest, due to both species diversity and age class diversity, make the H.J. Andrews Forest a nearly ideal location for studying the effects of management on biological and physical phenomena (McKee 1998). About one half of the H.J. Andrews Forest remains in old growth today. The remainder is a mosaic of variously aged stands subjected to various levels of intensive forest management (McKee 1998).

A large portion of the research which has occurred on the H.J. Andrews Forest has dealt with insects and other arthropods, including beetles. The results of many of these studies were compiled to produce a checklist of invertebrates occurring on the H.J. Andrews Forest (Parsons et al. 1991). Moldenke and Fichter (1988) researched the oribatid mites. Schowalter (1989, 1995) has looked extensively at canopy arthropod communities, including functional group distribution. Anderson et al. (1982) made a checklist of caddisflies. Krantz et al. (1973) studied the arthropods of a particular watershed within the forest. McIver et al. (1992) looked at spider communities in stands of various ages. Hammond and Miller (1998) looked at the diversity of Lepidoptera within the Andrews Forest. Two recent works have detailed various aspects of beetle communities within the H.J. Andrews Experimental Forest. Brenner (2000) looked at differences in beetle communities between riparian and upland sites. Work (2000) made a detailed analysis of forest edge effects on ground dwelling beetle communities.

The work of greatest relevance to the current project, occurring on the H.J. Andrews Forest, is that of Parsons (unpublished). Parsons looked at beetle communities from 29 distinct sites. The project was designed to: "1) determine the (beetle) species present, 2) compare the soil-litter arthropod diversity among the various habitat types and growth stages of the forest and 3) begin to determine the roles these arthropods perform in decomposition processes in the western coniferous forest system."

The current project addressed the use of beetle assemblages, in both inventory and monitoring roles (Kremen et al. 1993), to learn more about the H.J. Andrews Experimental Forest. The study was the first to rigorously describe the beetle communities of variously aged stands within the H.J. Andrews Forest. In addition, the communities were compared to assess the dynamic nature of insect communities associated with vegetation succession. The information obtained from this study may be used to establish monitoring programs which will contribute to the ways forests are managed.

This project began with an analysis of the Parsons data set, as this was never completed. Then, the original sites were resampled in order to examine changes in the beetle communities, at each of the sites, due to changes in the plant communities over time. The study addressed the following questions: 1) Are the early successional arthropod communities different from the late successional communities? 2) How can the community of arthropods (Coleoptera) which characterize each of the different ages of forest be described? 3) Are there patterns (relative abundance,

presence/absence) associated with vegetation associations and/or soil moisture levels?

4) In relation to the original data set, have the patterns of association and distribution, within the beetle communities, changed over time?

The following predictions have been generated as a means of addressing the above stated questions.

1) Beetle communities will differ according to forest stand age. Niemelä et al. (1993) found clear-cutting to affect beetle communities in boreal forest, and similar patterns are expected in other forested ecosystems.

2) Differences will be most pronounced when comparing recent clear-cut to old growth sites, and the differences will diminish as stand succession proceeds. Clear-cut and old growth stands represent the two habitat extremes, and beetles have been shown to be very sensitive to habitat differences (Lövei and Sunderland 1996). Also, McIver et al. (1992) found a greater difference in spider communities between recent clear-cut and old growth stands than between regenerating and old growth stands.

3) The diversity will be higher in young seral stands than in old growth stands. Niemelä et al. (1993) found young seral sites to have greater ground beetle diversity than mature forest sites.

4) Functional group composition will be different in different aged stands, with a higher proportion of predator, detritivore and fungivore specimens in old growth stands. These predictions are based on the work of Schowalter (1995) who found a higher proportion of predators and detritivores, in canopy communities, in old growth stands than in young seral stands. The higher litter biomass and fungal growth in old growth sites would appear to be able to support more detritivores and fungivores than clear-cut sites, thus a peak in abundance of these functional groups in

old growth sites is expected. Herbivore abundance is predicted to be higher in young seral stands. Schowalter (1989) found a greater biomass of herbivores in the canopies of young seral stands than old growth stands. 5) The diversity at wet sites will be greater than the diversity at dry sites. Again, many beetle species have been shown to have narrow larval habitat requirements (Lövei and Sunderland 1996), and many require moist sites. 6) The old growth sites should show little or no change in the beetle communities, due to time, between the historic samples and current samples. However, the young seral sites should show substantial change, as an indication of vegetation dynamics. Animal communities undergo succession just as the plant community does (Price 1975). The presumed consistency of the plant community in the old growth sites should be echoed in the insect community as well (Lattin 1993). Schowalter (1995) also reported less change in the canopy communities of old growth stands, than in managed stands.

METHODS AND MATERIALS

SITE SELECTION

In the 1982/1983 sampling period a total of 29 sites were sampled, and in the 1999 sampling period 18 sites were sampled, for ground dwelling beetles using pitfall traps. The sites sampled in 1982 and 1983 were selected based on vegetation associations described by Dyrness et al. (1974). Eight distinct habitats were sampled (Table 1). The traps were deployed in order to obtain samples from four forest stand seral stages in each of the eight habitats. Some seral stage x vegetation association combinations were unavailable on the H.J. Andrews Forest, so were omitted from the study (Table 3). Seral stages were defined as: 1) herb stage clear-cut, 2) shrub stage clear-cut, 3) tree stage clear-cut and 4) old growth forest (Table 1). Absolute ages for the classes were variable. At the time of the 1982 sampling date, time since cutting was as follows: herb stage: 5-14 years, shrub stage: 15-19 years, tree stage: 20-40 years, old growth: 250+ years.

A total of 18 sites were selected for sampling in 1999. Vegetation associations from 1982/1983 with similar plant communities were combined into broader categories in order to produce the desired number of sites. Ten of the sites (4 herb stage clear-cut and 6 old growth sites), were selected from the 1982/1983 study. These sites represented the broadest gradient of wet and dry soil conditions among the habitats used in 1982/1983. Eight additional sites were selected to provide replication for a soil moisture analysis (Table 2).

Table 1. 1982/1983 H.J. Andrews beetle and forest succession study design. Numbers represent individual sites. Sites marked with an X were not found on or near the H.J. Andrews at the time of sampling. Seral stages: 1) herb stage clear-cut, 2) shrub stage clear-cut, 3) tree stage clear-cut, 4) old growth forest.

Vegetation Association/Habitat Type	Stand Age Class			
	1	2	3	4
<i>Pseudotsuga menziesii/Holodiscus discolor</i> (PSME/HODI)	X	2	3	4
<i>Pseudotsuga menziesii-Tsuga heterophylla/Corylus cornutus</i> var. <i>californica</i> (PSME-TSHE/COCOA)	5	6	7	8
<i>Tsuga heterophylla/Castanopsis chrysophylla</i> (TSHE/CACH)	9	10	11	12
<i>Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon</i> (TSHE/RHMA/GASH)	13	14	15	16
<i>Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa</i> (TSHE/RHMA/BENE)	17	18	19	20
<i>Tsuga heterophylla/Acer circinatum/Polystichum munitum</i> (TSHE/ACCI/POMU)	21	22	23	24
<i>Tsuga heterophylla/Polystichum munitum</i> (TSHE/POMU)	25	X	27	28
<i>Tsuga heterophylla/Polystichum-Oxalis oregona</i> (TSHE/POMU-OXOR)	X	30	31	32

Table 2. 1999 H.J. Andrews beetle and forest succession study design. Sites 33-40 sampled only in 1999. All others sampled in 1982, 1983, and 1999.

Vegetation Association/Habitat Type	Stand Age Class					
	Clear-cut			Old growth		
<i>Pseudotsuga menziesii/Holodiscus discolor; Pseudotsuga menziesii-Tsuga heterophylla/corylus cornutus</i>	33	34	35	4	8	36
<i>Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon; Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa</i>	13	17	37	16	20	38
<i>Tsuga heterophylla/Polystichum munitum; Tsuga heterophylla/Polystichum munitum - Oxalis oregona</i>	21	25	39	28	32	40

Table 3. 1982, 1983 and 1999 H.J. Andrews beetle and forest succession study plots and years sampled.

Plot Number	Year		
	1982	1983	1999
1	<i>Seral Stage/Vegetation Association Combination Unavailable</i>		
2	X	X	-
3	X	X	-
4	X	X	X
5	X	X	-
6	X	X	-
7	X	X	-
8	X	X	X
9	X	X	-
10	X	X	-
11	X	X	-
12	X	X	-
13	X	X	X
14	X	X	-
15	X	X	-
16	X	X	X
17	X	X	X
18	X	X	-
19	X	X	-
20	X	X	X
21	X	X	X
22	X	X	-
23	X	X	-
24	X	X	-
25	X	X	X
26	<i>Seral Stage/Vegetation Association Combination Unavailable</i>		
27	X	X	-
28	X	X	X
29	<i>Seral Stage/Vegetation Association Combination Unavailable</i>		
30	X	X	-
31	X	X	-
32	X	X	X
33	-	-	X
34	-	-	X
35	-	-	X
36	-	-	X
37	-	-	X
38	-	-	X
39	-	-	X
40	-	-	X

SAMPLING AND PROCESSING METHODS

The ground dwelling fauna at each site was sampled with the use of pitfall traps. Traps consisted of 2.5 L plastic food containers, 18 cm in depth, with a diameter of 14 cm at the mouth and 12 cm at the bottom. The traps were fitted with aluminum funnels, with a 2-3 cm opening at the bottom of the funnel. Beneath the funnel, at the bottom of the trap, was either a 16 oz. plastic cup or pint mason jar, partially filled with a 50/50 ethylene glycol/water mixture. After placement in the ground, the traps were covered with a 20 x 20 cm piece of aluminum or particle board. The board or aluminum was suspended 2-3 cm above the trap by 20-penny nail legs to act as a rain guard.

Twelve traps were placed at each site the 1982/1983 study. The traps were placed to maximize the habitat diversity sampled at each of the sites. The traps were placed in haphazard arrangements, and were situated at a minimum distance of 5 m apart. A post-hole digger was used to dig a hole for the trap. The digger excavated a circular hole nearly the same diameter as the trap, for a minimum of disturbance at the site. The traps were placed in the holes by back filling, with the soil smoothed to the rim of the trap. Litter was repositioned around the edge of the trap to simulate natural conditions. The traps were then left unopened for a minimum of two weeks to reduce the "digging-in effect" (Digweed et al. 1995).

The protocols for the 1999 sampling season were similar to those of 1982/1983 with the exception of trap number. Five traps were placed at each sample site in 1999.

Sampling periods ran for three weeks, from June 26 to July 18 in 1982, from June 16 to July 7 in 1983, and from June 25 to July 16 in 1999. At the end of each sampling period, the trapped specimens were taken to the laboratory for cleaning and identification, and determining the number of individuals per species.

The samples were poured into a white bottomed sorting tray, and the large specimens were removed with forceps. Smaller specimens were separated from the ethylene glycol mixture with the use of small mesh nylon screen. The specimens were rinsed with ethanol, and sorted into respective taxa at the Ordinal level. The specimens were then stored in 70% ethanol, or pinned, using standard techniques. Voucher specimens were placed in the Oregon State Arthropod Collection.

Family level identification was performed using the keys in Borror, Triplehorn and Johnson (1989). Species level identification was performed using a reference collection from the Oregon State Arthropod Collection, and identification manuals for Pacific Northwest taxa (Hatch 1953, 1957, 1962, 1965, 1971; LaBonte unpublished). Counts were made of individuals per species per trap. Trap counts were pooled among all traps at each site, to obtain the number of individuals per species per site. The data were entered into a Paradox (Borland International 1996) database.

Measures of soil moisture were taken during the 1999 field season. Soil samples were taken within 1 m of each pitfall trap at the time of final trap collection. Plastic containers (200 mL), with tight fitting lids, were filled with field moist soil from each of the trap locations. Measurements on soil moisture content were conducted within 24 hours of collection. Each of the samples was sieved to remove

litter and other non-soil components of the sample. Sub-samples of soil (10 g) were placed into new plastic containers for drying. The soil was then placed into a drying oven at 100 °C for 12 hours. The samples were then weighed, to determine the weight loss due to evaporation.

STATISTICAL METHODS

Taxonomic Considerations

Chi square analysis was used to test the significance of mean abundance and species number values. The mean values were calculated for each seral stage for each year, and were then tested for significant differences within each year. The formula used was: $X^2 = (\text{observed value} - \text{expected value})^2 / \text{expected value}$. Paired comparisons were calculated for each seral stage combination. The observed value in each case was the mean abundance or species number of the seral stage of interest. The mean value of the older seral stage stand was used as the expected value. The calculated X^2 value was then compared to standard tables to obtain the p-value.

The soil moisture data were analyzed using simple linear models. The difference in weight, due to drying, of the soil samples was plotted against both abundance and species diversity to explore any correlation.

A multiple linear regression model was developed to assess the differences observed in the beetle communities among the sites, particularly due to time. Explanatory (independent) variables of interest included stand age (1982, 1983 and 1999) and soil moisture conditions (1999). A second model was tested using only

stand age as an explanatory variable for diversity. Simpson's biodiversity index was used as the response (dependent) variable in both models because it exhibits low bias and high efficiency (Mouillot and Leprêtre 1999). SAS v.8 (SAS Institute Inc. 1999) was used for the regression analysis.

Community Considerations

All community level analyses were conducted using PC-ORD v.4.28 (McCune and Mefford 1999).

Non-metric Multidimensional Scaling. The species data, for each site and year, were analyzed using Non-metric multidimensional scaling (NMS). NMS is an iterative ordination method based on ranked distances between sample units, and is especially useful for data that are non-normal. The data were split into several data sets, according to year or combination of years, depending on the question of interest. Each data set was then arranged into 2 data matrices, one for the species data, and one for any accompanying environmental data, such as soil moisture/vegetation association and seral stage. The species or environmental variables formed the columns and the sample sites formed the rows. Since the trapping effort was different between years, the data were relativized to number of beetles per species per trap when performing between year comparisons.

Pimentel (1985) suggested that NMS may work best if vector scores were input from some other ordination technique such as PCA (Principle Component Analysis) or ORD (Principal Coordinate Analysis). For this study, NMS was run independently, and with the input of scores from PCA. The resultant ordination plots

from each of the methods did not appear to differ substantially from one another, so NMS was used independently for final analysis.

Transformation of the data was necessary for the ordination analysis. Row and column skew and coefficient of variation (C.V.) were both examined. The values for both skew and C.V. were high, so rare species were eliminated. For this analysis, species which occurred in less than 5% of the sites were eliminated. The species removed from the data set were those represented as singletons, and species which occurred in only a single sampling site. Removal of a particular species was dependent upon the data subset because some species were numerous in one year and rare in another. Next, a $\log(x + 1)$ transformation was performed due to the large spread in the values of species abundance, and to further reduce the column skew and coefficient of variation for both rows and columns. The last step in data transformation was a relativization by column (species) maximum. Relativization equalized the weights between abundant and less abundant species by assigning a value of one to the site which had the highest abundance for a particular species. Values for that species in the other sites were then assigned in proportion to that site. This was done for each species to further reduce column coefficient of variation. No transformations were performed on the environmental matrices.

The data were also analyzed for the presence of outliers following the approach described by Tabachnick and Fidell (1989). The Sorensen distance measure was used for all tests. No species or sites were removed due to results of the outlier analysis.

Trial runs of non-metric multidimensional scaling were conducted using the data and the Sorensen distance measure. In all cases, 4 axes, 100 iterations, 15 runs of the real data and 30 randomized runs were used to determine the stress associated with different numbers of axes. In order to determine the number of axes appropriate for the final analysis, the instability and the plot of stress vs. dimensions were examined. A final run of the program was then performed, using the selected number of axes.

Table 4 lists the various data sets and the number of axes used in the final solution.

Table 4. Number of axes used for final NMS analyses. Forest succession sites, H.J. Andrews Experimental Forest, 1982, 1983, and 1999.

DATA SET	NUMBER OF AXES
1982	3
1983	3
1999	3
1982/1983	3
1982/1999	2

Multi-response Permutation Procedure. Multi-response permutation procedure (MRPP) and blocked MRPP (MRBP) were used to statistically examine differences in beetle community composition between groups. These techniques are often used to quantify the patterns observed in ordination analyses. This method compared the mean within group distances (from predetermined groups) to within group averages of randomly assigned groups. A low p-value (<0.05) indicates that the differences detected between the groups are greater than would be expected from random assignment to groups (H_0 = no difference between groups). MRPP was used in this analysis to examine differences between stand age classes in each of the data

sets. Blocked MRPP (MRBP) was used to examine the effects of time on the sites while blocking out effects which may be due to spatial differences. Euclidean distances were used for both MRPP and MRBP in this analysis.

Indicator Species Analysis. Indicator species analysis (Dufrêne and Legendre 1997) was used to identify species which may serve as indicators of a particular environmental condition. This method assigned indicator values to the species by assessing both the species abundance in a particular group and the faithfulness with which particular species occur in that group. Values range from 0 to 100, with a value of 100 suggesting perfect indication. The indicator values are then tested for significance using a randomization (Monte Carlo) procedure. In this study, indicator species analysis was used to assign indicator values to species based on time since clear-cut for the 1982, 1983 and 1999 data sets. In addition, the technique was used to help identify species which may be responsible for the change in beetle communities over time.

Functional Group Analysis

Adult feeding habits were used to assign each beetle species to a functional group. A total of twelve functional categories were used. In order to simplify analysis, the twelve narrow groups were reduced to five more inclusive groups. Functionally similar feeding categories were grouped together. These five groups (predators, herbivores, scavengers, fungivores, and unknown/non-feeding) were then used for comparisons both between seral stages and between years. Chi square analysis was used to statistically examine the significance of both abundance and

species diversity between years. The formula used was the same as that given above. The observed value was the 1982 value, and the expected value was taken as the 1999 value.

RESULTS AND DISCUSSION

TAXONOMIC CONSIDERATIONS

Families

Representatives of 49 beetle families were collected during the course of the project (Appendix 2). This represents 64% of the known beetle families (77) from the H.J. Andrews Experimental Forest (Parsons et al. 1991). Some families were rarely encountered in the traps, while others were very common. The families with the most individuals in all three sampling periods were: Carabidae (including Cicindellidae), Curculionidae, Leiodidae, and Staphylinidae. Carabids were also the most numerous group in the 1982 and 1999 samples, while Staphylinids were the most numerous group in 1983, with Carabids coming in second. The abundance values and the percent of total yearly catch may be seen in Table 5. In each sampling period, the combined catch from these four families represented more than 85% of the total yearly catch. The four most abundant families also accounted for nearly 89% of the total combined-year catch. Staphylinidae alone made up 37% of the total followed by Carabidae (24%), Curculionidae (14%) and Leiodidae (14%).

Numerous families were observed only in certain years. Samples from 1982 contained four families unique to the sampling period, Cerambycidae, Melandryidae, Meloidae and Mycetophagidae. In addition, 10 families which were found in 1983 and/or 1999 were not found in 1982. Similarly, the 1983 samples contained 6 unique families, Cleridae, Clydiidae, Coccinellidae, Cucujidae, Hydrophilidae and

Trogossitidae. Nine families were not found in 1983 samples. Finally, 4 families were unique to 1999, Cryptophagidae, Prostomidae, Pyrochroidae and Sphindidae. Twenty-five families were not found in the 1999 samples. The higher proportion of missing families from the 1999 data set, is most likely attributable to the reduced number of traps, and thus fewer "rare" species were collected.

Table 5. Abundance and percent of total yearly catch of the four most common beetle families. 1982, 1983, and 1999 H.J. Andrews forest succession sites.

	Carabidae	Curculionidae	Leiodidae	Staphylinidae	Total
1982	1123 (39%)	655 (23%)	268 (9%)	376 (13%)	2422 (85%)
1983	998 (15%)	715 (11%)	891 (13%)	3455 (52%)	6059 (91%)
1999	453 (38%)	91 (8%)	300 (25%)	186 (16%)	1028 (86%)

Abundance

The number of beetles captured was highly variable between years, between vegetation associations and between trap-sites. A total of 11,191 beetle specimens were collected from the pitfalls during the three sampling periods, 2,861 specimens from the 1982 season, 7,135 specimens from the 1983 season, and 1,195 specimens from the 1999 season. The number of beetles per trap-site per year is given in table 6. Rows in the table represent differing vegetation associations (Tables 1 and 2), and columns in the table represent four seral stages. Average abundance values per seral stage and the results of a chi square analysis comparing these values are in table 7.

No consistent pattern relating seral stage or vegetation association and beetle abundance was discernable from the raw data. However, the average values showed a consistent pattern relating seral stage and abundance among years. The old growth sites, had the highest average catch among all seral stages. This difference in

abundance was found to be significant among all seral stages in all years except for the tree stage clear-cuts in 1982 and 1999. Lenski (1982) also found significantly more individuals in uncut forest than in clear-cut forest. Beetle abundance in old growth sites was followed by the tree stage clear cuts, herb stage clear cuts, and lastly the shrub stage clear cuts (Table 7). From these data, it appears as if clear cutting is associated with a reduction in beetle abundance, and that further reductions occur through the earliest stages of succession. This reduction is then followed by an increase over time, through the later seral stages, until a maximum is reached in the old-growth stage.

Table 6. Beetle abundance per trap site per year. 1982, 1983, and 1999 H.J. Andrews forest succession sites. Sites as described in Appendix 1. H = herb stage, S = shrub stage, T = tree stage, O = old growth.

1982				1983				1999		
H	S	T	O	H	S	T	O	Clear-cut		
X	125	48	106	X	166	86	822	47	35	66
100	50	128	92	200	96	322	425	115	26	21
93	33	82	92	127	120	103	337	81	116	35
52	40	156	167	38	114	261	611	Old Growth		
99	63	123	153	143	78	362	286	38	12	35
66	70	112	211	85	87	278	330	66	59	184
136	X	117	52	107	X	170	204	57	22	178
X	39	124	132	X	81	418	211			

Table 7. Average number of beetle specimens per seral stage per year. 1982, 1983, and 1999 H.J. Andrews forest succession sites. Standard deviations given in parentheses.

	Herb stage	Shrub stage	Tree stage	Old growth
1982	91.5(30.3) ^b	60.0(31.3) ^a	111.4(32.7) ^{b,c}	125.5(50.6) ^c
1983	116.7(54.8) ^a	106.0(30.9) ^a	250.0(120.6) ^b	403.2(213.5) ^c
1999			60.2(36.6) ^a	72.3(64.1) ^a

Within year values with shared letters do not differ significantly using chi square analysis.

The results from this study differ from other similar studies. McIver et al. (1992) studied different taxa within the same plots as the current project. They found the greatest abundance of spiders in the herb stage clear-cuts, and a decrease in abundance over time. Niemelä et al. (1993) also studied ground dwelling beetles, but in a different habitat than the current study. They found ground beetle (Carabidae) abundance, in lodgepole pine forest in Canada, to be highest in recent clear-cuts and moist mature forest sites. The current data showed an increase in abundance with increasing stand age irrespective of soil moisture (Table 6).

Species

A total of 224 taxa were collected during the three sampling periods (Appendix 1). The total number of taxa included 193 "true" species, 24 genus level morpho-species, 3 groups not identified further than subfamily and 4 groups identified only to family. Because of the coarse level of identification of some groups, the true number of species is undoubtedly larger than indicated above. The number of species trapped at each site may be seen in table 8. Average values per seral stage and results of the chi square analysis comparing these values may be seen in table 9.

Like the abundance values, the number of species was highly variable between years. Several species were unique to each year. The 1982 samples contained 38 unique species, 1983 had 54, and 1999 had only 15 such species, perhaps due to reduced sampling effort. Seventy-three species were found in two separate sampling periods and 42 species were found in all three samples. The number of sampling periods in which a species was found was correlated with the total abundance of that

species, with the more abundant species being found more often in all three sampling periods.

Table 8. Number of beetle species per trap site per year. 1982, 1983, and 1999 H.J. Andrews forest succession sites. Sites as described in Appendix 1.
H = herb stage, S = shrub stage, T = tree stage, O = old growth.

1982				1983				1999		
H	S	T	O	H	S	T	O	Clear-cut		
X	25	20	23	X	34	23	28	19	15	20
31	17	22	18	38	25	32	29	15	9	12
30	25	20	22	20	25	27	20	9	13	12
21	15	22	17	20	21	26	21	Old Growth		
28	24	25	19	27	28	22	23	14	7	13
28	22	14	26	28	31	14	22	12	9	18
39	X	30	12	40	X	23	17	12	8	16
X	16	16	20	X	15	14	14			

Table 9. Average species richness for each seral stage. 1982, 1983, and 1999 H.J. Andrews forest succession sites. Standard deviations given in parentheses.

	Herb stage	Shrub stage	Tree stage	Old Growth
1982	29.5(5.8) ^{b,c}	20.6(4.4) ^a	21.1(5.0) ^{a,c}	19.6(4.2) ^a
1983	28.8(8.6) ^a	25.6(6.3) ^a	22.6(6.2) ^a	21.8(5.1) ^a
1999			13.8(3.6) ^a	12.1(3.9) ^a

Within year values with shared letters do not differ significantly using chi square analysis.

Several species were found in only one seral stage. Three species: *Microlestes nigrinus* Mannerheim, *Trachypachus holmbergi* Mannerheim, and *Bromius obscurus* Linnaeus were found only in the clear-cut stage (5-14 years post cut). Two species: *Zacotus mathewsii* LeConte and *Epuraea obtusicollis* Reitter were found only in old-growth sites (>250 years). Several other species showed age preferences, with exclusion from one or two seral stages. It was these species which primarily explained the differences in mean species richness among the four age classes (Table 9; see also indicator species analysis below).

In both 1982 and 1983, the clear cut sites had higher average species richness than any of the other age classes, and the old growth sites had the lowest average species richness, even though the old growth sites had the highest abundance. The tree stage sites had a higher average species richness than the old growth sites in 1999, which is similar in pattern to years 1982 and 1983. These results seem to support prediction number 3 above, but many of the differences are not significant. These results are similar to those obtained by Niemelä et al. (1993), who found higher beetle species richness in regenerating stands than in mature forest stands. Lenski (1982) also reported higher carabid species diversity in clear-cut stands than in uncut stands.

Soil Moisture Analysis

Soil moisture levels are thought to affect the suitability of habitat for certain beetle species (Rykken et al. 1997; Gardner 1991; Niemelä et al. 1992). The vegetation associations of 1982/1983 were utilized for site selection because they were believed to serve as a proxy for soil moisture levels, although no measurements were taken to confirm this. In 1999, vegetation associations were given less emphasis. Three broad vegetation types were sampled, each of which combined two of the eight 1982/1983 associations into a new association. In addition, quantitative soil moisture measurements were taken at each site. The soil moisture measurements, obtained in 1999, were analyzed along with species and abundance data (Figures 1 and 2) to explore any correlation between presence and abundance and soil moisture measurements (Table 10).

The relationship between soil moisture and beetle abundance is shown in figures 1 and 2. The data show an increase in beetle abundance with increasing soil moisture in the clear-cut sites, but a slight decrease in beetle abundance with increasing soil moisture in old growth sites. The relationship between soil moisture and ground beetles (Carabidae) was similar to that for all beetles, and therefore different than the results presented by Niemelä et al. (1993), who found abundance of Carabidae to be higher in moist mature forest sites.

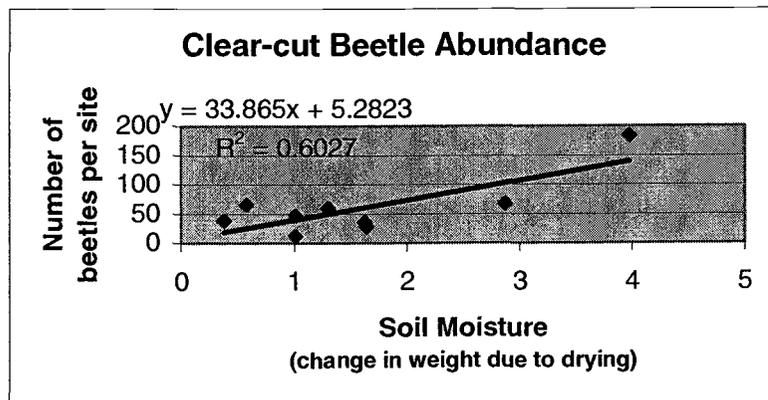


Figure 1. Relationship between soil moisture and beetle abundance ($n = 9$, $p = <0.05$) in 1999 H.J. Andrews forest succession clear-cut sites.

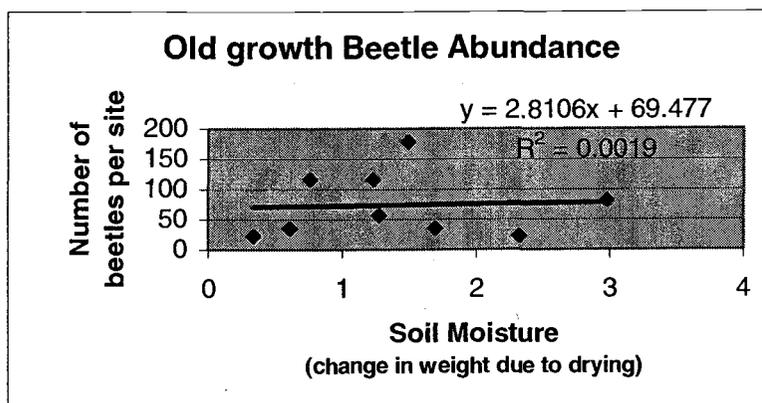


Figure 2. Relationship between soil moisture and beetle abundance ($n = 9$, $p = >0.05$) in 1999 H.J. Andrews forest succession old growth sites.

Table 10. Site soil moisture data for 1999 H.J. Andrews forest succession sites.

Site Number	Seral Stage	Mean post-drying weight (SD)
4	Old Growth	9.39 (0.27)
8	Old Growth	8.51 (0.31)
13	Clear-cut	8.99 (0.27)
16	Old Growth	9.24 (0.62)
17	Clear-cut	8.70 (0.40)
20	Old Growth	8.72 (0.52)
21	Clear-cut	8.36 (0.30)
25	Clear-cut	7.13 (0.70)
28	Old Growth	7.02 (0.74)
32	Old Growth	7.68 (0.20)
33	Clear-cut	9.42 (0.21)
34	Clear-cut	8.99 (0.74)
35	Clear-cut	9.62 (0.15)
36	Old Growth	9.66 (0.10)
37	Clear-cut	8.37 (0.35)
38	Old Growth	8.77 (0.72)
39	Clear-cut	6.02 (1.55)
40	Old Growth	8.30 (0.81)

Soil moisture analysis was also conducted using species richness data. The results are shown in figures 3 and 4. Increasing soil moisture was associated with a decrease in species richness in both clear-cut and old growth sites. This would lead to a rejection of prediction number 5 above, where diversity was predicted to be higher in wet sites than in dry sites. The decrease in species richness among the old growth sites was less than that observed in the clear-cut sites. The wetter clear-cut sites were more similar in forest structure to mature forest, including greater canopy formation, than the dryer clear-cut sites of comparable age. Perhaps the greater difference in species richness among the clear-cut sites could be attributed to not only the soil moisture conditions, but also the similarity of the wetter sites to mature forest stands.

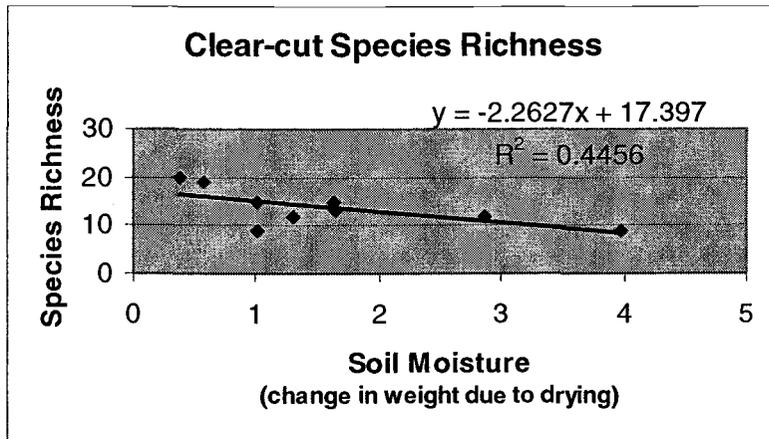


Figure 3. Relationship between soil moisture and species richness ($n = 9$, $p = <0.05$) in 1999 H.J. Andrews forest succession clear-cut sites.

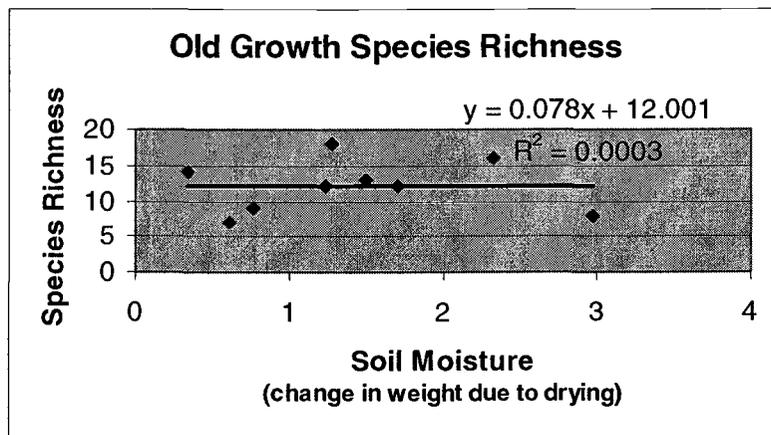


Figure 4. Relationship between soil moisture and species richness ($n = 9$, $p = >0.05$) in 1999 H.J. Andrews forest succession old growth sites.

The soil moisture analysis seems to indicate a strong relationship between beetle abundance and beetle species richness and soil moisture in young seral stands and a weak relationship among the same variables in old growth sites. These observations seem to support the prediction concerning the relative stability of old growth stands (prediction number 6).

Regression Analysis

Two linear regression models were tested for their adequacy in representing the relationship between soil stand age, soil moisture and beetle diversity at each of the study sites, for the 1982 and 1999 samples. The first linear regression model tested included quantitative stand age information and a categorical variable representing soil moisture (vegetation association), as quantitative soil moisture data was only available for 1999. The response variable was Shannon's biodiversity index. Soil moisture was found to be non-significant ($p = 0.25$) and was removed from the model. It was in actuality the vegetation association which was non-significant in the model, since soil moisture was only a categorical variable assigned according to the vegetation association.

A second model containing only stand age was then tested. Comparison between years was found to be inappropriate, due to the differences in sampling effort between years. The 12 traps per site used during the 1982 sampling period trapped a much higher proportion of "rare" species than did the 5 traps per site used in 1999. This resulted in higher diversity index values for the sites in 1982 than in 1999, making accurate comparisons between years impossible. Therefore, multiple linear regression analysis proved to be useful only for using linear contrasts to compare clear-cut and old growth sites within years.

The results showed moderate evidence for a difference in diversity between the clear-cut and mature forest sites in 1982 (p -value = 0.053; F -stat = 4.33; $df = 1$), and a non-significant difference between the same sites in 1999 (p -value = 0.474;

F-stat = 0.54; df = 1). Based on the results of the linear contrasts, it would seem that the differences observed in diversity between the clear-cut and old growth sites in 1982 were much reduced in 1999, presumably because the sites are now much more "old growth like" at least in terms of biodiversity of beetles.

Summary

Analysis of the abundance data and species data independently was adequate for answering only some of the questions of interest in this project. Average abundance and species presence/absence values showed that no pattern existed among the vegetation associations. Average values for the data also helped to show that the different seral stages did indeed have different numbers of both individuals and species. But the questions regarding the relationship of the beetle assemblages to soil moisture and the similarity of the beetle communities, in numbers of individual species, both within and between years remained.

The questions regarding soil moisture were readily answered using linear models and species number and abundance and the quantitative soil moisture measures from 1999. But still, no comparisons could be made between years.

A linear regression model was developed to help explore differences in beetle communities between years. The sites sampled in both 1982 and 1999 were compared using this method. The results showed that vegetation association was non-significant in modeling beetle diversity patterns. The results also showed that at least some of the sites had changed between the years 1982 and 1999. But, we were still left with no indication of the amount of change between years, or which species may have been

responsible for the change. Other methods were selected to help answer these questions.

COMMUNITY CONSIDERATIONS

Non-metric Multidimensional Scaling

Non-metric multidimensional scaling (NMS) (Kruskal 1964; Clarke 1993) is one of a number of multivariate statistical techniques commonly known as ordination. Ordination is a method used to arrange items along a scale or axes of a coordinate system (McCune 2000). Gauch (1982) stressed that the arrangement of the items on the coordinate system axes is done such that similar items are grouped close to one another, and dissimilar items far apart. The result is a systematic arrangement of items in a low dimensional (rather than multidimensional) space (Gauch, 1982). This space may then be viewed two dimensions at a time to help reveal relationships between the items.

In the case of community data, the sampling sites are most often the items analyzed with ordination techniques. The positions of the sites are determined by the values of the response variables, in this case the abundance and number of species. Theoretically the sites with highly similar communities will group near one another in the ordination space while those with dissimilar communities will group further apart in the same space. The results of NMS will be presented beginning with the 1982 and 1983 data sets, followed by comparison with the 1999 data.

NMS: 1982 data set. For the 1982 and 1983 data sets, since the sites were present in four discrete age classes (Figure 5), and eight vegetation associations (Figure 6), the questions of interest were: 1) to see if the beetle species assemblages would indicate differences in stand age and 2) to see if the assemblages would indicate differences in vegetation association. Ordination of the 1982 sites demonstrated that the seral stages exhibited different complexes of species. The clear cut sites and old growth sites in particular lay in distinct regions of the ordination space. The correlation between the ordination distances and the original multi-dimensional distances, was high ($r^2 = 0.84$) indicating a relatively accurate representation of the multi-dimensional data. The age of the stands had a high correlation with axis 2 ($r^2 = 0.70$). However, the vegetation associations did not show any discernable pattern. The eight vegetation associations were randomly scattered throughout the ordination space (Figure 6).

NMS: 1983 data set. The 1983 data (graphical presentation not shown), showed a very similar pattern to the 1982 data, with visually distinct seral stages, particularly the clear-cut and old growth sites. The 1983 ordination diagram showed slightly more overlap between the shrub, tree and old growth age classes than the 1982 diagram. The correlation between ordination space and multidimensional space was lower in 1983 than in 1982 ($r^2 = 0.70$). The correlation between age and the ordination axes was also lower in 1983 ($r^2 = 0.39$ for axis 2). The 1983 ordination diagram also showed no discernable pattern in beetle communities due to differences in vegetation association.

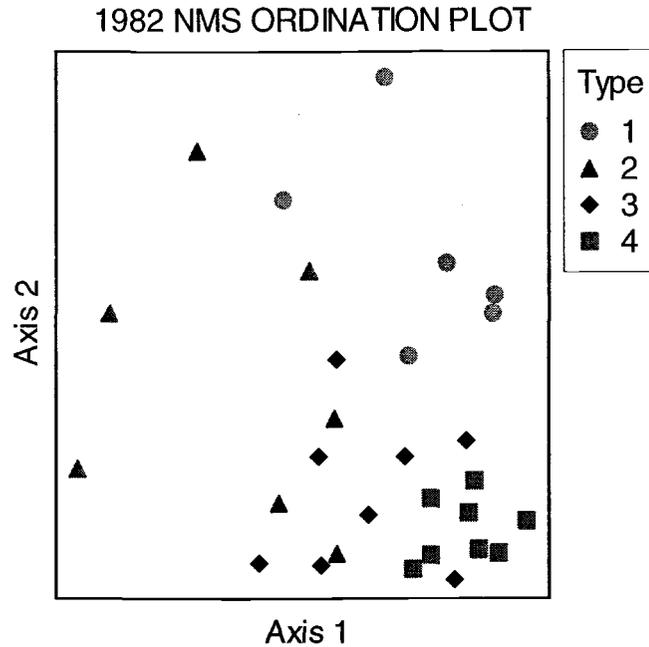


Figure 5. Ordination of 1982 H.J. Andrews forest succession sites in beetle species space. Types 1-4 indicate age classes: 1) 5-14 years; 2) 15-19 years; 3) 20-40 years; 4) 250+ years.

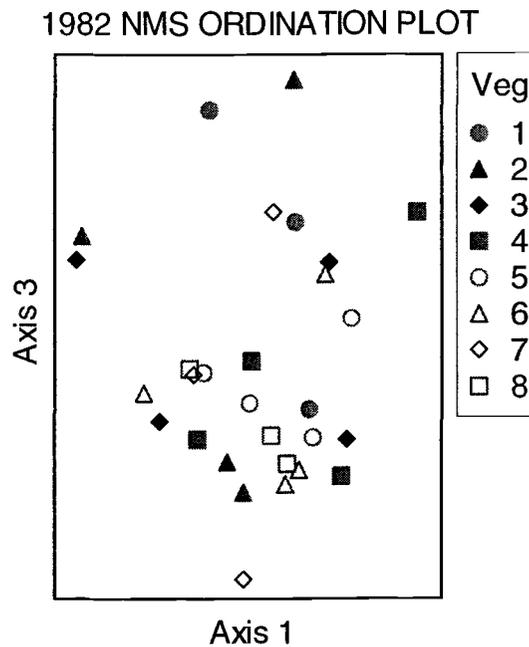


Figure 6. Ordination of 1982 H.J. Andrews forest succession sites in beetle species space. Veg 1-8 indicate vegetation associations. 1) *PSME/HODI*; 2) *PSME-TSHE/COCOA*; 3) *TSHE/CACH*; 4) *TSHE/RHMA/GASH*; 5) *TSHE/RHMA/BENE*; 6) *TSHE/ACCI/POMU*; 7) *TSHE/POMU*; 8) *TSHE/POMU-OXOR*

NMS: Combined 1982/1983 data set. Ordination of the combined 1982/1983 data set (Figure 7) showed close association of comparable age classes between years. The old growth sites in particular exhibited strong grouping between years. As was predicted, the 1983 clear-cut sites showed more similarity to the older age classes than did the same sites in 1982. The correlation between axis 2 and stand age was still relatively high ($r^2 = 0.54$). Multivariate space correlation was also high ($r^2 = 0.76$).

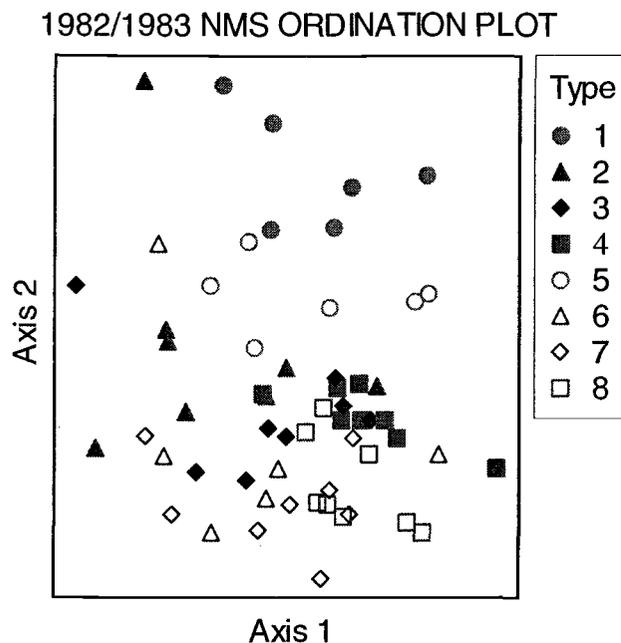


Figure 7. Ordination of 1982/1983 H.J. Andrews forest succession sites in beetle species space. Types 1-4 indicate 1982 age classes, and 5-8 indicate 1983 age classes: 1/5) 5-14 years; 2/6) 15-19 years; 3/7) 20-40 years; 4/8) 250+ years.

Some differences in species number and abundance were evident between 1982 and 1983. Forty-two species were found in the 1982 samples, which were not found in the 1983 sample. Likewise, 57 species were found in the 1983 samples which were not encountered in 1982. Of these 99 total species unique to one or the

other of the sampling years, 67 were not included in the ordination analyses, because they were considered rare (see methods section above). Of the remaining 32 species, 12 of them were exclusive to the 1982 samples and 20 were exclusive to the 1983 samples. Three of the twelve 1982 species and nine of the twenty from the 1983 samples were staphylinids. Of the remaining species, two from 1982 and three from 1983 are members of families rarely encountered in pitfall traps; Cerambycidae, Chrysomelidae and Cantharidae. The remainder were less common members of the following ground dwelling families: Melandryidae, Scarabaeidae, Byrrhidae, Lathridiidae, Leiodidae, Pselaphidae and Scydmaenidae.

NMS: 1999 data set. The 1999 data set showed two broadly overlapping groups, the herb stage clear-cuts from 1982/1983 and the old growth sites, indicating their increased similarity due to time. Axis correlation with age was low ($r^2 = 0.30$). The three vegetation associations sampled in 1999 were also differentiated based on beetle assemblages (ordination diagram not shown). The three associations were selected to represent wet, medium and dry soil moisture conditions, and combined associations from the 1982/1983 study design whose plant composition were similar.

NMS: combined 1982/1999 data set. Comparison of the sites sampled in both 1982 and 1999, using data from both years, resulted in the separation of the 1982 sites from the 1999 sites in the ordination diagram. By pairing each site by year, the lengths of the connecting lines may be considered to represent a measure of the amount of change observed in the beetle communities at each of the sites (Figure 8). As was predicted, the clear-cut sites appeared to trend toward old growth sites

between 1982 and 1999. In addition, the clear-cuts underwent substantial change, while the old growth sites underwent considerably less change.

The mean length of the lines connecting the clear-cut sites across time was significantly longer than the mean length of the lines connecting the old growth sites across the same amount of time ($t = 2.71$, $p = 0.026$, $df = 8$). The direction of change in the ordination space was consistent among all but one of the sites. Site four was the unique site in both its direction and amount of change, particularly among the old growth sites.

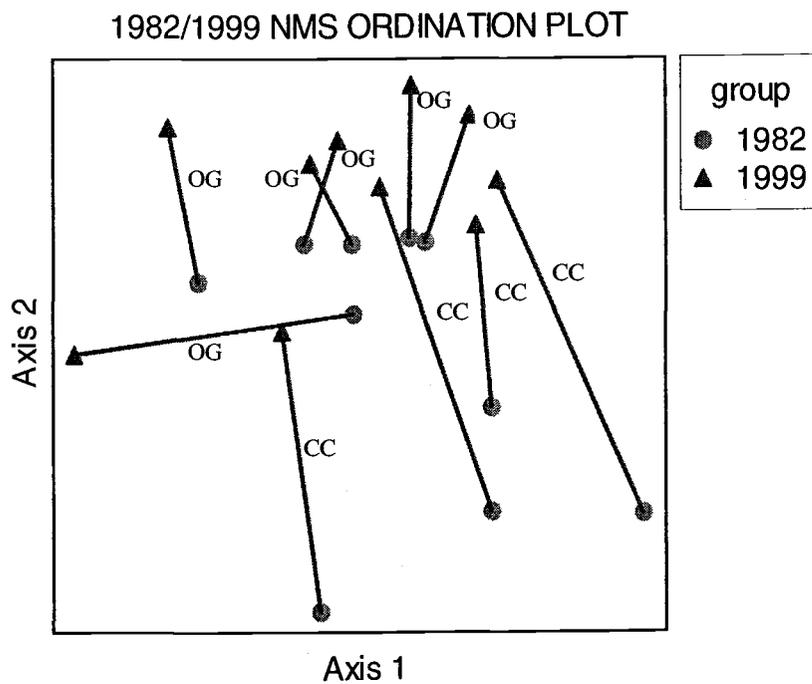


Figure 8. Ordination of 1982/1999 H.J. Andrews forest succession sites in beetle species space. Lines connect individual sites separated by time. CC = Clear cut sites and OG = old growth sites.

Site four was very different from any of the other sites sampled. It was a dry old growth site, located in a very rare plant community on the H. J. Andrews. The

over story vegetation consisted of Douglas fir (*P. menziesii*) and Oregon white oak (*Quercus garryana* Dougl.), the only stand of Oregon white oak on the H.J. Andrews. It was on a south facing slope, with very shallow soils overlaying bedrock. The 1982 samples yielded a total of 25 species from this site, while the 1999 samples contained only 7 species. The difference in number of species alone, could explain the pattern observed in the ordination diagram. In addition, one of the five traps placed at the site in 1999 did not trap any beetles. The trap appeared to be fully functional and remained undamaged through the course of the sampling. Only 12 individuals were trapped at the site in 1999 versus 106 in 1982. The site also produced a millipede species and a scorpion species (*Uroctonus mordax* Thorell) which were trapped nowhere else during the entire study. The stand received no major treatment during the period between 1982 and 1999.

The 1999 clear-cut sites were compared with the complete 1982 data set in order to further evaluate the amount of change which occurred in the clear-cut sites over the 17 years between 1982 and 1999 (Figure 9). The ordination diagram showed six of the nine 1999 clear-cut sites (type 5) ordinating near the tree stage sites (type 3) from the 1982 data set. This supports the prediction concerning the magnitude of change, via succession, in the clear-cut communities over the 17 year time span. Based on this ordination, the 1999 clear-cut sites were more similar to comparable age sites from 1982 than to their condition 17 years earlier. The remaining three sites (33, 34 and 35 in Figure 9) still lay near the 1982 clear-cut sites in the ordination diagram. These three sites were very dry sites and have developed a canopy more slowly than

the wetter sites. In addition, they were slightly younger than the other sites in this age class (Appendix 2). Consequently, the beetle communities still resembled those of early seral sites. Clear-cut and old growth sites, as in previous ordinations, remained the most distinct.

1982/1999 NMS ORDINATION PLOT

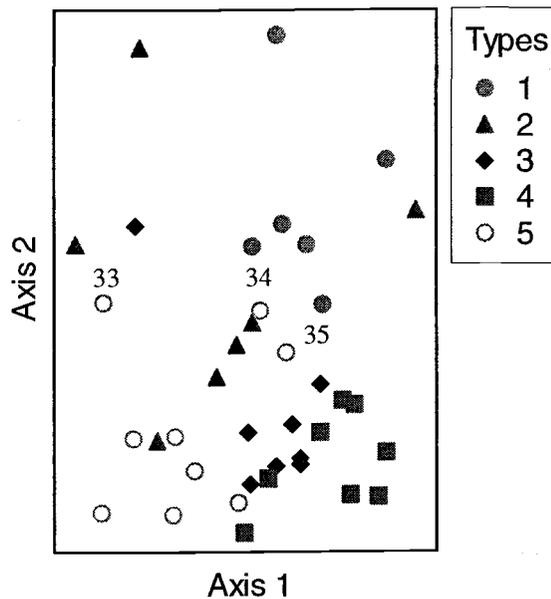


Figure 9. Ordination of 1982/1999 H.J. Andrews forest succession sites in beetle species space. Types 1-4 represent 1982 sites as described in previous figures. Type 5 represents 1999 clear-cut sites.

The 1982/1999 combined data set was split into various subsets and then subjected to ordination analyses in order to more fully understand the effect of time on the sites. The first subset consisted of two complementary groups, the first being the combined year clear-cut sites and the other the combined year old growth sites. The resulting patterns showed clear distinction between the two different ages of clear-cuts, while the old growth sites were randomly scattered in the ordination space, as

would be expected considering the presumed stability of the old growth sites. The data set was then split into years. Only those sites which were sampled in both 1982 and 1999 were included (Figure 10).

When the sites were plotted based on the 1982 data, the clear-cut sites occupied a different area of the ordination space than did the old growth sites. Conversely, when the sites were subjected to ordination according to the 1999 data, the clear-cut and old growth sites occupied widely overlapping regions of the ordination space, indicating their increased similarity.

The differences observed between 1982 and 1999 in the ordination diagrams were due to differences in the beetle communities. Eighty-two species were found in the 1982 samples which were not encountered in 1999. Ten species were likewise encountered in 1999 but not in 1982. Of the 92 combined species unique to one or the other of the sampling years, ten were immediately eliminated from the NMS analysis because they were staphylinids. Except for two species, the Staphylinidae were not identified beyond the family level in the 1999 samples. Another 55 species were eliminated from the analysis because they were considered rare (see methods section above).

Of the remaining 27 species unique to one or the other sampling period, 24 were unique to the 1982 samples, and 3 to the 1999 samples. The three species unique to 1999, were: *Ellychnia hatchi* Fender, *Isorhipis obliqua* Say and *Pterostichus* new species. The *Pterostichus* species is unique to the 1999 samples, because it was unknown in 1982. This species has yet to be officially described, and this work is in

progress by a local researcher. Examination of the voucher specimens from 1982, seemed to indicate that *Pterostichus* new species, was most likely included with *Pterostichus herculaneus* Mannerheim. That was the assumption throughout the analysis of these data. Both of the other species unique to 1999, were collected in 1982, but at sites not included in this historical analysis. Likewise, several of the species unique to 1982 were also collected in 1999, but again, at sites not included in this analysis. Of those unique to 1982, five were restricted to old growth sites, eleven to clear-cut sites, and six were found in both old growth and clear-cut sites. The higher proportion of clear-cut specialists, and lower proportion of old growth specialists, helps explain the pattern observed in figure 7, where the old growth sites are relatively stable between years, while the clear-cut sites underwent significantly more change. The eleven clear-cut exclusive species are members of six families, and many were characteristic of disturbed areas.

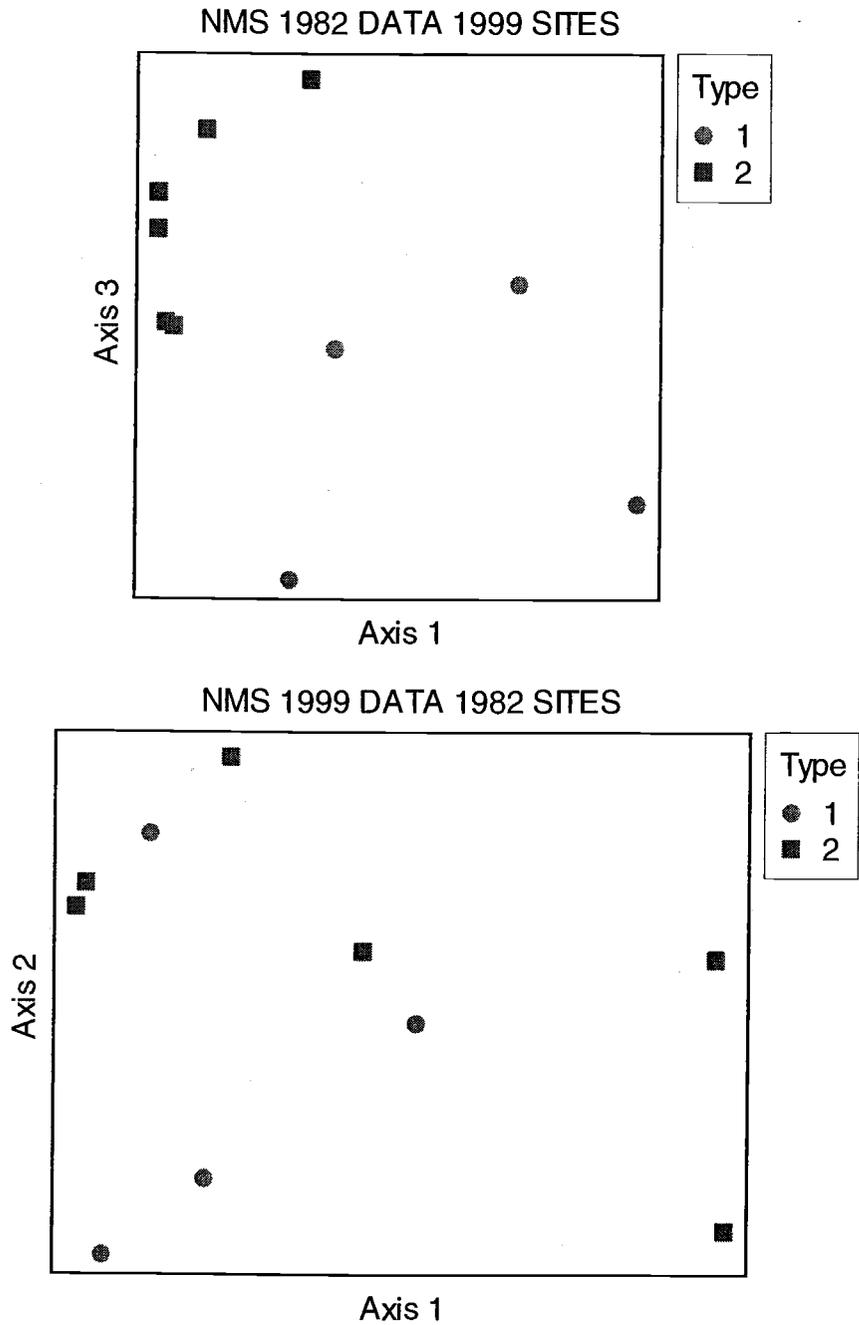


Figure 10. Ordination of 1982/1999 H.J. Andrews forest succession sites in beetle species space. Types: 1) clear-cut sites; 2) old growth sites.

Top: Ordination of 1982/1999 shared sites for data collected in 1982
 Bottom: Ordination of 1982/1999 shared sites for data collected in 1999.

NMS: summary. Several patterns seemed to be consistent throughout the results of the ordination analyses. First, the 1982 and 1983 data sets suggested that forest stands of various seral stages could be identified based on their beetle communities. This pattern was especially true for clear-cut and old growth sites, with more overlap among the mid-seral stands (Figures 4 and 6). The differentiation of forest stands based on beetle communities was consistent with the findings of Niemelä et al. (1993) who also found beetle communities to differ according to stand age although ordination was not used in their analysis. Rykken et al. (1997) used ordination and also found beetle communities to differ according to site conditions. Second, the data showed that beetle assemblages at these sites are not good indicators of the narrow 1982/1983 vegetation associations as defined by Dyrness et al. (1974) (Figure 6). The vegetation associations of 1999, three broad groups each made of two similar 1982 communities, were found to be differentiated by the associated beetle communities. This was not surprising, as the three associations were selected to represent wet, medium, and dry soil moisture conditions, and the effect of soil moisture on beetle presence and abundance has already been established. Third, it was apparent that beetle communities in old growth sites were relatively stable, while those in early seral sites were changing as a result of vegetation dynamics (Figures 7 and 9). Fourth, we gained some indication of the magnitude of the change in the clear-cut sites due to time (Figure 9). Seventeen years had passed between 1982 and 1999. This would put the 1999 clear-cuts in the same age class as the 1982 tree stage stands, and the ordinations seemed to confirm this. Last, within site species differences, between

years, were given above. Few conclusions could be drawn using this superficial analysis. A more detailed examination of the species responsible for the observed changes in the beetle communities, due to time, was conducted and will be presented below in the indicator species analysis.

Multi-response Permutation Procedure

Multi-response permutation procedure (MRPP), and the related technique blocked MRPP (MRBP), were used to test the significance of groups observed in the ordinations. Unlike ordination, where the results are graphically presented in reduced dimensional space, MRPP (and MRBP) tests the relationships of entities in the original multidimensional space. In general, the results of the MRPP analysis substantiated what was already found in the ordination analysis (Table 11). But, MRPP provided p-values for evaluating the significance of the observed patterns.

MRPP: 1982, 1983 and combined 1982/1983 data sets. The 1982 data set, when viewed in ordination space consisted of four distinct groups according to age class. MRPP showed significant differences, in the multi-dimensional space, among each of the four groups as was predicted ($p = <0.01$). Likewise, the MRPP analysis of the 1983 data set showed significant differences among the four groups. The combined 1982/1983 data set showed significant differences among stand age classes as well, with all eight age classes occupying separate regions of the multi-dimensional space. MRPP showed non-significant groups based on vegetation association. The ordination diagram also showed no grouping pattern in the sites due to vegetation association.

Table 11. Statistics and results of MRPP and MRBP tests. H.J. Andrews forest succession and beetle community study, 1982, 1983, and 1999.

Data set and Groups Tested	Test	t-statistic	A-statistic	p-value	Associated Figure
<u>1982</u> ; four age classes	MRPP	-8.91	0.072	<0.001	Figure 5
<u>1982</u> ; eight vegetation associations	MRPP	0.50	-0.007	0.676	Figure 6
<u>1983</u> ; four age classes	MRPP	-5.98	0.395	<0.001	Not shown
<u>1982/1983</u> ; eight age classes	MRPP	-13.99	0.113	<0.001	Figure 7
<u>1999</u> ; clear-cut vs. old growth	MRPP	-1.93	0.018	0.043	Not shown
<u>1999</u> ; three vegetation associations	MRPP	-1.89	0.025	0.042	Not shown
<u>1982/1999</u> ; 1982 vs. 1999	MRBP	-3.06	0.072	0.003	Figure 8
<u>1982 all/1999</u> clear-cuts; 1982/1999 tree stage vs. other age classes	MRPP	-4.72	0.024	0.001	Figure 9
<u>1982/1999</u> ; 1982 clear-cuts vs. 1999 clear-cuts	MRPP	-3.82	0.114	0.006	Not shown
<u>1982/1999</u> ; 1982 old growth vs. 1999 old growth	MRPP	-1.15	0.029	0.126	Not shown
<u>1982/1999</u> sites, 1982 data; clear-cut vs. old growth	MRPP	-4.36	0.142	0.002	Figure 10a
<u>1982/1999</u> sites, 1999 data; clear-cut vs. old growth	MRPP	-0.38	0.012	0.289	Figure 10b

MRPP: 1999 and combined 1982/1999 data sets. The difference between the two age classes in 1999 was supported by moderate evidence from the MRPP analysis ($p = 0.04$). In the ordination diagram, the two age classes were broadly overlapping, indicating more similarity now than in 1982, and the MRPP analysis provided similar evidence, with a relatively high p-value. In addition, the difference between the three vegetation associations sampled in 1999 was also supported by moderate evidence from the MRPP analysis ($p = 0.042$).

The combined 1982/1999 data set, when subjected to blocked MRPP analysis (MRBP) showed significant differences in multi-dimensional space associated with time. MRBP blocked out spatial differences between the sites and looked only at differences due to time. The MRBP results support the results from Figure 8 where the sites were shown to change over time.

In order to discover whether the differences shown using MRBP in the combined 1982/1999 data set were due to the clear-cut sites or the old growth sites, the data set was split into two separate units, one for the clear-cut sites and another for the old growth sites. Ordination results were discussed above, and the MRPP tests substantiate those results. A significant difference was found to exist within the multi-dimensional space between the clear-cut sites from the two different years ($p = <0.01$). By contrast, the old growth site groups were found to be non-significant between years ($p = 0.13$). This indicated that the low p-value observed for the complete combined 1982/1999 data set could be attributed to differences between the clear-cut sites and not the old-growth sites. This also served as further evidence for the relative lack of change within the old-growth sites.

Given the suggested consistency of the beetle assemblages in the old-growth sites, one may wonder how much change has occurred in the clear-cut sites due to time. As discussed above, the length of the lines in the 1982/1999 combined ordination space gave some indication, but further analysis provided further clarification. As was also discussed above, the 1999 clear-cut sites were compared with the complete 1982 data set, and the ordination showed grouping of the 1999

clear-cut sites with the later seral stages from the 1982 data set. MRPP showed these results to be significant. A test was run to compare the 1982 tree stage clear-cuts plus the 1999 clear-cuts (similar in age since cut) to the rest of the 1982 data set. The results were significant ($p = 0.03$), indicating that the grouping was less random than would be expected by chance.

Two other MRPP tests were run on the subdivided 1982/1999 combined data set. The data set was split into the two years, so that clear-cuts were compared to old-growth sites independently for both 1982 and 1999. The results showed significant differences between the groups in 1982 ($p = <0.01$), and non-significant differences between the groups for 1999 ($p = 0.21$). These data further suggested that the beetle communities in the clear-cuts of 1982 changed significantly with respect to the communities at the same sites in 1999.

MRPP: summary. The MRPP/MRBP analyses confirmed what was found in the ordination analyses. First, MRPP showed that forest stands of various ages have different beetle communities. Again, clear-cut and old growth sites in particular, are very different from one another in ordination and multi-dimensional space. Second, the broad vegetation associations, sampled in 1999, were found to have different beetle communities, unlike the more narrow vegetation associations of 1982/1983. Third, the MRPP analysis gave further indication of the relative stability of the beetle communities in old growth sites, and of changing communities in the young seral stands. Last, the MRPP analysis provided further measure of the magnitude of change observed in the clear-cut stands between 1982 and 1999.

Indicator Species Analysis

Several patterns emerged when the results from the indicator species analysis were examined (Table 12). Species which appeared to be indicators of specific age classes will be discussed first, followed by the species indicative of year. The herb stage clear-cuts had the most species identified as having a unique or near unique association with a certain seral stage. Eleven species were identified as indicators based on the 1982 data, and five were identified according to the 1983 data. Of these species, two were common to both years; *Bolboceras obesus* (Leconte) and *Neocyrta sternalis* Hatch. One of the species, *N. sternalis*, was found only in clear-cuts in both the 1982 and 1983 samples, and had the highest indicator value of any of the clear-cut species with a value of 83.3 for 1982. The second species, *B. obesus*, occurred in herb, shrub, and tree stage clear-cuts although its highest abundance was in the herb stage clear-cut sites, hence its identification as an indicator.

The shrub stage sites had the lowest incidence of potential indicator species of all the seral stages. The 1982 data set yielded a single indicator species, while the 1983 data set had no species identified as indicators. The species identified as an indicator, for shrub stage clear-cuts, in the 1982 data set was *Malthodes* sp. This species had the greatest abundance in the shrub stage, but was encountered in low numbers in all three other seral stages, and therefore had a relatively low indicator value (54.4).

Table 12. Indicator species for both age class and year with associated indicator values and P. All species with indicator value ≥ 50.0 are reported.

Data set and group indicated	Species	Indicator Value*	P**	
1982; clear-cut age class	<i>Neocyrta sterna</i>	83.3	0.002	
	<i>Boreocanthon simplex</i>	66.7	0.001	
	<i>Microlestes nigrinus</i>	66.7	0.001	
	<i>Harpalus cautus</i>	62.1	0.001	
	<i>Trixagus sericeus</i>	57.3	0.005	
	<i>Batrissodes albionicus</i>	50.7	0.006	
	<i>Bolbocerus obesus</i>	50.0	0.01	
	<i>Bromius obscurus</i>	50.0	0.007	
	<i>Hynobius longulus</i>	50.0	0.005	
	<i>Longitarsus</i> sp.	50.0	0.003	
	<i>Metabletus americanus</i>	50.0	0.006	
	1982; shrub age class	<i>Malthodes</i> sp.	54.4	0.004
	1982; tree age class	<i>Lepesoma granicollis</i>	65.2	0.002
<i>Nemocestes puncticollis</i>		52.7	0.007	
1982; old growth age class	<i>Zacotus matthewsii</i>	87.5	0.001	
	<i>Tachinus semirufus</i>	71.7	0.001	
	<i>Clinidium calcaratum</i>	50.0	0.011	
1983; clear-cut age class	<i>Bolbocerus obesus</i>	66.7	0.002	
	<i>Leiodes morula</i>	66.7	0.002	
	<i>Coelocnemus californicus</i>	51.6	0.005	
	<i>Altica tombacina</i>	50.0	0.011	
	<i>Neocyrta sterna</i>	50.0	0.007	
1983; old growth age class	<i>Philonthus</i> sp.	67.4	0.002	
	<i>Epuraea obtusicollis</i>	50.0	0.007	
	<i>Zacotus matthewsii</i>	50.0	0.012	
1999; clear-cut age class	<i>Lobosoma horridum</i>	59.9	0.065	
1999; old growth age class	<i>Zacotus matthewsii</i>	73.7	0.002	
	<i>Tachinus semirufus</i>	63.9	0.016	
	<i>Omus dejeani</i>	50.6	0.358	
	<i>Omus dejeani</i>	55.5	0.021	
1982/1983; 1982	<i>Tachinus semirufus</i>	81.0	0.001	
1982/1983; 1983	<i>Nemadus decipiens</i>	68.4	0.001	
	<i>Pterostichus lama</i>	57.5	0.008	
	<i>Lobosoma horridum</i>	55.2	0.083	
	<i>Scaphinotus angulatus</i>	52.8	0.001	
	<i>Promecognathus laevissimus</i>	50.8	0.001	
	1982/1999; 1982	<i>Lophoderus similis</i>	70.0	0.005
		<i>Steremnius carinatus</i>	54.8	0.290
1982/1999; 1999	<i>Catops basilaris</i>	56.1	0.048	

*Indicator value = % of perfect indication, based on combining values for relative abundance and relative frequency.

**P = proportion of randomized trials with indicator value equal to or exceeding the observed indicator value.

The shrub stage sites had the lowest incidence of potential indicator species of all the seral stages. The 1982 data set yielded a single indicator species, while the

1983 data set had no species identified as indicators. The species identified as an indicator, for shrub stage clear-cuts, in the 1982 data set was *Malthodes* sp. This species had the greatest abundance in the shrub stage, but was encountered in low numbers in all three other seral stages, and therefore had a relatively low indicator value (54.4).

The tree stage sites also had few species identified as indicators. Two species were found for 1982 (*Lepesoma granicollis* (LeConte) and *Nemocestes puncticollis* Casey) and no species for 1983. In 1999, the 1982 herb stage clear-cuts had vegetation similar to the 1982 tree stage clear-cuts. One species, *Lobosoma horridum* Mannerheim, was found to be an indicator of these sites. All three of these species are weevils. A review of the trap records for weevils showed that except for *Steremnius carinatus* Boheman, which was unusually widespread, weevils were extremely rare in herb stage clear-cuts, and reached their peak abundance in the shrub and tree stage clear-cut sites. In addition, 1982 and 1983 each had ten weevil species with an indicator value assigned for various seral stages. In both years, five of the ten species indicated tree stage sites.

Old growth sites had two indicator species identified for each year. In both 1982 and 1999, *Tachinus semirufus* Horn was shown to be indicative of old growth sites, and *Z. matthewsii* was identified in 1982, 1983 and 1999 as an indicator species. The 1983 sampling period produced 2,790 of the 2,990 total individuals of *T. semirufus*. Peak abundance occurred in the old growth stage, but its widespread

distribution in 1983 resulted in a relatively low indicator value (32.8) for that year. *Z. matthewsii* was trapped in old growth sites only for all years.

Based on the indicator species analysis, suites of species appear to be useful as indicators of seral stage, within the H.J. Andrews Experimental Forest, for two of the four defined classes. Kremen et al. (1993) reported that the use of several taxa for community monitoring is probably better than the use of a single taxon for each area of interest. In addition, the commonly used EPT test (Ephemeroptera, Plecoptera, Trichoptera), used by aquatic ecologists and hydrologists for water quality monitoring, uses multiple species from three insect families for most reliable results (e.g. Berkman et al. 1986).

For clear-cut sites, the combined presence of *B. obesus* and *N. sternita* would, except in rare exceptions, indicate a clear-cut site. No species or suite of species appears to be consistently indicative of the shrub or tree stage sites. However, further exploration of the abundance of weevils in tree stage sites would be worth while.

Old growth sites are characterized by *T. semirufus* and *Z. matthewsii*. This assemblage may be the most useful from a management standpoint, because old growth sites are valued from an ecological and a cultural standpoint, and evidence that a stand has indeed reached "old growth" conditions may be important to those charged with managing our natural resources. Although *T. semirufus* reached peak abundance in old growth stands, its distribution was ubiquitous. On the other hand *Z. matthewsii* appears, based on these data, to be limited in distribution to the old growth sites, and as such may serve as an old growth indicator independently. It has the highest

indicator value listed for any species in any of the age classes, with a value of 87.5 for 1982 old growth sites. Had individuals been trapped in every old growth site, an indicator value of 100 would have been assigned. Lindroth (1961-1969) commented on the relatively narrow habitat requirements, of this species, which are found in the old growth environment. Hatch (1953) considered *Z. matthewsii* rare, but was found to be locally abundant, in this study, in many of the old growth trap sites.

The remainder of the indicator species testing was most valuable in helping to identify species which may have been responsible for the changes observed in the ordination analyses, due to time. Analysis of the 1982/1983 combined data set identified one species indicative of the 1982 sample, and six species of the 1983 sample. The 1982 indicator was also found in the 1983 samples, although in much reduced abundance. Likewise, all six species indicative of 1983 were also found in 1982, again, in reduced numbers. These observed differences are probably sampling artifacts and not true differences due to time.

The results of the 1982/1983 combined analysis must be interpreted carefully, because the results of the trapping effort in 1983 were undoubtedly affected by the trapping done in 1982. Hundreds of specimens were removed from the trap sites during the 1982 sampling period, and subsequent resampling not discussed in this paper. The altered community structure may have affected the composition of the community the following year. Common species may have been reduced in abundance, while rare species may have increased in abundance due to the decreased competition with the more abundant species. Brenner (2000) also addressed the

effects of sampling over time. He suggested that permanent sampling sites, such as those used in this study, could very well have negative impacts on local populations of beetles, and therefore affect subsequent samples.

The combined 1982/1999 data set yielded two indicator species for 1982 and a single species for 1999. *Lophoderus similis* Marsh and *S. carinatus* were the species listed as indicators of 1982 conditions. *Steremnius carinatus* was found in the 1999 samples, while *L. similis* was not. It is not surprising then that *L. similis* has one of the highest indicator values reported (70.0). *Catops basilaris* (Say) was identified as a possible indicator of 1999 conditions. This species was present in both 1982 and 1999 samples, and was extremely abundant in 1999, with 291 of the total 442 individuals trapped during that sampling period. This is especially surprising when considering the reduced trapping effort during the 1999 season, with 90 traps, compared to the 348 present during the 1982 and 1983 seasons.

Indicator species analysis: summary. The indicator species analysis suggests that it was species relative abundance more than presence/absence which was responsible for the changes observed in the ordination diagrams. Relatively few species were found in a single sampling period (see NMS results). Even fewer species remained in the data set for NMS analyses because they were classified as rare and removed. However, many species had abundance values which varied widely between years. These differences in abundance were relativized to individuals per species per trap for comparison of the 1982 and 1999 data sets, but large differences in some species still occurred.

There has been some concern expressed over the reliability of using invertebrates as indicator species for environmental assessment. As mentioned above, the practice is already widely accepted in aquatic systems, and many believe that terrestrial systems may be as adequately served through invertebrate sampling. Murtaugh (1996, p. 138) warns that “indicators must be screened rigorously and quantitatively before they are put forth as meaningful surrogates for the responses we are really interested in.” Brenner (2000) suggests that this may be a good practice when there is concern over a critically endangered species or ecosystem, but that for general use, this level of intense screening may be cost prohibitive, and other approaches may be more useful.

FUNCTIONAL GROUP ANALYSIS

Adult beetle feeding habits were used to assign species to 12 functional groups: detritivores, dung feeders, flower feeders, fungivores, herbivores, moss feeders, non-feeders, predators, seed feeders, scavengers, xylophages and unknown (Table 13). Because many of the functional groups were represented by only a few individuals, groups sharing general trophic function were combined to create 5 categories which were then used for analysis. The 5 groups were: scavengers (scavengers, detritivores, and dung feeders), herbivores (flower feeders, herbivores, moss feeders, seed feeders and xylophages), fungivores, predators and unknown/non-feeding. Comparisons were conducted based on numbers of individuals and numbers of species (Figures 11 and 12, and Table 14).

Table 13. The abundance, family affiliation, and adult functional group for beetles collected in 1982, 1983 and 1999, H.J. Andrews Experimental Forest. Species listed by decreasing total abundance. Functional Groups (FG) from Parsons et al. (1991).

D = detritivore, Dg = dung feeder, Fl = flower feeder, Fu = fungivore,
H = herbivore, Ms = moss feeder, nf = non-feeding stage, Pr = predator,
Sd = seed feeder, Sv = scavenger, X = xylophagous, unk = unknown.

SPECIES	1982	1983	1999	TOTAL	FAMILY	FG
<i>Tachinus semirufus</i> Horn	91	2790	109	2990	Staphylinidae	unk
Aleocharinae spp.	242	1052	0	1294	Staphylinidae	Pr
<i>Nemadus decipiens</i> Horn	124	747	4	875	Leiodidae	Sv
<i>Lobosoma horridum</i> Mannerheim	297	486	50	833	Curculionidae	H
<i>Omus dejeani</i> Reiche	268	117	150	535	Cicindellidae	Pr
<i>Pterostichus herculeanus</i> Mannerheim	228	192	68	488	Carabidae	Pr
<i>Catops basilaris</i> (Say)	74	77	291	442	Leiodidae	Sv
<i>Steremnius carinatus</i> Boheman	273	136	27	436	Curculionidae	H
<i>Pterostichus lama</i> Menetries	105	154	89	348	Carabidae	Pr
Ptiliidae sp.	0	213	0	213	Ptiliidae	Fu
<i>Zacotus matthewsii</i> LeConte	103	29	48	180	Carabidae	Pr
<i>Harpalus cautus</i> LeConte	93	65	5	163	Carabidae	Sd
<i>Scaphinotus rugiceps rugiceps</i> Horn	46	60	40	146	Carabidae	Pr
<i>Aphodius opacus</i> LeConte	60	35	13	108	Scarabaeidae	Dg
<i>Amara littoralis</i> Mannerheim	31	66	0	97	Carabidae	Sd
<i>Cychrus tuberculatus</i> Harris	33	43	15	91	Carabidae	Pr
<i>Carabus taedatus</i> Fabricius	2	74	6	82	Carabidae	Pr
<i>Pterostichus protractus</i> LeConte	60	15	0	75	Carabidae	Pr
<i>Promecognathus laevis</i> Dejean	9	64	1	74	Carabidae	Pr
Staphylinidae spp.	0	0	71	71	Staphylinidae	unk
<i>Nicrophorus defodiens</i> Mannerheim	0	0	66	66	Silphidae	Sv
<i>Leiodes morula</i> (LeConte)	39	21	1	61	Leiodidae	Fu
<i>Coelocnemis californicus</i> Mannerheim	20	34	1	55	Tenebrionidae	H
<i>Scaphinotus angulatus</i> Harris	6	42	2	50	Carabidae	Pr
<i>Trachypachus holmbergi</i> Mannerheim	47	2	0	49	Carabidae	Pr
<i>Lophoderus similis</i> Marsh	24	24	0	48	Scydmaenidae	unk
<i>Epuraea obtusicollis</i> Reitter	7	39	0	46	Nitidulidae	Fu
<i>Geodercodes latipennis</i> Casey	14	32	0	46	Curculionidae	H
Philonthus sp.	19	19	0	38	Staphylinidae	Pr
<i>Phausis skelleyi</i> Fender	16	14	7	37	Lampyridae	unk
<i>Scaphinotus marginatus</i> Fischer	12	18	7	37	Carabidae	Pr
<i>Pterostichus inopinus</i> (Casey)	10	24	0	34	Carabidae	Pr
<i>Lepesoma lecontei</i> Casey	18	10	5	33	Curculionidae	H
<i>Ditylus gracilis</i> LeConte	27	3	1	31	Oedemeridae	Fl
<i>Dasytes cruralis</i> Leconte	19	10	0	29	Melyridae	Pr
<i>Platyceroides laticollis</i> Casey	17	8	4	29	Lucanidae	nf
<i>Timarcha intricata</i> Haldeman	12	13	0	25	Chrysomelidae	H
<i>Pactopus horni</i> LeConte	22	1	1	24	Throscidae	unk
Acrotrichus sp.	2	20	0	22	Ptiliidae	Fu
<i>Aulonothroscus validus</i> LeConte	11	8	3	22	Throscidae	Pr
<i>Neoclytus sternita</i> Hatch	16	4	2	22	Leiodidae	Fu

Table 13 (Continued)

<i>Agriotes oregonensis</i> Beck	7	6	8	21	Elateridae	unk
<i>Metabletus americanus</i> Dejean	12	9	0	21	Carabidae	Pr
<i>Phellopsis porcata</i> LeConte	4	9	8	21	Zopheridae	Fu
<i>Batrisodes albionicus</i> (Aube)	14	6	0	20	Pselaphidae	Pr
<i>Bolboceras obesus</i> (LeConte)	7	6	7	20	Scarabaeidae	D
<i>Boreocanthon simplex</i> (LeConte)	12	8	0	20	Scarabaeidae	Dg
<i>Colon</i> sp.	7	13	0	20	Leiodidae	Sv
<i>Nemocestes puncticollis</i> Casey	9	11	0	20	Curculionidae	H
<i>Oropus</i> sp.	10	10	0	20	Pselaphidae	Pr
<i>Pterostichus new species</i>	0	0	19	19	Carabidae	Pr
<i>Lepesoma productus</i> Hatch	8	10	0	18	Curculionidae	H
<i>Microlestes nigrinus</i> Mannerheim	16	1	0	17	Carabidae	Pr
<i>Lepesoma granicollis</i> (LeConte)	10	6	0	16	Curculionidae	H
<i>Malthodes</i> sp.	9	7	0	16	Cantharidae	unk
<i>Calosoma tepidum</i> LeConte	13	2	0	15	Carabidae	Pr
<i>Ellychnia hatchi</i> Fender	1	7	6	14	Lampyridae	unk
<i>Panscopus gemmatus</i> LeConte	6	5	3	14	Curculionidae	H
<i>Metrius contractus</i> Eschscholtz	2	3	8	13	Carabidae	Pr
<i>Empelus brunnipennis</i> (Mannerheim)	1	11	0	12	Clambidae	Fu
<i>Orobanus tarsalis</i> Hatch	6	6	0	12	Staphylinidae	unk
<i>Otiorhynchus rugosostriatus</i> (Goeze)	6	5	1	12	Curculionidae	H
<i>Triarthron lecontei</i> Horn	1	10	0	11	Leiodidae	Fu
<i>Troglomethes oregonensis</i> Wittmer	0	11	0	11	Cantharidae	unk
<i>Bromius obscurus</i> Linnaeus	8	2	0	10	Chrysomelidae	H
<i>Dermestes talpinus</i> Mannerheim	3	1	6	10	Dermestidae	Sv
<i>Hydnobius longulus</i> LeConte	4	4	1	9	Leiodidae	Fu
<i>Megapenthes caprella</i> (LeConte)	5	3	1	9	Elateridae	unk
<i>Mycetoporus</i> sp.	0	9	0	9	Staphylinidae	unk
<i>Pselaptrichus rothi</i> Park	5	4	0	9	Pselaphidae	Pr
<i>Pterostichus amethystinus</i> Mannerheim	4	5	0	9	Carabidae	Pr
<i>Staphylinus rutilicauda</i> Horn	2	1	6	9	Staphylinidae	Pr
<i>Trixagus sericeus</i> LeConte	9	0	0	9	Throscidae	unk
<i>Isorhipis obliqua</i> Say	1	0	7	8	Eucnemidae	unk
<i>Leiodes</i> sp.	1	6	1	8	Leiodidae	Fu
<i>Lordithon</i> sp.	0	8	0	8	Staphylinidae	unk
<i>Lucifotychus</i> sp.	0	8	0	8	Pselaphidae	Pr
<i>Mordella atrata</i> Melsheimer	6	0	2	8	Mordellidae	H
<i>Nicrophorus vespilloides</i>	7	1	0	8	Silphidae	Sv
<i>Thalycra murrayi</i> Horn	4	4	0	8	Nitidulidae	Fu
<i>Amara sinuosa</i> Casey	2	5	0	7	Carabidae	Sd
<i>Xestocis</i> spp.	3	4	0	7	Ciidae	unk
<i>Altica tombacina</i> Mannerheim	3	3	0	6	Chrysomelidae	H
<i>Clinidium calcaratum</i> LeConte	4	2	0	6	Rhysodidae	Fu
<i>Cupila</i> sp.	0	6	0	6	Pselaphidae	Pr
<i>Enicmus cordatus</i> Belon	4	2	0	6	Lathridiidae	Fu
<i>Pterostichus tuberculo-femoratus</i> Hatch	3	1	2	6	Carabidae	Pr
<i>Quedius</i> spp.	0	6	0	6	Staphylinidae	Pr
<i>Tachyporinae</i> sp.	3	3	0	6	Staphylinidae	unk

Table 13 (Continued)

<i>Xenomycetes laversi</i> Hatch	2	4	0	6	Endomychidae	Fu
<i>Hylastes nigrinus</i> (Mannerheim)	1	4	0	5	Scolytidae	H
<i>Listemus formosus</i> Casey	4	1	0	5	Byrrhidae	Ms
<i>Otiorhynchus ovatus</i> (Linnaeus)	2	2	1	5	Curculionidae	H
<i>Plinthodes taeniatus</i> LeConte	2	3	0	5	Curculionidae	H
<i>Anaspis seposita</i> Liljeblad	4	0	0	4	Melandryidae	Fl
<i>Anotylus nitidulus</i> Gravenhorst	3	1	0	4	Staphylinidae	Pr
<i>Athous varius</i> Benton	3	1	0	4	Elateridae	unk
<i>Cnemogonus lecontei</i> Dietz	2	2	0	4	Curculionidae	H
<i>Dacne californica</i> Horn	1	3	0	4	Erotylidae	Fu
<i>Limonius maculicollis</i> Motschulsky	3	1	0	4	Elateridae	H
<i>Megarafonus</i> sp.	3	1	0	4	Pselaphidae	Pr
<i>Mycetochara caseyi</i> Hatch	2	2	0	4	Alleculidae	Fl
<i>Mycetophagus californicus</i> Horn	4	0	0	4	Mycetophagidae	Fu
<i>Mycetoporus consors</i> LeConte	4	0	0	4	Staphylinidae	unk
<i>Notiophilus sylvaticus</i> Eschscholtz	2	2	0	4	Carabidae	Pr
<i>Podabrus piceatus</i> Fender	0	4	0	4	Cantharidae	Pr
<i>Proteinus limbatus</i> Maklin	0	4	0	4	Staphylinidae	Pr
<i>Pseudopanscopus costatus</i> Buchanan	2	2	0	4	Curculionidae	H
<i>Pterostichus crenicollis</i> LeConte	2	2	0	4	Carabidae	Pr
<i>Rhyncolus brunneus</i> Mannerheim	3	1	0	4	Curculionidae	X
<i>Serica curvata</i> (LeConte)	4	0	0	4	Scarabaeidae	H
<i>Usechus nucleatus</i> Casey	1	2	1	4	Zopheridae	Fu
<i>Ampedus rhodopus</i> LeConte	1	2	0	3	Elateridae	unk
<i>Aphodius</i> sp.	3	0	0	3	Scarabaeidae	Dg
<i>Aridius nodifer</i> Westwood	0	3	0	3	Lathridiidae	Fu
<i>Caenocyrtia picipennis</i> LeConte	1	2	0	3	Leiodidae	Fu
<i>Ctenicera</i> sp.	2	1	0	3	Elateridae	unk
<i>Hemicrepidius morio</i> LeConte	2	1	0	3	Elateridae	unk
<i>Iphthimimus serratus</i> Mannerheim	2	1	0	3	Tenebrionidae	unk
<i>Lioon simplicipes</i> Mannerheim	0	3	0	3	Byrrhidae	Ms
<i>Longitarsus</i> sp.	3	0	0	3	Chrysomelidae	H
<i>Megarathrus pictus</i> Motschulsky	0	3	0	3	Staphylinidae	unk
<i>Mordellistena aspersa</i> Melsheimer	2	1	0	3	Mordellidae	H
<i>Phyllotreta</i> sp.	0	3	0	3	Chrysomelidae	H
<i>Stenus costalis</i> Casey	0	3	0	3	Staphylinidae	Pr
<i>Xestoleptura crassipes</i> (LeConte)	3	0	0	3	Cerambycidae	Fl
<i>Agathidium jasperinum</i> Fall	0	2	0	2	Leiodidae	Fu
<i>Amara lunicollis</i> Schiodte	1	1	0	2	Carabidae	Sd
<i>Amara sanjuanensis</i> Hatch	1	1	0	2	Carabidae	Sd
<i>Amecocerus larsoni</i> Hatch	0	0	2	2	Melyridae	Fl
<i>Aphodius rogersi</i> Hatch	1	0	1	2	Scarabaeidae	Dg
<i>Bolitobius kremeri</i> (Malkin)	1	1	0	2	Staphylinidae	unk
<i>Bradycellus nigrinus</i> Dejean	2	0	0	2	Carabidae	Pr
<i>Ctenicera opacula</i> (LeConte)	0	1	1	2	Elateridae	unk
<i>Dasyrhadus impressicollis</i> Fall	1	1	0	2	Melyridae	Pr
<i>Harpalus innocuus</i> LeConte	2	0	0	2	Carabidae	Sd
<i>Helops permitens</i> LeConte	1	1	0	2	Tenebrionidae	unk

Table 13 (Continued)

<i>Hydnobius pumilus</i> LeConte	0	2	0	2	Leiodidae	Fu
<i>Hyperaspis postica</i> LeConte	0	2	0	2	Coccinellidae	Pr
<i>Mathrilaenum subcostatum</i> (Maklin)	0	2	0	2	Staphylinidae	Fl
<i>Micrathous brevis</i> (VanDyke)	1	0	1	2	Elateridae	unk
<i>Mycetoporus punctatissimus</i> Hatch	2	0	0	2	Staphylinidae	unk
<i>Necrophilus hydrophiloides</i> Guerin-Meneville	0	1	1	2	Silphidae	Sv
<i>Nemocestes incomptus</i> Horn	1	1	0	2	Curculionidae	H
<i>Ontholestes cingulatus</i> Gravenhorst	0	2	0	2	Staphylinidae	Pr
<i>Otiorhynchus sulcatus</i> (Fabricius)	0	0	2	2	Curculionidae	H
<i>Panscopus costatus</i> Buchanan	0	0	2	2	Curculionidae	H
<i>Phaedon prasinellus</i> LeConte	0	2	0	2	Chrysomelidae	H
<i>Philonthus cruentatus</i> Gmelin	2	0	0	2	Staphylinidae	Pr
<i>Psylliodes</i> sp.	1	1	0	2	Chrysomelidae	H
<i>Saprinus lubricus</i> LeConte	2	0	0	2	Histeridae	Pr
<i>Scydmaenus</i> sp.	0	2	0	2	Scydmaenidae	unk
<i>Silis pallida</i> Mannerheim	1	1	0	2	Cantharidae	unk
<i>Sitona californicus</i> Fahraeus	0	2	0	2	Curculionidae	H
<i>Uloma longula</i> LeConte	2	0	0	2	Tenebrionidae	unk
<i>Xestolinus frontalis</i> Hatch	0	2	0	2	Staphylinidae	Pr
<i>Agasphaerops nigra</i> Horn	0	1	0	1	Curculionidae	H
<i>Agathidium pulchrum</i> LeConte	1	0	0	1	Leiodidae	Fu
<i>Agrilus arbuti</i> Fisher	0	1	0	1	Buprestidae	Fl
<i>Anaspis rufa</i> Say	1	0	0	1	Melandryidae	Fl
<i>Aphodius aleutes</i> Eschscholtz	0	0	1	1	Scarabaeidae	Dg
<i>Aphodius cribratulus</i> Schmidt	0	1	0	1	Scarabaeidae	Dg
<i>Aphodius haemorrhoidalis</i> (Linnaeus)	1	0	0	1	Scarabaeidae	Dg
<i>Astenus longiusculus</i> Mannerheim	0	1	0	1	Staphylinidae	Pr
<i>Astenus robustulus</i> Casey	0	1	0	1	Staphylinidae	Pr
<i>Atomaria longipennis</i> Casey	0	0	1	1	Cryptophagidae	unk
<i>Atrechus punctiventris</i> (Fall)	0	1	0	1	Staphylinidae	unk
<i>Bembidion</i> sp.	1	0	0	1	Carabidae	Pr
<i>Bradycellus conformis</i> Fall	0	1	0	1	Carabidae	Pr
<i>Buprestis aurulenta</i> Linnaeus	1	0	0	1	Buprestidae	H
<i>Byrrhus wickhami</i> Casey	1	0	0	1	Byrrhidae	H
<i>Colon celatum</i> Horn	0	0	1	1	Leiodidae	Fu
<i>Crenitis rufiventris</i> Horn	0	1	0	1	Hydrophilidae	H
<i>Crenitis snoqualmie</i> Miller	0	1	0	1	Hydrophilidae	H
<i>Cryptolestes ferrugineus</i> Stephens	0	1	0	1	Cucujidae	Sd
<i>Ctenicera falsifica angularis</i> LeConte	1	0	0	1	Elateridae	unk
<i>Elonium rugosa</i> (Hatch)	0	1	0	1	Staphylinidae	Fl
<i>Enoclerus</i> sp.	0	1	0	1	Cleridae	Pr
<i>Epuraea truncatella</i> Mannerheim	0	0	1	1	Nitidulidae	unk
<i>Eronyxa pallidus</i> (Motschulsky)	0	1	0	1	Trogositidae	Fl
<i>Eutheia morae</i> Marsh	0	1	0	1	Scydmaenidae	unk
<i>Eutheia scitula</i> Maklin	0	1	0	1	Scydmaenidae	unk
<i>Gabrius</i> sp.	1	0	0	1	Staphylinidae	unk
<i>Harpalus animosus</i> Casey	1	0	0	1	Carabidae	Sd
<i>Harpalus fuliginosus</i> Duftschmid	1	0	0	1	Carabidae	Sd

Table 13 (Continued)

<i>Helops edwardsii</i> Horn	1	0	0	1	Tenebrionidae	unk
<i>Homaetarsus californicus</i> LeConte	0	1	0	1	Staphylinidae	Pr
<i>Hydnobius</i> sp.	0	1	0	1	Leiodidae	Fu
<i>Ischalia vancouverensis</i> Harris	0	0	1	1	Pyrochroidae	unk
<i>Leiodes horni</i> Hatch	0	1	0	1	Leiodidae	Fu
<i>Limonius</i> sp.	0	0	1	1	Elateridae	unk
<i>Lytta stygica</i> LeConte	1	0	0	1	Meloidae	Fl
<i>Megasternum posticatum</i> Mannerheim	0	1	0	1	Hydrophilidae	unk
<i>Megataphrus tenuicornis</i> Casey	0	1	0	1	Clydiidae	Pr
<i>Morychus oblongus</i> LeConte	0	0	1	1	Byrrhidae	H
<i>Mycetochara procera</i> Casey	1	0	0	1	Alleculidae	Fl
<i>Mycetophagus pluriguttatus</i> LeConte	1	0	0	1	Mycetophagidae	Fu
<i>Nicrophorus investigator</i> Zetterstedt	1	0	0	1	Silphidae	Sv
<i>Octotemnus laevis</i>	1	0	0	1	Ciidae	Fu
<i>Odontospindus clavicornis</i> Casey	0	0	1	1	Sphindidae	Fu
Omalinae sp.	0	1	0	1	Staphylinidae	unk
<i>Omocita discoidea</i> Fabricius	0	0	1	1	Nitdulidae	Sv
<i>Phthora americana</i> Horn	1	0	0	1	Tenebrionidae	unk
<i>Platycholeus opacellus</i> Fall	0	1	0	1	Leiodidae	Sv
<i>Podabrus piniphilus</i> Dejean	1	0	0	1	Cantharidae	Pr
<i>Podabrus pruinosus diversipes</i> Fall	1	0	0	1	Cantharidae	Pr
<i>Prostomus mandibularis</i> Fabricius	0	0	1	1	Prostomidae	Pr
Pselaphidae sp.	1	0	0	1	Pselaphidae	Pr
<i>Pseudocistela pacifica</i> (Hopping)	1	0	0	1	Alleculidae	Fl
<i>Pseudohylesinus nebulosus</i> (LeConte)	0	1	0	1	Scolytidae	X
<i>Pterostichus campbelli</i> Bosquet	1	0	0	1	Carabidae	Pr
Ptiliidae sp.	1	0	0	1	Ptiliidae	Fu
<i>Saprinus lugens</i> Erichson	0	1	0	1	Histeridae	unk
<i>Scymnus caurinus</i> Horn	0	1	0	1	Coccinellidae	Pr
<i>Sitona lineatus</i> (Linnaeus)	1	0	0	1	Curculionidae	H
<i>Sonoma</i> sp.	0	1	0	1	Pselaphidae	Pr
<i>Stenolophus conjunctus</i> Say	1	0	0	1	Carabidae	Pr
<i>Stethorhaxis borealis</i> Blaisdell	0	1	0	1	Endomychidae	Fu
<i>Stictocranium</i> sp.	0	1	0	1	Staphylinidae	unk
<i>Sunius</i> sp.	0	1	0	1	Staphylinidae	unk
<i>Tachinus basalis</i> Erichson	0	1	0	1	Staphylinidae	unk
<i>Tychius stepheni</i> Schonherr	1	0	0	1	Curculionidae	H
<i>Xanthochroa testacea</i> Horn	1	0	0	1	Oedemeridae	Fl
<i>Zalobius serricollis</i> LeConte	0	1	0	1	Staphylinidae	unk
TOTALS	2861	7135	1195	11191		

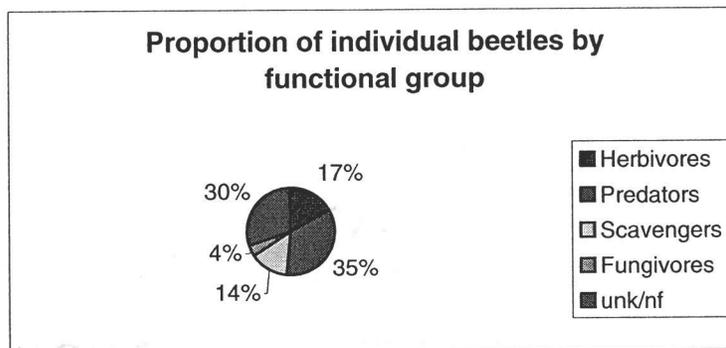


Figure 11. Proportion of beetle specimens per functional group. H. J. Andrews Experimental Forest 1982, 1983, and 1999.

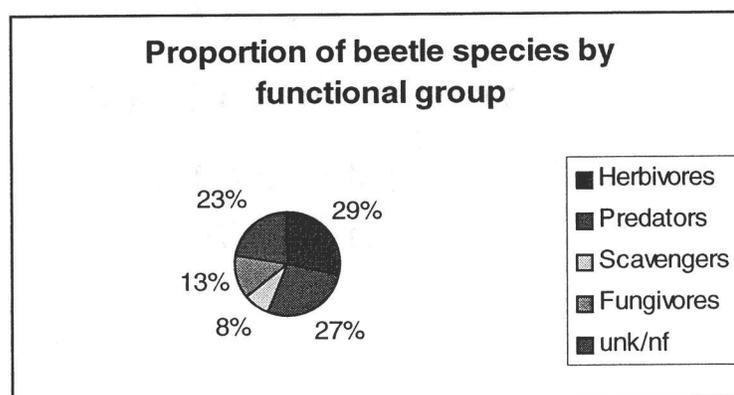


Figure 12. Proportion of beetle species per functional group. H.J. Andrews Experimental Forest 1982, 1983, and 1999.

Table 14. Beetle functional group differences between 1982 and 1999, H.J. Andrews Experimental Forest. Yes indicates significant differences, No indicates non-significant differences.

Functional Group		Seral Stage	
		Clear-cut	Old Growth
Predators	Abundance	No	No
	Number of species	No	No
Herbivores	Abundance	Yes	Yes
	Number of species	Yes	No
Fungivores	Abundance	Yes	No
	Number of species	No	Yes
Scavengers	Abundance	Yes	Yes
	Number of species	Yes	No

The total number of individuals collected was 11,191. The predator group comprised 35% of this amount, and represented the largest functional group. The predators were followed in abundance by the unknown/non-feeders (30%), herbivores (17%), scavengers (14%), and then fungivores (4%) (Figure 11). Individual years were different in terms of proportion of individuals in each functional group. In 1982, the largest group was the predators (45%), followed by herbivores (31%), scavengers (10%), unknown/non-feeders (10%), and then fungivores (4%). In 1983, the predator group was not the largest functional category. The unknown/non-feeding group was most abundant (41%), followed by predators (28%), scavengers (16%), herbivores (13%), and fungivores (2%). In 1999, the predators were the most numerous functional category (39%), followed by scavengers (33%), unknown/non-feeders (18%), herbivores (9%), and lastly fungivores (1%). Although each year had a slightly different functional group composition, in each case fungivores comprised the smallest group, and predators one of the largest.

The total number of species collected was 224. Numbers of species varied widely between years (Table 9). The herbivore group comprised the greatest proportion of species in the total catch (29%), followed by predators (27%), unknown/non-feeders (23%), fungivores (13%), and scavengers (8%) (Figure 12). Functional group composition by species varied between years. In 1982, predators comprised the largest species group (41%), followed by herbivores (32%), scavengers (11%), fungivores (9%), and unknown/non-feeders (5%). The pattern in ranked species number in 1983 was exactly the same as in 1982. Predators comprised the

largest group (44%), followed by herbivores (27%), scavengers (13%), fungivores (10%) and lastly unknown/non-feeders (6%). In 1999, the pattern in species number was different than 1982 and 1983. Predators still comprised the largest group (25%), but the unknown/non-feeding group was second in terms of species number (24%). The unknown/non-feeders were followed by herbivores (22%), scavengers (16%), and fungivores (13%). In each individual year, predators comprised the largest group in terms of number of species, while in the combined year data set, herbivores were the largest group. This was due to the large overlap in predator species between years, and little overlap among herbivorous species between years.

Predators

The predator group was the largest in terms of total number of individuals (Figure 11). The predaceous beetles represented 35% ($n = 3806$) of the total number of individuals. The old growth sites had the highest average number of predaceous individuals in each year. The ranking of the other seral stages was variable among years, but in both 1982 and 1983 the shrub stage clear-cuts had the lowest average abundance (avg. = 19.4 (6.6) and 38.9 (14.6)). In 1999, the clear-cut sites had a lower average abundance (avg. = 25.5 (23.8)) than did the old growth sites (avg. = 38.1 (29.1)) (Table 15). The greater number of predaceous individuals in the old growth sites was discovered to be consistent with the findings of Schowalter (1995) who reported a greater abundance of canopy dwelling predaceous insects in old growth sites.

Table 15. Average predator beetle abundance and species number (S.D.) per seral stage and year. Data from 1982, 1983, and 1999 forest succession sites, H.J. Andrews Experimental Forest.

Seral stage at time of sampling	Data Type	YEAR		
		1982	1983	1999
Herb Stage Clear-cut	Abundance	39.8 (21.4)	62.0 (42.0)	X
	Number of Species	9.3 (2.5)	10.0 (3.8)	X
Shrub Stage Clear-cut	Abundance	19.4 (6.6)	38.9 (14.6)	X
	Number of Species	7.6 (1.8)	8.9 (1.2)	X
Tree Stage Clear-cut	Abundance	38.9 (22.2)	66.9 (26.9)	25.5 (23.8)
	Number of Species	7.2 (2.0)	8.8 (2.7)	5.2 (2.0)
Old Growth	Abundance	74.6 (36.8)	104.8 (29.7)	38.1 (29.1)
	Number of Species	8.0 (1.4)	9.1 (1.9)	6.2 (1.6)

The proportion of predaceous individuals decreased slightly in both clear-cut and old growth stands between 1982 and 1999, although the differences proved to be non-significant. The proportion of predators in clear-cut sites decreased from 43% to 36% between 1982 and 1999 ($X^2 = 1.36$, $p = 0.24$). The proportion of predators in old growth sites decreased from 65% to 53% through the same amount of time ($X^2 = 2.71$, $p = 0.10$) (Table 16).

Although predators were the most abundant functional group in terms of individuals, the group ranked second to herbivores in terms of number of species. Predaceous species comprised 27% ($n = 60$) of the total species number (Figure 12). Average numbers of predaceous species varied minimally between seral stages. In 1982, average values ranged from 7.2 (2.0) species per seral stage for the tree stage clear-cuts to 9.3 (2.5) species per seral stage for the herb stage clear-cuts. Similarly in 1983, average species number ranged from 8.8 (2.7) to 10.0 (3.8) for the tree stage and shrub stage clear-cuts consecutively (Table 15). Schowalter (1989, 1995) found predator species diversity to be highest in old growth sites, among canopy dwelling insects.

Table 16. Number of beetle specimens and species per site. Proportion of site total given in parentheses. 1982 and 1999 forest succession sites, H.J. Andrews Experimental Forest.

	Site		1982				1999			
			Fu	H	Pr	Sv	Fu	H	Pr	Sv
CC	13	Individuals	3 (6%)	29 (56%)	14 (27%)	3 (6%)	0 (0%)	7 (33%)	5 (24%)	9 (43%)
		Species	1 (5%)	8 (40%)	7 (35%)	1 (5%)	0 (0%)	2 (40%)	2 (40%)	1 (20%)
	17	Individuals	9 (9%)	20 (20%)	51 (51%)	9 (9%)	0 (0%)	5 (31%)	11 (69%)	1 (6%)
		Species	4 (14%)	6 (21%)	10 (34%)	4 (14%)	0 (0%)	3 (38%)	4 (50%)	1 (12%)
	21	Individuals	12 (18%)	18 (27%)	19 (29%)	6 (9%)	1 (1%)	7 (7%)	27 (28%)	61 (64%)
		Species	2 (7%)	11 (41%)	6 (22%)	2 (7%)	1 (10%)	2 (20%)	4 (40%)	3 (30%)
	25	Individuals	20 (15%)	19 (14%)	68 (50%)	9 (7%)	0 (0%)	5 (22%)	17 (74%)	1 (4%)
		Species	7 (18%)	12 (30%)	13 (32%)	3 (8%)	0 (0%)	2 (20%)	7 (70%)	1 (10%)
	Totals	Individuals	44 (12%)	86 (24%)	152 (43%)	27 (8%)	1 (1%)	24 (14%)	60 (36%)	81 (49%)
		Species	6 (10%)	25 (43%)	20 (34%)	7 (12%)	1 (6%)	4 (24%)	8 (47%)	4 (24%)
OG	4	Individuals	4 (4%)	24 (25%)	53 (55%)	15 (16%)	0 (0%)	1 (10%)	10 (90%)	0 (0%)
		Species	3 (16%)	5 (26%)	7 (37%)	4 (21%)	0 (0%)	1 (17%)	5 (83%)	0 (0%)
	8	Individuals	1 (1%)	39 (48%)	40 (49%)	1 (1%)	1 (4%)	5 (18%)	19 (70%)	2 (7%)
		Species	1 (7%)	4 (29%)	8 (57%)	1 (7%)	1 (10%)	1 (10%)	6 (60%)	2 (20%)
	16	Individuals	2 (1%)	38 (24%)	106 (66%)	14 (9%)	3 (5%)	5 (9%)	48 (86%)	0 (0%)
		Species	2 (15%)	2 (15%)	8 (62%)	1 (8%)	1 (14%)	2 (28%)	4 (57%)	0 (0%)
	20	Individuals	2 (1%)	21 (15%)	108 (76%)	12 (8%)	1 (1%)	10 (6%)	67 (38%)	96 (55%)
		Species	2 (12%)	2 (12%)	10 (63%)	2 (12%)	1 (7%)	4 (28%)	8 (57%)	1 (7%)
	28	Individuals	0 (0%)	17 (38%)	27 (61%)	0 (0%)	0 (0%)	2 (20%)	5 (50%)	3 (30%)
		Species	0 (0%)	5 (45%)	6 (54%)	0 (0%)	0 (0%)	2 (28%)	4 (57%)	1 (14%)
	32	Individuals	3 (2%)	13 (11%)	99 (84%)	3 (2%)	3 (2%)	5 (3%)	89 (51%)	76 (44%)
		Species	3 (18%)	4 (24%)	8 (47%)	2 (12%)	1 (10%)	2 (18%)	7 (64%)	1 (10%)
	Totals	Individuals	17 (2%)	152 (23%)	433 (65%)	66 (10%)	8 (2%)	28 (6%)	238 (53%)	177 (39%)
		Species	6 (18%)	7 (21%)	16 (48%)	4 (12%)	1 (5%)	6 (29%)	12 (57%)	2 (10%)

Differences in proportion of predator species between 1982 and 1999 were found to be non-significant. Both clear-cut and old growth sites showed an increase in the proportion of predaceous species between years 1982 and 1999 despite a decrease in the proportion of predaceous individuals. The proportion of predaceous species increased from 34% in 1982 to 47% in 1999 in clear-cuts ($X^2 = 3.60$, $p = >0.05$), and from 48% to 57% in old growth sites ($X^2 = 1.42$, $p = >0.20$).

Of the ten most common species trapped during the study, four were predators. The most abundant predator species in the total catch were Aleocharinae spp. (n = 1,294), *Omus dejeani* Reiche (n = 535), *P. herculaneus* (n = 488), and *Pterostichus lama* Menetries (n = 348).

Aleocharinae spp. were most abundant in 1983, with 1,052 of the 1,294 individuals trapped during this season. Consequently, the average number of predaceous individuals was much higher in all seral stages in 1983 than in 1982 despite the same sampling effort. Aleocharinae had a higher abundance in old growth stands although they were trapped in all seral stages.

Individuals from the genus *Pterostichus* were very common in this study, and are very prevalent and widespread throughout the Pacific Northwest. The most common *Pterostichus* species in this study was *P. lama* and was collected from nearly every trap site within the study.

There are thirteen described species within the genus *Omus*, five of which occur in the Pacific Northwest (Hatch 1953). The only species trapped in this study was *O. dejeani* which is the largest member of this genus and is flightless. Like the

other members of the tiger beetle family (Cicindellidae), *O. dejeani* is a voracious predator in both the larval and adult forms (Parsons et al. 1991). There were no patterns in distribution of *O. dejeani* related to either seral stage or vegetation association.

Herbivores

The herbivore group ranked third following predators and unknown/non-feeders in terms of total number of individuals (Figure 11). The herbivorous beetles represented 17% (n = 1,935) of the total number of individuals. The tree stage clear-cut sites had the highest average number of herbivorous individuals in each year, followed by old growth, shrub stage clear-cut, and herb stage clear-cut sites (Table 17). This pattern in abundance was found to be consistent with the prediction that herbivores would occur in a higher abundance in young seral stands than in old growth stands. These results are similar to those reported by Schowalter (1989), who found greater herbivore biomass, of canopy dwelling species, in young seral sites than in old growth sites.

Table 17. Average herbivore beetle abundance and species number (S.D.) per seral stage and year. Data from 1982, 1983 and 1999 forest succession sites, H.J. Andrews Experimental Forest.

Seral stage at time of sampling	Data Type	YEAR		
		1982	1983	1999
Herb Stage Clear-cut	Abundance	26.0 (9.1)	20.3 (14.1)	X
	Number of Species	9.0 (2.2)	7.2 (2.9)	X
Shrub Stage Clear-cut	Abundance	26.0 (33.6)	28.7 (34.4)	X
	Number of Species	5.6 (3.4)	5.9 (3.1)	X
Tree Stage Clear-cut	Abundance	43.0 (19.4)	46.9 (24.4)	7.3 (2.7)
	Number of Species	7.1 (2.4)	6.2 (1.7)	2.8 (1.7)
Old Growth	Abundance	27.1 (13.2)	29.6 (13.0)	4.1 (2.7)
	Number of Species	3.9 (1.2)	3.9 (1.5)	1.7 (1.0)

The abundance of herbivorous individuals decreased significantly in both clear-cut and old growth stands between 1982 and 1999 (Table 16). In 1982, herbivores comprised 24% and 23% of the total yearly catch in clear-cut and old growth stands consecutively. The values for percent catch were reduced to 14% ($X^2 = 7.1$, $p = <0.01$) and 6% ($X^2 = 48.2$, $p = <0.001$) for clear-cut and old growth stands in 1999.

Although herbivores ranked third in terms of numbers of individuals, the group ranked first in terms of number of species. Herbivorous species comprised 29% ($n = 65$) of the total number of species (Figure 12). Average numbers of herbivorous species were highest in herb stage clear-cuts and lowest in old growth sites in both 1982 and 1983. In 1999 the clear-cut sites had a higher species richness (avg. = 2.8 (1.7)) than did the old growth sites (avg. = 1.7 (1.0)) (Table 17).

The proportion of herbivorous species in clear-cut sites decreased significantly from 43% to 24% ($X^2 = 15.0$, $p = <0.001$) between 1982 and 1999, similar to the drop in abundance at the same sites. However, the proportion of herbivorous species in old growth sites showed a non-significant change from 21% to 29% ($X^2 = 2.2$, $p = >0.10$) during the same period of time.

Of the ten most abundant species trapped during the study, two were herbivores. The most abundant herbivore species in the total catch were *L. horridum* ($n = 833$) and *S. carinatus* ($n = 436$). Both species are members of the family Curculionidae.

L. horridum had a higher abundance in old growth sites, although it was found in nearly every sampled site. The 1983 samples had the greatest number of *L. horridum*, with 486 of the total 833 specimens trapped that year. Little is known about the life cycle of *L. horridum*.

The other common herbivorous species, *S. carinatus*, is widely studied due to its role as a vector of black-stain root disease in Douglas fir (Witcosky et al. 1986). The distribution of *S. carinatus* showed no pattern among seral stages or vegetation associations. The 1982 samples had the greatest number of *S. carinatus*, with 273 of the 436 total specimens trapped that year.

Fungivores

The fungivore group was the smallest in terms of total number of individuals (Figure 11). The fungivorous beetles represented only 4% ($n = 482$) of the total number of individuals. No consistent pattern was observed in average fungivore abundance among years. In 1982 the greatest average number of fungivorous specimens was found in the herb stage clear-cut sites (avg. = 9.7 (6.5)), while in 1983 the highest average number was found in the old growth sites (avg. = 9.9 (13.1)). In 1999, the old growth sites had a higher average number (avg. = 1.1 (1.3)) of fungivorous specimens than did the clear-cut sites (avg. = 0.7 (0.7)) (Table 18). This lack of pattern in abundance is not consistent with the prediction that fungivores would be most abundant in old growth sites.

The proportion of fungivorous individuals decreased significantly in the clear-cut sites between 1982 and 1999. No change in the proportion of fungivores was

observed within old growth sites in the same period of time. In 1982 the fungivores comprised 12% of the total catch while in 1999 the fungivores comprised only 1% of the yearly catch ($X^2 = 121$, $p = <0.001$). Within old growth sites, 2% of the catch were fungivores in both 1982 and 1999.

Table 18. Average fungivore beetle abundance and species number (S.D.) per seral stage and year. Data from 1982, 1983, and 1999 forest succession sites, H.J. Andrews Experimental Forest.

Seral stage at time of sampling	Data Type	YEAR		
		1982	1983	1999
Herb Stage Clear-cut	Abundance	9.7 (6.5)	6.2 (5.5)	X
	Number of Species	3.5 (2.2)	2.5 (1.8)	X
Shrub Stage Clear-cut	Abundance	2.4 (1.9)	2.6 (3.9)	X
	Number of Species	1.6 (1.5)	1.9 (2.5)	X
Tree Stage Clear-cut	Abundance	1.1 (1.7)	2.4 (2.2)	0.7 (0.7)
	Number of Species	0.9 (1.1)	1.6 (1.2)	0.4 (0.7)
Old Growth	Abundance	2.2 (2.0)	9.9 (13.1)	1.1 (1.3)
	Number of Species	1.8 (1.3)	2.4 (1.3)	0.7 (0.7)

Although fungivores comprised only 4% of the total abundance for the study, the group represented 13% ($n = 30$) of the total number of species collected (Figure 12). Like abundance, fungivore species diversity lacked consistent pattern among seral stage and years. In 1982 the herb stage clear-cut sites had the highest average species diversity (avg = 3.5 (2.2)). By contrast, in 1983 the greater diversity was found in both herb stage clear-cuts and old growth sites, with an average of 2.5 (1.8) and 2.4 (1.3) species consecutively. In 1999 the old growth sites had a slightly greater average species number (avg. = 0.7 (0.7)) than did the clear-cut sites (avg. = 0.4 (0.7)).

The proportion of fungivorous species decreased in both clear-cut and old growth sites between 1982 and 1999. In the clear-cut sites, the decrease in fungivore

species richness was shown to be non-significant ($X^2 = 2.7$, $p = 0.10$). The proportion of fungivores in clear-cut sites decreased from 10% to 6%. In the old growth sites the reduction was significant ($X^2 = 33.8$, $p = <0.001$). The proportion of fungivores in old growth sites decreased from 18% to 5% (Table 16).

Of the ten most abundant species trapped during the study, only one was a fungivore. The most abundant fungivore in the study was an unidentified species from the family Ptiliidae (Table 13). A total of 213 individuals of Ptiliidea sp. were collected, all within the 1983 sampling period. All known members of this family, occurring within the H.J. Andrews Forest, are forest litter dwellers, who feed on fungi, or fungal spores, in both the larval and adult stages (Parsons et al. 1991). This species showed a greater affinity for older seral stages, with only 2 of 213 individuals being collected in herb stage clear-cuts.

The next most abundant fungivore was *Leiodes morula* (LeConte). A total of 61 individuals of *L. morula* were trapped, making it number 22 in terms of total abundance. The majority of the trapped individuals, of this species, were found in 1982 (39) although it was present in all three sampling periods. This species was most common in young seral stands, with only a single individual collected from an old growth site.

Scavengers

The scavenger group was fourth largest in terms of total number of individuals (Figure 11). The scavenging beetles represented 14% ($n = 1582$) of the total number of individuals. No pattern in average scavenger abundance was observed among

years. In 1982 the highest average abundance of scavenging beetles (avg. = 18.0 (15.0)) was found in the tree stage clear-cuts. In 1983 and 1999 the greatest average number of scavenging individuals was found in the old growth sites (avg. = 73.6 (88.6) and 24.7 (35.6)) (Table 19). Schowalter (1995) reported a greater abundance of detritivores in the canopies of old growth forests than in the canopies of young stands.

The proportion of scavenging individuals was found to have increased significantly between 1982 and 1999 in both clear-cut and old growth sites. In 1982 the proportion of scavenging beetles was 8% and 10% for clear-cut and old growth sites consecutively. By 1999, those numbers had increased to 49% for clear-cut sites ($X^2 = 34.3$, $p = <0.001$) and 39% ($X^2 = 21.5$, $p = <0.001$) for old growth sites (Table 16).

Scavengers comprised the smallest functional group in terms of number of species. Scavenging species comprised 8% ($n = 18$) of the total species number (Figure 12). Average numbers of scavenging species were highest in herb stage clear-cuts in 1982 (avg. = 2.8 (1.5)) and 1983 (avg. = 4.3 (1.4)). The ranking of the other seral stages varied between years. Average scavenger numbers were highest in 1999 in the clear-cut sites (avg. = 1.9 (1.0)).

The proportion of scavenging species in clear-cuts increased significantly from 12% to 24% ($X^2 = 6$, $p = <0.02$), between 1982 and 1999. The proportion of species in old growth sites decreased from 12% to 10% within the same period of time, but this difference was found to be non-significant ($X^2 = 0.4$, $p = >0.25$)

(Table 16).

Table 19. Average scavenger beetle abundance and species number (S.D.) per seral stage and year. Data from 1982, 1983, and 1999 forest succession sites, H.J. Andrews Experimental Forest.

Seral stage at time of sampling	Data Type	YEAR		
		1982	1983	1999
Herb Stage Clear-cut	Abundance	7.2 (2.3)	18.7 (13.2)	X
	Number of Species	2.8 (1.5)	4.3 (1.4)	X
Shrub Stage Clear-cut	Abundance	5.7 (5.6)	21.3 (15.3)	X
	Number of Species	1.7 (1.4)	2.4 (1.8)	X
Tree Stage Clear-cut	Abundance	18.0 (15.0)	32.5 (26.4)	18.8 (23.7)
	Number of Species	2.1 (1.0)	2.1 (0.6)	1.9 (1.0)
Old Growth	Abundance	8.9 (6.9)	73.6 (88.6)	24.7 (35.6)
	Number of Species	2.2 (1.7)	2.0 (0.5)	1.1 (0.9)

Of the ten most common species trapped during the study, two were scavengers. The most abundant scavenging species in the total catch were *Nemadus decipiens* Horn (n = 875), and *C. basilaris* (n = 442). Both species are members of the family Leiodidae. Members of this family are commonly called round fungus beetles, and were locally abundant within the sites sampled.

The majority of the *N. decipiens* specimens were trapped in 1983, with 747 of the total 875 coming from that sampling period. *Nemadus decipiens* appeared to be most prevalent in the old growth sites.

Of the 442 total specimens of *C. basilaris*, 291 were collected in 1999. The old growth sites seemed to have a higher abundance of *C. basilaris* than did the young seral sites, particularly the herb stage clear-cut sites. No explanation has been offered for the greater abundance of *C. basilaris* in 1999 despite the reduced sample size.

Functional Groups: Conclusions and Speculations

Prediction number four outlined the changes in functional group composition expected with changes in forest structure due to clear cutting. The abundance of

predators, scavengers, and fungivores was expected to increase with increasing stand age. Herbivores were predicted to decrease in abundance with increasing stand age. The results showed the average abundance of predators to be highest in old growth stands as predicted. A significant increase in the proportion of predators between years 1982 and 1999 would have given further support, but this was not the case. Both fungivores and scavengers had contradictory results regarding the highest average abundance. In the case of the fungivores, the highest average value was found in a different seral stage for each of the three years. Fungivore abundance increased significantly in both clear-cut and old growth sites between 1982 and 1999. The scavenger group had the highest average abundance in the old growth sites for two years, and the tree stage clear-cut for another. The proportion of scavenging individuals also decreased significantly between 1982 and 1999 instead of the predicted increase. Herbivores were most abundant in tree stage clear-cuts. A decrease in abundance was noted for both clear-cut and old growth sites between 1982 and 1999.

The results of the functional group analysis do not give clear support either way for the predictions outlined above. The 1983 sample was undoubtedly affected by the previous years samples, so should be interpreted with care. In addition, the reduced sample size of 1999 introduces other difficulties into the analysis. It remains clear however that functional group composition changes with vegetation dynamics, and thus is influenced by forest management.

CONCLUSIONS

The goal of this study was to conduct an inventory of the beetle communities within a portion of the H.J. Andrews Experimental Forest, and then to use the data regarding the composition of those communities in a monitoring program. Monitoring would be used to assess the impact of forest management and subsequent regeneration on the beetle communities and on the forest system. Sampling protocol is critical to bioinventory and monitoring studies. Pitfall trapping is the most common and convenient method used to study ground dwelling Coleoptera, despite the fact that much criticism of the method has been offered (e.g. Spence and Niemelä 1994). This is due in part to the fact that no other “similarly convenient method” has been devised (Lövei and Sunderland 1996, p. 233). Spence and Niemelä (1994) expressed concern over the multitude of factors which may influence capture efficiency and interpretation, including trap construction, preservative material, temperature, moisture and surrounding vegetation. Several recent papers, including Halsall and Wratten (1988) and Digweed et al. (1995), have helped to alleviate some of these concerns with the use of pitfalls as a sampling technique. Pitfalls were used in this study despite the criticisms for many of the reasons cited above.

Several questions and predictions were posed regarding the beetle communities. The first question addressed the differences between early and late successional beetle communities. This study suggested that different ages of forest do have different beetle communities. The second question addressed the correlation between environmental variables and the observed beetle communities. The eight

vegetation associations, as described by Dyrness et al. (1974), seemed to have no discernable effect on beetle communities. However, the three broadly defined vegetation associations, used in the 1999 analysis, did show significantly different beetle communities. Increasing soil moisture was shown to have a negative effect on species richness, and a positive effect on beetle abundance. The effects of varying soil moisture were most evident in the clear-cut sites. In response to the third question, clear-cut sites and old growth sites showed the greatest difference in regards to their beetle communities.

This study indicates a change in clear-cut sites over time such that the older the site, the more "old growth" like, in regards to its beetle communities, it appears. The study also provides evidence of change along a gradient from clear-cut to old growth in the beetle communities. Plant communities have been observed to undergo succession in a relatively predictable manner. This study provides evidence for a similar parallel phenomenon in animal communities.

The accuracy of the predictions varied. 1) Beetle communities did differ according to forest stand age as predicted. This is consistent with other similar studies (e.g. Niemelä et al. 1988; Niemelä et al. 1993). 2) Prediction number two was also accurate, as clear-cut and old growth sites were indeed the most dissimilar in beetle community composition. Again, this was found to be consistent with other published results (e.g. McIver et al. 1992). 3) The diversity was indeed found to be higher in young seral stands than in old growth stands. This is consistent with other work involving studies of beetles in regenerating forest stands (e.g. Niemelä et al. 1993). 4)

Functional group composition was different between stands of varying age as predicted. Predators were most prevalent in old growth stands as predicted. This is consistent with what Schowalter (1995) found in forest canopies. Fungivores and detritivores were predicted to be most abundant in old growth sites. The results of this portion of the analysis were not consistent between years. Depending on year, the mean abundance was highest in clear-cut or old growth sites. Explanation of this is unavailable. 5) The prediction regarding soil moisture and beetle diversity was also refuted based on these results. This study showed a decrease in beetle diversity with increasing soil moisture, opposite than predicted. No prediction was made regarding the effect of soil moisture on abundance, but the effect was shown to be a positive one. 6) Last, this study further supports the assumed stability of old growth stands. The ordinations showed that the beetle communities in the old growth stands changed very little due to time.

This study served as a major contribution to our understanding of biodiversity in the H.J. Andrews Experimental Forest. The results from the 1982/1983 sampling period were the basis for the listing of Coleoptera in "Invertebrates of the H.J. Andrews Experimental Forest, Western Cascade Range, Oregon. V: An Annotated List of Insects and Other Arthropods" (Parsons et al. 1991).

Continued monitoring of these sites would further contribute to understanding the nature of succession in the beetle community following major disturbance. The current study provided an indication of the time scale required for the beetle communities to regain some of their "old growth" characteristics. It is predicted that

further monitoring would eventually show complete return to old growth conditions of both the vegetative community and animal communities, including the beetles.

However, confounding factors must also be taken into account if accurate information is to be gained from this work.

Confounding factors in this study include several differences in site characteristics. Site characteristics differing between sites include the nature of the management, such as burned vs. unburned, planted vs. unplanted, and thinned vs. unthinned. Other site differences have been observed on the H.J. Andrews Forest including rate of vegetation succession. All of these factors could potentially influence the rate and pattern of succession in the beetle communities. Each of these confounding variables could form the basis of a separate study, and should be included in any future monitoring of these sites.

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APPENDICES

Appendix 1. Site descriptions for 1982, 1983 and 1999. 1982 (*), 1983 (#), and 1999 (^). Age class listed (i.e. herb stage clear-cut), designate conditions present at time of initial sampling.

*# SITE 1 - HERB STAGE CLEAR-CUT PSME/HODI

NO SAMPLE SITE AVAILABLE ON OR NEAR H.J.A.

*# SITE 2 - SHRUB STAGE CLEAR-CUT PSME/HODI

LOCATION: T15S, R5E, Sec.28, NE 1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 approx. 1/4 mile past concrete bridge to rd. 330. Proceed to rd. 332. Site at end of rd. 332 below road in clear-cut.

ELEVATION: 2300' ASPECT: S

CC DATA: S2 strip, 1.3 acres clear-cut and burned 1954. S2a strip, 1.3 acres clear-cut and burned in 1963. (Site covers top of both strips.)

*# SITE 3 - TREE STAGE CLEAR-CUT PSME/HODI

LOCATION: T15S, R5E, Sec.31, NE 1/4

ACCESS: From rd. 15-130 jct., take rd. 130 NE approx. 1/2 mi. past administration site to clear-cut B133. Take trail down top of ridge to site.

ELEVATION: 1800' ASPECT: SW

CC DATA: B133 - 28 acres clear-cut and burned 1960.

*# ^ SITE 4 - OLD GROWTH PSME/HODI

LOCATION: T15S, R5E, Sec.31, NE 1/4

ACCESS: From rd. 15 - 130 jct., take rd. 130 NE approx. 1.75 mi. to rd. 134. Proceed on rd. 134 approx. 0.25 mi. Take trail running E from road into stand approx. 100 m.

ELEVATION: 2300' ASPECT: S

*# SITE 5 - HERB STAGE CLEAR-CUT PSME-TSHE/COCOA

LOCATION: T16S, R5E, Sec.8, SW1/4

ACCESS: From Hwy. 126, take rd. 2633 N approx. 2 mi. to rd. 720. Take rd. 720 W approx. 0.75 mi. to short skid rd. S of rd. 720. Proceed 0.25 m. into clear-cut to landing. Site on slope above landing.

ELEVATION: 1800' ASPECT: SE

CC DATA: Stand # 7115-27, 27 acres clear-cut 1968, planted 1969, replanted 1970.

*# SITE 6 - SHRUB STAGE CLEAR-CUT PSME-TSHE/COCOA

LOCATION: T15S, R5E, Sec.27, NW1/4

ACCESS: From rd. 15-1506 jct. Take rd. 1506 approx. 1 mi. past concrete bridge to bottom of clear-cut S4A. Site just above road.

ELEVATION: 1900' ASPECT: S

CC DATA: S4A, 8.9 acre narrow strip from top of ridge down to road, clear-cut and broadcast burned 1963.

*# SITE 7 - TREE STAGE CLEAR-CUT PSME-TSHE/COCOA

LOCATION: T15S, R5E, Sec.27, NW1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 approx. 1 mi. past concrete bridge to bottom of clear-cut S4 (above rd.). Take trail E up into site between S4 and S4a.

ELEVATION: 1900' ASPECT: S

CC DATA: S4 - 8.9 acre strip clear-cut and burned 1954-55.

*# ^ SITE 8 - OLD GROWTH PSME-TSHE/COCOA

LOCATION: T15S, R5E, Sec.31, NW 1/4

ACCESS: From rd. 15 - 130 jct., take rd. 130 NE approx. 1 mi. to 1st drainage into ccB133. Site NW up slope from where road crosses drainage (above clearcut).

ELEVATION: 1900' ASPECT: ESE

*# SITE 9 -HERB STAGE CLEAR-CUT TSHE/CACH

LOCATION: T15S, R5E, Sec.31, NW1/4

ACCESS: From rd. 15-130 jct. take rd. 130 NE 1.75 mi. to rd. 134. Take rd. 134 SW to top of water shed 10. Site at NE corner of clear-cut.

ELEVATION: 2100' ASPECT: S

CC DATA: Water shed 10, 24 acres clearcut 1975, not burned.

*# SITE 10 - SHRUB STAGE CLEAR-CUT TSHE/CACH

LOCATION: T16S, R5E, Sec.6, NW1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 approx. .25 mi. NE. Take water shed 1 trail through old growth up into clear-cut. Site just below ridgeline.

ELEVATION: 1700' ASPECT: SW

CC DATA: Water shed 1, 202 acres clearcut 1963-66, burned 1966.

*# SITE 11 - TREE STAGE CLEAR-CUT TSHE/CACH

LOCATION: T15S, R5E, Sec.33, NW1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 NE approx. 2.25 mi. to rd. 1507. Take rd. 1507 approx. 2 mi. SE to clear-cut L202. Site located along ridgeline, at south end of clear-cut.

ELEVATION: 2900' ASPECT: W

CC DATA: L202, 48 acres clear-cut and broadcast burned 1951.

*# SITE 12 - OLD GROWTH TSHE/CACH

LOCATION: T15S, R5E, Sec.31, NW1/4

ACCESS: From rd. 15-130 jct. take rd. 130 NE approx. 1 mi. to W side of clear-cut B133. Site on top of ridgeline above road.

ELEVATION: 1700' ASPECT: SSE

*# ^ SITE 13 - HERB STAGE CLEAR-CUT TSHE/RHMA/GASH

LOCATION: T15S, R5E, Sec.31, NW 1/4

ACCESS: From rd. 15 - 1506 jct., take rd. 15 approx. .75 mi. N to rd. 143. Take 143 NE approx. .15 mi. to gauging station at bottom of WS -10. Take trail approx. 200 m up N side of clearcut. Site on slope above trail.

ELEVATION: 1700' ASPECT: SSE

CC DATA: WS - 10, 24 acres clearcut 1975 (not burned).

*# SITE 14 - SHRUB STAGE CLEAR-CUT TSHE/RHMA/GASH

LOCATION: T16S, R5E, Sec.6, NW1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 approx. .25 mi. NE. Take water shed 1 trail through old growth up into clear-cut. Main trail winds through site in lower NE corner of clear-cut.

ELEVATION: 1700' ASPECT: SW

CC DATA: Water shed 1, 202 acres clear-cut 1963-66, burned 1966.

*# SITE 15 - TREE STAGE CLEAR-CUT TSHE/RHMA/GASH

LOCATION: T15S, R5E, Sec.33, NW1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 NE approx. 2.25 mi. to rd. 1507. Take rd. 1507 approx. 2 mi. SE to clear-cut L202. Site located below ridgeline, at south end of clear-cut.

ELEVATION: 2850' ASPECT: WSW

CC DATA: L202, 48 acres clear-cut and broadcast burned 1951

*# ^ SITE 16 - OLD GROWTH TSHE/RHMA/GASH

LOCATION: T15S, R5E, Sec. 32, NW 1/4

ACCESS: From rd. 15-1506 jct., take rd 1506 approximately 1.75 mi. to rd. 305. Take rd. 305 to slide, and then proceed on foot (approximately .5 mi.). Where road enters historic clearcut, take trail NW along ridge to site.

ELEVATION: 1750' ASPECT: SW

*# ^ SITE 17 - HERB STAGE CLEAR-CUT TSHE/RHMA/BENE

LOCATION: T15S, R5E, Sec.31, NW 1/4

ACCESS: From rd. 15 - 130 jct., take rd. 130 NE 1.75 mi. to rd. 134. Proceed on rd. 134 to top of WS - 10. From landing, take trail along ridge approx. 200 m. into clearcut. Site on slope below ridge.

ELEVATION: 1850' ASPECT: NW

CC DATA: WS - 10, 24 acres clearcut 1975 (not burned).

*# SITE 18 - SHRUB STAGE CLEAR-CUT TSHE/RHMA/BENE

LOCATION: T16S, R5E, Sec.6, NE1/4

ACCESS: At rd. 15-1506 jct. take short side road up to upper landing at bottom of water shed 1. Take trail up SW side of clear-cut approx.. 0.5 mi. Just before trail crosses creek to NE side, take side trail up from main trail. Site along side trail immediately above main trail.

ELEVATION: 1900' ASPECT: NE

CC DATA: Water shed 1, 202 acres clear-cut 1963-66, burned 1966.

*# SITE 19 - TREE STAGE CLEAR-CUT TSHE/RHMA/BENE

LOCATION: T15S, R5E, Sec.32, NW1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 NE approx. 2 mi. to W side of clear-cut L102. Take trail leading into W side of clear-cut. Trail leads through site.

ELEVATION: 1750' ASPECT: SW

CC DATA: L102, 40 acres clear-cut 1950, broadcast burned 1951

*# ^ SITE 20 - OLD GROWTH TSHE/RHMA/BENE

LOCATION: T15S, R5E, Sec.32, NW1/4

ACCESS: From rd. 15 - 1506 juct. Take rd. 1506 approx. 1.25 mi. to rd. 300. 20m from rd 1506 - 300 jct., take trail NE into and through R.S. 2 to site.

ELEVATION: 1550' ASPECT: NW

*# ^ SITE 21 - HERB STAGE CLEAR-CUT TSHE/ACCI/POMU

LOCATION: T15S, R5E, Sec.31, NW1/4

ACCESS: From rd. 15 - 1506 jct. take rd. 15 approx. .75 mi. N to rd. 143. Take rd. 143 NE approx. .15 mi. to guaging station at bottom of WS -10. Take S trail approx. 20 m. above guaging station into clearcut. Most of site on hill above weather station.

ELEVATION: 1550' ASPECT: N

CC DATA: Water shed -10, 24 acres clearcut 1975 (not burned).

*# SITE 22 - SHRUB STAGE CLEAR-CUT TSHE/ACCI/POMU

LOCATION: T15S, R5E, Sec.35, NE1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 approx. 3.2 mi. to rd. 360. Take rd. 360 appros. 2.75 mi. to clear-cut L110. Site just below road.

ELEVATION: 2450' ASPECT: E

CC DATA: L110, 9 acres clear-cut and broadcast burned 1965.

*# SITE 23 - TREE STAGE CLEAR-CUT TSHE/ACCI/POMU

LOCATION: T15S, R5E, Sec.32, NW1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 NE approx. 2 mi. to E side of clear-cut L102. Where road crosses creek, take trail up slope toward ridgeline on E side of clear-cut. Trail runs through site.

ELEVATION: 1850' ASPECT: NE

CC DATA: L102, 40 acres clear-cut 1950 and broadcast burned 1951.

*# SITE 24 - OLD GROWTH TSHE/ACCI/POMU

LOCATION: T15S, R5E, Sec.32, NE1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 NE approx. 2.25 mi. to rd. 1507. Take rd. 1507 approx. 1.4 mi. SE to top of clear-cut L201. Site is in old growth approx. 100 yds. W of jct. of rds. 1507 and 465.

ELEVATION: 2600' ASPECT: N

*# ^ SITE 25 - HERB STAGE CLEAR-CUT TSHE/POMU

LOCATION: T15S, R5E, Sec.27, SE1/4

ACCESS: From rd. 15 - 1506 jct., take rd. 1506 E approx. 3.2 mi. to rd. 360. Take rd. 360 approx. 1.25 mi. to cc L107B. Site just above rd. on slope of clearcut.

ELEVATION: 2200' ASPECT: N

CC DATA: L107B (Mack Salvage #6), 11 acres clearcut 1976. Broadcast burned 1979.

SITE 26 - SHRUB STAGE CLEAR-CUT TSHE/POMU

NO SAMPLE SITE AVAILABLE ON OR NEAR H.J.A.

*# SITE 27 - TREE STAGE CLEAR-CUT TSHE/POMU

LOCATION: T15S, R5E, Sec.32, SE1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 NE approx. 2.25 mi. to rd. 1507. Take rd. 1507 approx. 0.5 mi. S to rd. 455. Take rd. 455 to clear-cut L221. Site on slope in clear-cut above road just beyond stream crossing.

ELEVATION: 2400' ASPECT: NNW

CC DATA: L221, 28 acres clear-cut and broadcast burned 1963.

*# ^ SITE 28 - OLD GROWTH TSHE/POMU

LOCATION: T15S, R5E, Sec.31, SE1/4

ACCESS: From rd. 15 - 1506 jct., take 1506 approx. 1.25 mi. to rd. 300. Take rd. 300 S to end. Take trail up slope (South) from gauging station. Site about 20 m up trail.

ELEVATION: 1900' ASPECT: NE

SITE 29 - HERB STAGE CLEAR-CUT TSHE/POMU-OXOR

NO SAMPLE SITE AVAILABLE ON OR NEAR H.J.A.

*# SITE 30 - SHRUB STAGE CLEAR-CUT TSHE/POMU-OXOR

LOCATION: T16S, R5E, Sec.6, NE1/4

ACCESS: From rd. 15-1506 jct., take short toad up to upper landing at bottom of water shed 1. Take trail up SW side of clear-cut approx. 100 yds. above landing. Trail runs through site.

ELEVATION: 1600' ASPECT: NE

CC DATA: Water shed 1, 202 acres clear-cut 1963-66 and burned 1966.

*# SITE 31 - TREE STAGE CLEAR-CUT TSHE/POMU-OXOR

LOCATION: T15S, R5E, Sec.32, NW1/4

ACCESS: From rd. 15-1506 jct., take rd. 1506 approx. 2 mi. to E side clear-cut L102. Where road crosses stream, take trail up along stream on E side of clear-cut. Trail loops through site on slope just above stream.

ELEVATION: 1750-1800' ASPECT: NE

CC DATA: L102, 40 acres clearcut 1950 and broadcast burned 1951.

*# ^ SITE 32 - OLD GROWTH TSHE/POMU-OXOR

LOCATION: T15S, R5E, Sec.31, SE 1/4

ACCESS: From rd. 15 - 1506 jct., take rd. 1506 approx. .75 mi. to trail into R.S. - 7.

Site is on slope above first 50 m of trail.

ELEVATION: 1500' ASPECT: NW

^ SITE 33 - SHRUB STAGE CLEAR-CUT PSME/HODI

LOCATION: T16S, R5E, Sec. 5, SE 1/4

ACCESS: Take rd. 2633 N approx. 3.5 mi. to the top of the hairpin turn. Park on S side of road. Site below road.

ELEVATION: 2300' ASPECT: S

CC DATA: Stand #7115-19, 50 acres clear-cut 1986, broadcast burned 1987, planted 1987, precommercial thinned 1996

^ SITE 34 - TREE STAGE CLEAR-CUT PSME-TSHE/COCOA

LOCATION: T16S, R5E, Sec.7, NE 1/4

ACCESS: Take rd. 2633 N to junction of rd. 1501 (approx. 4 mi.). Continue on rd. 1501 to junction of rd. 202 (approx. .75 mi.). Continue on rd. 202 approx. 0.3 mi. to site. Site below road.

ELEVATION: 2600' ASPECT: S

CC DATA: Stand #1105-130, clear-cut 1975, planted 1976, replanted 1978, precommercial thinned 1988

^ SITE 35 - OLD GROWTH PSME/HODI

LOCATION: T16S, R5E, Sec.6, SW 1/4

ACCESS: Take rd. 15 towards the entrance to the HJA Forest. Approx. 0.2 mi. before entrance to forest (junction of rd. 1506), take small service rd. west of rd. 15. Take trail NW of gauging station to site.

ELEVATION: 1800' ASPECT: WSW

^ SITE 36 - TREE STAGE CLEAR-CUT TSHE/RHMA/GASH

LOCATION: T15S, R5E, Sec.22, SW1/4

ACCESS: From rd. 15 - 1506 jct., take rd. 1506 approx. 4 mi. to jct. of rd. 1506 - 320. Take rd. 320 approx. .5 mi. to jct. of rd. 320 - 322. Take rd. 322 approx. 0.15 mi. to clearcut L502. Site is across road and uphill from meadow.

ELEVATION: 2050' ASPECT: SE

CC DATA: L502, 25 acres clearcut 1959, broadcast burned with natural regeneration.

^ SITE 37 - OLD GROWTH TSHE/RHMA/BENE

LOCATION: T15S, R5E, Sec.28, NW1/4

ACCESS: From rd. 15 - 1506 jct., take rd. 1506 E approx. 3.5 mi to the jct. of rds. 1506 - 412. Take rd. 412 approx. 1.0 mi. to pull-out. Site is above rd.

ELEVATION: 2200' ASPECT: SE

^ SITE 38 - TREE STAGE CLEAR-CUT *TSHE/POMU-OXOR*

LOCATION: T15S, R5E, Sec.31, NW1/4

ACCESS: From rd. 15 - 1506 jct., take rd. 15 approx. .75 mi. N to rd. 143. Take rd. 143 NE approx. .25 mi, (pass gauging station) to slide. Park here, and continue on foot approx. 200 m. to site upslope from rd.

ELEVATION 1800' ASPECT: NE

CC DATA: Chem-Shed Hi-15 (1104-167/1000864) cut 1975. Planted 1976 and 1977.

^ SITE 39 - OLD GROWTH *TSHE/POMU-OXOR*

LOCATION: T15S, R5E, Sec.32, NE1/4

ACCESS: From rd. 15 - 1506 jct., take rd. 1506 approx. 1.5 mi. to jct. of rd. 1506 - 304. Take rd. 304 approx. 0.15 mi. to site. Site uphill from rd., between rds. 304 and 1506.

ELEVATION: 1600' ASPECT: NE

^ SITE 40 - SHRUB STAGE CLEAR-CUT *PSME/HODI*

LOCATION: T16S, R5E, Sec. 8

ACCESS: Take rd. 2633 N approx. 2 mi. to rd. 720. Proceed through gate, take rd. to left 0.75 mi. past gate. Continue 0.2 mi. from rd. fork to small landing. Take trail E of landing onto site.

ELEVATION: 1800' ASPECT: SE

CC DATA: Stand #7115-23, 32 acres clear-cut 1986, burned 1986, planted 1987, replanted 1990, precommercial thinned 1996

Appendix 2. Species list by family. 1982 (*), 1983 (#), and 1999 (^).

ALLECULIDAE

Mycetochara caseyi Hatch *#
Mycetochara procera Casey *
Pseudocistela pacifica (Hopping) *

BUPRESTIDAE

Agrilus arbuti Fisher #
Buprestis aurulenta Linnaeus *

BYRRHIDAE

Byrrhus wickhami Casey *
Lioon simplicipes Mannerheim #
Listemus formosus Casey *#
Morychus oblongus (LeConte) ^

CANTHARIDAE

Malthodes sp. *#
Podabrus piceatus Fender #
Podabrus piniphilus Dejean *
Podabrus pruinosus diversipes Fall *
Silis pallida Mannerheim *#
Trogolmethes oregonensis Wittmer #

CARABIDAE

Amara littoralis Mannerheim *#
Amara lunicollis Schiodte *#
Amara sanjuanensis Hatch *#
Amara sinuosa Casey *#
Bembidion sp. *
Bradycellus conformis Fall #
Bradycellus nigrinus Dejean *
Calosoma tepidum LeConte *#
Carabus taedatus Fabricius *# ^
Cychrus tuberculatus Harris *# ^
Harpalus animosus Casey *#
Harpalus cautus LeConte * ^
Harpalus fuliginosus Duftschmid *
Harpalus innocuus LeConte *
Metabletus americanus Dejean *#
Metrius contractus Eschscholtz *# ^
Microlestes nigrinus Mannerheim *#
Notiophilus sylvaticus Eschscholtz *#

Promecognathus laevis Dejean *# ^
Pterostichus amethystinus Mannerheim *#
Pterostichus campbelli Bosquet *
Pterostichus crenicollis LeConte *#
Pterostichus herculaneus Mannerheim *# ^
Pterostichus inopinus (Casey) *#
Pterostichus lama Menetries *# ^
Pterostichus new species ^
Pterostichus protractus LeConte *#
Pterostichus tuberculo-femoratus Hatch *# ^
Scaphinotus angulatus Harris *# ^
Scaphinotus marginatus Fischer *# ^
Scaphinotus rugiceps rugiceps Horn *# ^
Stenolophus conjunctus Say *
Trachypachus holmbergi Mannerheim *#
Zacotus matthewsii LeConte *# ^

CERAMBYCIDAE

Xestoleptura crassipes (LeConte) *

CHRYSOMELIDAE

Altica tombacina Mannerheim *#
Bromius obscurus Linnaeus *#
Longitarsus spp. *
Phaedon prasinellus LeConte #
Phyllotreta denticornis Horn #
Phyllotreta spp. #
Psylliodes sp. *#
Timarcha intricata Haldeman *#

CICINDELLIDAE

Omus dejeani Reiche *# ^

CIIDAE

Octotemnus laevis Casey *
Xestocis spp. *#

CLAMBIDAE

Empelus brunnipennis (Mannerheim) *#

CLERIDAE

Enoclerus sp. #

CLYDIIDAE*Megataphrus tenuicornis* Casey #**COCCINELLIDAE***Hyperaspis postica* LeConte #*Scymnus caurinus* Horn #**CRYPTOPHAGIDAE***Atomaria longipennis* Casey ^**CUCUJIDAE***Cryptolestes ferrugineus* Stephens #**CURCULIONIDAE***Agasphaerops nigra* Horn #*Cnemogonus lecontei* Dietz *#*Dyslobus granicollis* (LeConte) *#*Dyslobus lecontei* Casey *# ^*Dyslobus productus* Hatch *#*Geodercodes latipennis* Casey *#*Lobosoma horridum* Mannerheim *# ^*Nemocestes incomptus* Horn *#*Nemocestes puncticollis* Casey *#*Otiorhynchus ovatus* (Linnaeus) *# ^*Otiorhynchus rugosostriatus* (Goeze) *# ^*Otiorhynchus sulcatus* (Fabricius) ^*Panscopus costatus* Buchanan ^*Panscopus gemmatus* LeConte *# ^*Plinthodes taeniatus* LeConte *#*Pseudopanscopus costatus* Buchanan *#*Rhyncholus brunneus* Mannerheim *#*Sitona californicus* Fahraeus #*Sitona lineatus* (Linnaeus) **Steremnius carinatus* Boheman *# ^*Tychius stepheni* Schonherr ***DERMESTIDAE***Dermestes talpinus* Mannerheim *# ^**ELATERIDAE***Agriotes oregonensis* Beck *# ^*Ampedus rhodopus* LeConte *#*Athous varius* Benton *#*Ctenicera falsifica angularis* LeConte *

Ctenicera opacula (LeConte) # ^
Ctenicera spp. *#
Hemicrepidius morio LeConte *#
Limonius maculicollis Motschulsky *#
Megapenthes caprella (LeConte) *# ^
Micrathous brevis (VanDyke) * ^

ENDOMYCHIDAE

Stethorhanis borealis Blaisdell #
Xenomycetes laversi Hatch *#

EROTYLIDAE

Dacne californica Horn *#

EUCNEMIDAE

Isorhipis obliqua Say * ^

HISTERIDAE

Saprinus lubricus LeConte *
Saprinus lugens Erichson #

HYDROPHILIDAE

Crenitis rufiventris Horn #
Crenitis snoqualmie Miller #
Megasternum posticatum Mannerheim #

LAMPYRIDAE

Ellychnia hatchi Fender *# ^
Phausis skelleyi Fender *# ^

LATHRIDIIDAE

Aridius nodifer Westwood #
Enicmus cordatus Belon *#

LEIODIDAE

Agathidium jasperinum Fall #
Agathidium pulchrum LeConte *
Caenocyrtia picipennis LeConte *#
Catops basilaris (Say) *# ^
Colon celatum Horn ^
Colon spp. *#
Hydnobius longulus LeConte *# ^
Hydnobius pumilus LeConte #
Hydnobius sp. #
Leiodes horni Hatch #

Leiodes morula (LeConte) *# ^

Leiodes spp. *# ^

Nemadus decipiens Horn *# ^

Neocyrtusa sternita Hatch *# ^

Platycholeus opacellus Fall #

Triarthron lecontei Horn *#

LUCANIDAE

Platyceroides laticollis Casey *# ^

MELANDRYIDAE

Anaspis rufa Say *

Anaspis seposita Liljeblad *

MELOIDAE

Lytta stygica LeConte *

MELYRIDAE

Amecocerus larsoni Hatch ^

Dasyrhadus impressicollis Fall *#

Dasytes cruralis Leconte *#

MORDELLIDAE

Mordella atrata Melsheimer * ^

Mordellistena aspersa Melsheimer *#

MYCETOPHAGIDAE

Mycetophagus californicus Horn *

Mycetophagus pluriguttatus LeConte *

NITIDULIDAE

Epuraea obtusicollis Reitter *#

Epuraea truncatella Mannerheim ^

Omocita discoidea Fabricius ^

Thalycra murrayi Horn *#

OEDEMERIDAE

Ditylus gracilis LeConte *# ^

Xanthochroa testacea Horn *

PROSTOMIDAE

Prostomus mandibularis Fabricius ^

PSELAPHIDAE*Batrisodes albionicus* (Aube) *#*Cupila* sp. #*Lucifotychus* sp. #*Megarafonus* sp. *#*Oropus* spp. *#*Pselaphidae* sp. **Pselaptrichus rothi* Park *#*Sonoma* sp. #**PTILLIDAE***Acrotrichus* sp. *#

Ptillidae spp. *#

PYROCHROIDAE*Ischalia vancouverensis* Harris ^**RHYSODIDAE***Clinidium calcaratum* LeConte *#**SCARABAEIDAE***Aphodius aleutes* Eschscholtz ^*Aphodius cribratulus* Schmidt #*Aphodius haemorrhoidalis* (Linnaeus) **Aphodius opacus* LeConte *# ^*Aphodius rogersi* Hatch * ^*Aphodius* sp. **Bolboceras obesus* (LeConte) *# ^*Boreocanthon simplex* (LeConte) *#*Serica curvata* (LeConte) ***SCOLYTIDAE***Hylastes nigrinus* (Mannerheim) *#*Pseudohylesinus nebulosus* (LeConte) #**SCYDMAENIDAE***Eutheia morae* Marsh #*Eutheia scitula* Maklin #*Lophoderus similis* Marsh *#*Scydmaenus* sp. #**SILPHIDAE***Nicrophorus defodiens* ^*Necrophilus hydrophiloides* Guerin-Meneville # ^

Nicrophorus investigator Zetterstedt *
Nicrophorus vespilloides Herbst*#

SPHINDIDAE

Odontospindus clavicornis Casey ^

STAPHYLINIDAE

Aleocharinae spp. *#
Anotylus nitidulus Gravenhorst *#
Astenus longiusculus Mannerheim #
Astenus robustulus Casey #
Atrechus punctiventris (Fall) #
Bolitobius kremeri (Malkin) *#
Elonium rugosa (Hatch) #
Gabrius sp. *
Homaeotarsus californicus LeConte #
Lordithon spp. #
Mathrilaenum subcostatum (Maklin) #
Megarthus pictus Motschulsky #
Mycetoporus consors LeConte *
Mycetoporus punctatissimus Hatch *
Mycetoporus spp. #
 Omaliinae sp. #
Ontholestes cingulatus Gravenhorst #
Orobanus tarsalis Hatch *#
Philonthus cruentatus Gmelin *
Philonthus spp. *#
Proteinus limbatus Maklin #
Quedius spp. #
 Staphylinidae spp. ^
Staphylinus rutilicauda Horn *# ^
Stenus costalis Casey #
Stictocranium sp. #
Sunius sp. #
Tachinus basalis Erichson #
Tachinus semirufus Horn *# ^
 Tachyporinae spp. *#
Xestolinus frontalis Hatch #
Zalobius serricollis LeConte #

TENEBRIONIDAE

Coelocnemis californicus Mannerheim *# ^
Helops edwardsii Horn *
Helops pernitens LeConte *#

Ipthimimus serratus Mannerheim *#
Phthora americana Horn *
Uloma longula LeConte *

THROSCIDAE

Aulonthroscus validus LeConte *# ^
Pactopus horni LeConte *# ^
Trixagus sericeus LeConte *

TROGOSITIDAE

Eronyxa pallidus (Motchulsky) #

ZOPHERIDAE

Phellopsis porcata LeConte *# ^
Usechus nucleatus Casey *# ^