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Forest Ecology and Management 179 (2003) 123–134

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Ground dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA

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Received 12 March 2002; accepted 12 September 2002

Abstract

Regrowth and old-growth Douglas-fir stands were sampled for ground dwelling beetles using pitfall traps in 1982, 1983 and 1999. Species richness and abundance was compared within and among years, plots, and age of forest using multivariate techniques. Representatives of 49 families and 224 taxa were collected for a total of 11,191 specimens. The abundance and species richness of ground dwelling beetles suggested four notable relationships. First, different ages of forest had significantly different beetle communities. For instance, the herb stage regrowth stands supported a number of seral specialists including: *Microlestes nigrinus* Mannerheim and *Trachypachus holmbergi* Mannerheim. Second, specifically defined plant communities were associated with unique beetle communities. Ordination analysis showed that the grouping of stands, based on beetle communities, was correlated with differences in vegetative characteristics. Third, over a 17-year-period, beetle communities in old-growth stands remained relatively stable while beetle communities in regrowth stands exhibited a high degree of change. Ordination analysis grouped old-growth stands regardless of year sampled, while young seral stands changed significantly in regards to their ordination position depending on sampling year. Fourth, beetle communities in regrowth stands changed in a manner that paralleled the predictable transformation of young plant communities into mature forest stands. Ordination analyses found that beetle communities in the herb stage regrowth stands of 1982 had changed significantly and exhibited characteristics of beetle communities in tree stage regrowth stands.

Keywords: Beetle; Succession; Insect communities; Forest management

1. Introduction

Dynamics of ecosystems are influenced by naturally occurring disturbances such as wind, water, fire, insects, and disease. These disturbances have created and maintained forest habitat heterogeneity for centuries (Waring and Schlesinger, 1985). Habitat heterogeneity in forests can be observed as an irregular mosaic of old-growth and young regeneration forest stands. During the last century, the effect of many natural disturbances has been minimized as a result of modern forest management techniques (Kimmins, 1997). Thus, forest cutting now rivals natural disturbance for the creation of habitat heterogeneity (Hansen et al., 1991; Franklin and Forman, 1987). After many decades of tree harvest, the coniferous forests of the Pacific Northwest and elsewhere, have been shaped into a patchwork of young plantations, mature forest stands and non-forest sites. The ecological

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PII: S0378-1127(02)00490-5

ramifications from decisions regarding forest management range in scale from local to global and suggest that an assessment of the effects of forest management practices become a priority in scientific research (Lubchenco et al., 1991).

Various forest management practices, including clear-cutting, have been associated with changes in resident biota on the scale of species, populations, communities, and ecosystems (Franklin, 1989). Intensive forest management has been shown to have a significant effect on both plant and animal biodiversity (Harris, 1984; Schoonmaker and McKee, 1988). Management practices that result in changes in the flora further influence the ecosystem by affecting the fauna, including both vertebrates (Hansen et al., 1991; Hayes et al., 1997) and invertebrates (Schowalter, 1995; Miller, 1993). Two of the most common components to understanding impacts of forest management on populations and communities of vertebrates are breeding habitat and food relationships. Concerning the food relationships, insects serve an important role and are being included in measures of biota relating to management (Spence et al., 1999; Hammond and Miller, 1998). Insects are important components in food webs and the dynamics of populations, communities, and ecosystems (Miller, 1993). Furthermore, insects possess several characteristics that make them particularly suitable for use in environmental monitoring, including their diversity, small size, reproductive capacity, and acute sensitivity to environmental change (Weaver, 1995). Among the insects, beetles (Coleoptera) have been particularly well studied and may serve as useful indicator organisms. Beetles: (1) are abundant, with over 300,000 described species (Wilson, 1992), (2) are relatively well known taxonomically, (3) have been shown to be highly sensitive to habitat change (Refseth, 1980), and (4) may be collected using standardized techniques (Niemelä et al., 1993).

Numerous studies have focused on forest management and the effect on arthropods (Jennings et al., 1986; Schowalter, 1989, 1995; Niemelä et al., 1993; Niemelä et al., 1992; Lenski, 1982). In general, these studies have demonstrated that forest management, particularly clear-cutting, significantly alters species abundance, richness and diversity. Jennings et al. (1986) reported a greater abundance of ground dwelling beetles in uncut forest than in clear-cut forest stands. However, species richness, in ground dwelling beetles, has been found to be higher in regenerating stands (following clear-cut) than in mature forest stands (Niemelä et al., 1993; Lenski, 1982; Jennings et al., 1986). Niemelä et al. (1993) reported a general pattern of recovery, in ground beetle communities, following logging and a predictable increase or decrease of various specialist species. Schowalter (1989, 1995) reported greater arthropod species diversity in the canopies of old-growth trees than in young trees. Also, Schowalter (1995) reported less variability in arthropod diversity and abundance in old-growth stands than in partially harvested stands. Although, the pattern in species diversity in the forest canopy may be different than that found in ground dwelling insect group, forest management was still shown to have a significant effect on insect communities.

In the present study, we investigated the relationships between forest regeneration following clear-cutting and beetle communities in order to address the following questions: (1) How can the beetle communities best be described? (2) Are beetle communities in early vegetation seral stages different than the beetle communities found in late seral stages? (3) Are patterns in the beetle communities (relative abundance, presence/absence) associated with specific plant communities? (4) How do the patterns of association and distribution, within the beetle communities, change over time? These questions address the following general hypothesis: that as a result of vegetation change (expressed in plant community types), over both time and space, the composition of beetle communities is dynamic and directly related to the vegetative variation.

2. Methods

2.1. Study area

This study was conducted in the H.J. Andrews Experimental Forest, located approximately 80 km east of Eugene, Oregon, in the Cascade Mountain Range of western Oregon. With elevations ranging from 410 to 1630 m, the H.J. Andrews Forest is representative of the mountain landscapes prevalent in the west slope of the Cascade Mountains of the Pacific Northwest. Dyrness et al. (1974) described 23 vegetation associations from the Western Cascades, including the H.J. Andrews Forest. On the H.J. Andrews Forest, these vegetation associations are distributed within two major zones: the Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco)/western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone generally below 1050 m in elevation, and the Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) zone above 1050 m in elevation. The separation of the two zones is a function of temperature (elevation), while the distribution of the various vegetation associations within each zone is determined primarily by moisture availability as affected by slope, aspect and other environmental variables (Dyrness et al., 1974).

The H.J. Andrews Experimental Forest was designated a Biosphere Reserve as part of the United Nation's Man and Biosphere Program in 1976, and in 1980 became part of the National Science Foundation's Long Term Ecological Research (LTER) Program (McKee, 1998).

2.2. Stand selection

Twenty-nine forest stands were sampled in 1982/1983 and eighteen forest stands were sampled in 1999. Site selection was based on the availability of desired age and vegetation association combinations. The 29 stands sampled in 1982 and 1983 encompassed eight vegetation associations from the Douglas-fir/Western Hemlock Zone (Dyrness et al., 1974), and four seral stages within each of the vegetation associations, with three vegetation association/seral stage combinations lacking within the forest. The four seral stages were defined as: (1) herb stage regrowth (5–14 years post-harvest), (2) shrub stage regrowth (15–19 years post-harvest, (3) tree stage regrowth (20–40 years post-harvest) and (4) old-growth forest (growth since fire episodes of 125 and 400 years before present). The eight vegetation associations were: (1) *Pseudotsuga menziesii/Holodiscus discolor*, (2) *Pseudotsuga menziesii-Tsuga heterophylla/Corylus cornutus*, (3) *Tsuga heterophylla/Castanopsis chrysophylla*, (4) *Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon*, (5) *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa*, (6) *Tsuga heterophylla/Acer circinatum/Polystichum munitum*, (7) *Tsuga heterophylla/Polystichum munitum*, and (8) *Tsuga heterophylla/Polystichum munitum-Oxalis oregona*.

A subset of the stands sampled in 1982/1983 was resampled in 1999. For the 1999 sampling season, six of the eight vegetation associations from 1982/1983 sampling were used. These six associations were combined into three broader vegetation associations, because preliminary analyses suggested that the level of definition of the original vegetation associations was too specific to detect differences in the beetle communities. The three vegetation associations used in 1999 were: (1) *Pseudotsuga menziesii/Holodiscus discolor/Pseudotsuga menziesii-Tsuga heterophylla/Corylus cornutus*, (2) *Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon*; *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa*, (3) *Tsuga heterophylla/Polystichum munitum*; *Tsuga heterophylla/Polystichum munitum-Oxalis oregona*. Ten of the 18 stands were selected from the 1982/1983 study, four stands originally classified as herb stage regrowth and six old-growth stands. The four herb stage regrowth stands from 1982 had advanced to stage 3 (above) by 1999. The 10 resampled stands represented the broadest gradient of wet and dry soil conditions among the habitats used in 1982/1983. The additional eight stands (five tree stage regrowth, three old-growth) were selected to maximize the micro-habitat diversity sampled in the watershed because no apriori management was performed for this study.

2.3. Sampling and processing methods

The ground dwelling beetle fauna within each stand was sampled using pitfall traps consisting of 2.5 l plastic food containers (18 cm depth, 14 cm diameter 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 a 16 oz collection vessel partially filled with a 50/50 ethylene glycol/water mixture. After placement in the ground, the traps were covered with a 20 cm × 20 cm piece of mat finish aluminum or particle board, suspended 2–3 cm above the trap by 20-penny nail legs to act as a rain guard. Differences in the traps were limited to rain cover material. Studies of pitfall methodology indicate that pitfall size and shape are the greatest determinants of catch size and composition (Greenslade, 1964; Spence and Niemelä, 1994; Work et al., 2002), and both were held constant in this study. In addition, ordination analyses, of beetle catches from old-growth sites, routinely showed similar beetle communities irrespective of rain cover material.

Twelve traps were placed in each sampled stand in 1982 and 1983, five traps were placed in each stand in 1999. The 1999 trap array was reduced in size to reduce the time required for cleaning, identifying and vouchering. The traps were placed in a haphazard arrangement a minimum distance of 5 m apart, flush with the surrounding soil. Litter was repositioned around the edge of the trap to simulate natural conditions. The traps were then left unopened for a minimum of 2 weeks to reduce the "digging-in effect" (Digweed et al., 1995). Each sample consisted of a 3-week-period: (1) from 26 June to 18 July in 1982, (2) from 16 June to 7 July in 1983, and (3) from 25 June to 16 July in 1999. At the end of each sampling period, the trapped specimens were taken to the laboratory for cleaning, identification, and enumeration.

Family level identification was performed using Borror et al. (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 per 3-week-period. Trap counts were pooled among all traps from each stand to obtain the number of individuals per species per stand per 3-week-period. Voucher specimens were placed in the Oregon State Arthropod Collection, Corvallis, OR, USA.

2.4. Statistical methods

All community level analyses were conducted using PC-ORD version 4.28 (McCune and Mefford, 1999). Species data, for each stand and year, were analyzed using Non-metric Multi-dimensional Scaling (NMS) (Kruskal, 1964). NMS is an iterative ordination method based on ranked distances between sample units, and is especially useful for data that are non-normal (Clarke, 1993). NMS was chosen for this study because it allows the researcher to maintain a biologically meaningful view of the data (Clarke, 1993). The data were split into several data sets, according to year or combination of years, depending on the question of interest. For example, the 1982 data were analyzed independently, to examine spatial differences, as well as with the 1983 data and with the 1999 data, to examine temporal differences. Each data set was then arranged into two data matrices, one for the species data, and one for any accompanying data, such as soil moisture/vegetation association and seral stage. Since the trapping effort was different among years, the data were relativized, to number of beetles per species per trap per 3-week time period, when performing comparisons between years. This was done by dividing the yearly total 3 weeks catch, for each species, by the number of traps used at each site.

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. The values for skew and coefficient of variation were high, so rare species were eliminated. Rare species were those represented by singletons, and species that occurred in only a single sampled stand. Removal of a particular species was dependent upon the data subset because some species were numerous in 1 year and rare in another. The rare species may have been of ecological interest, but could not be examined using multivariate techniques due to the statistical "noise" generated by these data. Next, a $\log(x + 1)$ transformation was performed due to the large spread in the values of species abundance, and to further reduce the skew and coefficient of variation of the data. 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 stand that had the highest abundance for a particular species. Values for that species in the other stands were then assigned in proportion to that stand. This was done for each species to further reduce overall coefficient of variation. No transformations were performed on the matrices containing the accompanying environmental data. All data were analyzed for the presence of outliers following the approach described by Tabachnik and Fidell (1989), however, this did not result in the removal of any species or stands. The Sorensen distance measure (Faith et al., 1987) was used for all tests.

Trial runs of NMS were conducted using the appropriate data and the Sorensen distance measure. In all cases, four 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 versus dimensions were examined. A final run of the program was then performed, using the selected number of axes.

Fig. 3 was produced by first determining that a two-dimensional representation of the data was appropriate, using the above described procedure. Then, an ordination diagram was produced using NMS. The diagram was then imported into our word processing software and lines were drawn manually to connect the appropriate points. The longest line was assigned the value of 1, with the lengths of the other lines assigned accordingly. A paired *t*-test was used to statistically compare line length.

Multi-response permutation procedure (MRPP) and blocked MRPP (MRBP) were used to statistically examine differences in beetle community composition between groups (Biondini et al., 1988). Unlike ordination, where the results are graphically presented in reduced dimensional space, MRPP (and MRBP) tests the relationships of entities in the original multi-dimensional space. MRPP compares the mean within group distances (from predetermined groups) to within group means 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). Using Euclidean distances, MRPP was used to examine differences between stand seral stages in each of the data sets, and MRBP was used to examine the effects of time on the stands while blocking out effects that may be due to spatial differences.

3. Results

3.1. Taxonomic scope

Individuals from 49 beetle families were collected during the course of the project, totaling 64% of the 77 known beetle families from the H.J. Andrews Experimental Forest (Parsons et al., 1991). The families with the most individuals in all three sampling periods were Carabidae (including Cicindellidae) (2574 individuals), Curculionidae (1461 individuals), Leiodidae (1459 individuals), and Staphylinidae (4017 individuals). Carabids were the most numerous group in the 1982 and 1999 samples (1123 and 453 individuals, respectively), while Staphylinids were the most numerous group in 1983 (3455 individuals). In each sampling period, the combined catch from these four families represented more than 85% of the total yearly catch and 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%).

Total beetle abundance was highly variable between years, between vegetation associations and between forest stands. An overall total of 11,191 individual beetles were collected from the pitfall traps during the three sampling periods, including 2861 specimens from the 1982 season, 7135 specimens from the 1983 season, and 1195 specimens from the 1999 season. The totals are in part a result of different levels of sampling intensity (see earlier), however, when standardized values were calculated on a per trap basis the number of individuals collected between years was similar. The average catch per trap was 13.2 individuals in 1982 and 8.2 individuals in 1999. The differences were not significantly different due to a large standard deviation.

The old-growth stands had the highest average abundance among all seral stages, followed by the tree stage regrowth, herb stage regrowth, and lastly the shrub stage regrowth stands (Table 1). No consistent pattern in beetle abundance was observed among the vegetation associations, with abundance fluctuating between years and sites.

A total of 224 beetle taxa were collected during the three sampling periods. The total number of taxa included 193 identified species, 24 genus level morpho-species, three morpho-species not identified further than subfamily and four morpho-species identified only to family. Because of the coarse level of identification of some groups, the true number of species is potentially larger than indicated above.

Species richness (including morpho-species) differed among seral stages (Table 2). In both 1982

Table 1
Average number of beetles (S.D.) per seral stage per year

Sample year	Herb stage	Shrub stage	Tree stage	Old-growth
1982	91.5 (30.3) b	60.0 (31.3) a	111.4 (32.7) bc	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

H.J. Andrews Experimental Forest, Oregon, 1982, 1983, and 1999. Letters indicate differences within a given sample year (χ^2).

Table 2
Average species richness (S.D.) per seral stage per year

Sample year	Herb stage	Shrub stage	Tree stage	Old-growth
1982	29.5 (5.8) bc	20.6 (4.4) a	21.1 (5.0) ac	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

H.J. Andrews Experimental Forest, Oregon, 1982, 1983, and 1999. Letters indicate differences within a given sample year (χ^2).

and 1983, the herb stage regrowth stands had higher average species richness (S.D.), 29.5 (5.8) species and 28.8 (8.6) species, respectively, than any of the other seral stages. The old-growth stands (sampled in 1982 and 1983) had the lowest average species richness, 19.6 (4.2) species and 21.8 (5.1) species, respectively, even though the old-growth stands, in both years, had the highest values for beetle abundance. In 1999, the tree stage regrowth stands (herb stage regrowth from 1982) had a higher average species richness (13.8 (3.6) species) than the old-growth stands (12.1 (3.9) species), which is similar in pattern to years 1982 and 1983.

3.2. Community considerations

Ordination analyses of the 1982 forest stands demonstrated that the seral stages did exhibit different assemblages of species (Fig. 1). In particular, the herb stage regrowth and old-growth stands were clearly separated from one another in the ordination. The correlation between the ordination distances and the original multi-dimensional distances was high ($r^2 = 0.84$) indicating an accurate representation of the multi-dimensional data. The age of the stands had a high correlation with axis 2 ($r^2 = 0.70$), while axis 1 showed no strong correlation with any of the environmental data. Statistical measures from MRPP showed significant differences in the multi-dimensional space among each of the four seral stages ($P < 0.01$) (Table 3). The eight vegetation associations (Fig. 2) did not show any discernable pattern in the ordination diagram. Also, MRPP showed non-significant groups based on vegetation association for the 1982 data set (Table 3). The 1983 data (no figure shown) showed a very similar pattern to the 1982 data. Thus, the data for years 1982 and 1983 were combined.

Ordination of the combined 1982/1983 data (Fig. 3) showed close association of comparable seral stages between years. The old-growth stands in particular

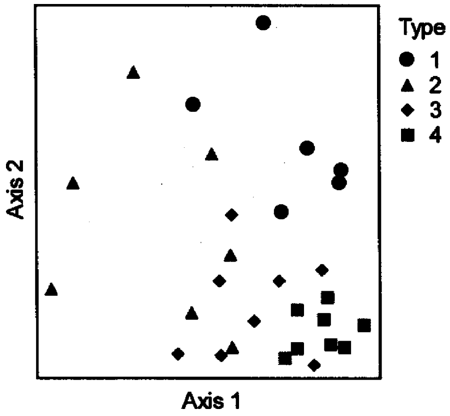

Fig. 1. Ordination of 1982 beetle species data illustrating the similarity of beetle communities among forest stands of differing seral stage. Types 1–4 indicate seral stages: (1) herb stage regrowth, 5–14 years post-harvest; (2) shrub stage regrowth, 15–19 years post-harvest; (3) tree stage regrowth, 20–40 years post-harvest; (4) old-growth, >125 years. H.J. Andrews Experimental Forest, Oregon.

Table 3
Results of multi-response permutation procedure (MRPP) and blocked multi-response permutation procedure (MRBP) tests for each year

Groups tested and data set	Test	t-statistic	A-statistic	P-value
Four seral stages; 1982	MRPP	−8.91	0.072	<0.001
Eight vegetation associations; 1982	MRPP	0.50	−0.007	0.676
Four seral stages; 1983	MRPP	−5.98	0.395	<0.001
Eight seral stages; combined 1982, 1983	MRPP	−13.99	0.113	<0.001
Regrowth vs. old-growth; 1999	MRPP	−1.93	0.018	0.043
Three vegetation associations; 1999	MRPP	−1.89	0.025	0.042
1982 vs. 1999; combined 1982, 1999	MRBP	−3.06	0.072	0.003
Tree stage regrowth vs. all other seral stages; combined 1982, 1999	MRPP	−4.72	0.024	0.001
1982 herb stage regrowth vs. 1999 regrowth; combined 1982, 1999	MRPP	−3.82	0.114	0.006
1982 old-growth vs. 1999 old-growth; combined 1982, 1999	MRPP	−1.15	0.029	0.126
Regrowth vs. old-growth; 1982	MRPP	−4.36	0.142	0.002
Regrowth vs. old-growth; 1999	MRPP	−0.38	0.012	0.289

H.J. Andrews Experimental Forest, Oregon, 1982, 1983, and 1999.

exhibited strong grouping between years illustrating the constancy of old-growth stands over time. The correlation between axis 2 and stand age was still relatively high ($r^2 = 0.54$). Multivariate space correlation was also high ($r^2 = 0.76$). An MRPP analysis of the combined 1982/1983 data set showed significant differences among stand seral stages, with all eight seral stages (four seral stages for each of 2 years) occupying separate regions of the multi-dimensional space. The MRPP analysis showed non-significant groups based on vegetation association for the

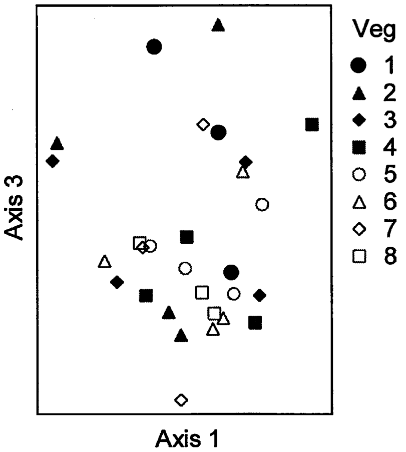

Fig. 2. Ordination of 1982 beetle species data illustrating the similarity of beetle communities among forest stands of differing vegetative association. Veg 1–8 indicate vegetation associations: (1) *Pseudotsuga menziesii/Holodiscus discolor*; (2) *Pseudotsuga menziesii-Tsuga heterophylla/Corylus cornutus*; (3) *Tsuga heterophylla/Castanopsis chrysophylla*; (4) *Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon*; (5) *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa*; (6) *Tsuga heterophylla/Acer circinatum/Polystichum munitum*; (7) *Tsuga heterophylla/Polystichum munitum*; (8) *Tsuga heterophylla/Polystichum munitum-Oxalis oregona*. H.J. Andrews Experimental Forest, Oregon.

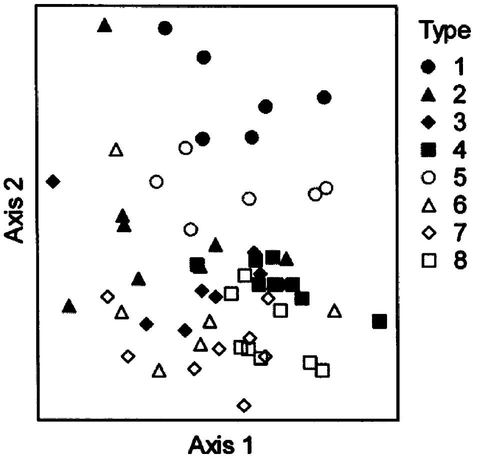

Fig. 3. Ordination of 1982/1983 beetle species data illustrating the similarity of beetle communities among forest stands of differing seral stage and year. Types 1–8 indicate seral stages: (1) 1982 herb stage regrowth, 5–14 years post-harvest; (2) 1982 shrub stage regrowth, 15–19 years post-harvest; (3) 1982 tree stage regrowth, 20–40 years post-harvest; (4) 1982 old-growth, >125 years; (5) 1983 herb stage regrowth, 5–14 years post-harvest; (6) 1983 shrub stage regrowth, 15–19 years post-harvest; (7) 1983 tree stage regrowth, 20–40 years post-harvest; and (8) 1983 old-growth, >125 years.

combined data set. The ordination diagram also showed no grouping pattern in the stands due to vegetation association. The results of the vegetation association analysis of 1982 and 1983 led to the creation of three rather than eight vegetation associations for the 1999 sampling period.

Ordination of the 1999 data set showed two broadly overlapping groups, the tree stage regrowth (herb stage regrowth from 1982/1983) and the old-growth stands, indicating their increased similarity due to time (no figure shown). Axis correlation with stand age was low ($r^2 = 0.30$). The difference between the two seral stages in 1999 was supported by only moderate evidence from the MRPP analysis ($P = 0.04$) (Table 3). The three vegetation associations sampled in 1999 were differentiated based on beetle assemblages. The difference between the three vegetation associations sampled in 1999 was supported by evidence from the MRPP analysis ($P = 0.04$) (Table 3).

Ordination of the stands sampled in both 1982 and 1999, using data from both years, resulted in the separation of the 1982 stands from the 1999 stands in the ordination diagram (Fig. 4). By pairing each stand by year, the relative lengths of the connecting lines could be considered to represent a measure of the relative amount of change observed in the beetle communities at each of the stands. The mean length of the lines connecting the regrowth stands across time was significantly longer than the mean length of the lines connecting the old-growth stands across the same amount of time (paired t-test, $t = 2.71$, d.f. $= 8$, $P = 0.03$). The direction of change in the ordination space was consistent among all but one of the stands. Stand four was unique in both its direction and amount of change (Fig. 4). An MRBP analysis of the combined 1982/1999 data set showed significant differences in multi-dimensional space associated with time (Table 3).

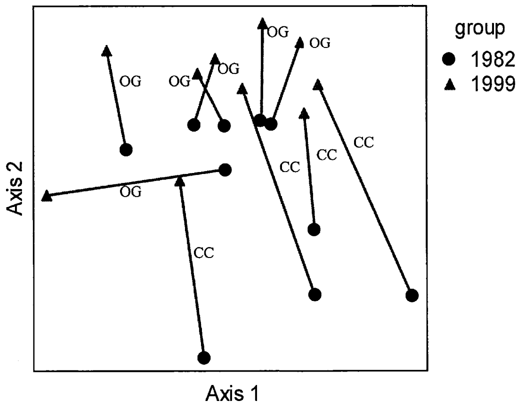

Fig. 4. Ordination of 1982/1999 beetle species data illustrating relative amount of change in beetle communities in regrowth (CC) and old-growth (OG) stands. Lines connect individual stands separated by time. Changes in beetle communities indicated by relative length of lines. H.J. Andrews Experimental Forest, Oregon.

The 1999 tree stage regrowth stands were compared with the complete 1982 data set in order to further evaluate the amount of change which occurred in the regrowth stands over the 17 years between 1982 and 1999 (Fig. 5). The ordination diagram showed six of the nine 1999 tree stage regrowth stands (type 5—all sampled in 1982) grouping near the 1982 tree stage regrowth stands (type 3) from the 1982 data set. The remaining three stands (33, 34 and 35 in Fig. 5—not sampled in 1982) were more closely associated with the 1982 shrub stage regrowth stands. As in the other ordinations, regrowth and old-growth stands remained distinct from one another. An MRPP analysis showed the ordination results to be significant ($P \leq 0.01$). MRPP was run to compare the 1982 tree stage

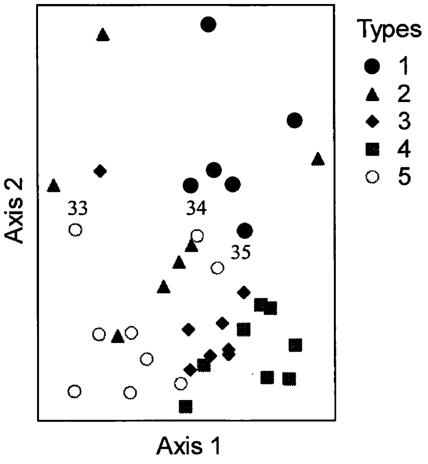

Fig. 5. Ordination of 1982/1999 beetle species data illustrating the similarity of beetle communities between 1999 regrowth stands (1982 herb stage regrowth) and 1982 tree stage regrowth stands. Types 1–4 indicate seral stages: (1) herb stage regrowth, 5–14 years post-harvest; (2) shrub stage regrowth, 15–19 years post-harvest; (3) tree stage regrowth, 20–40 years post-harvest; (4) old-growth, >125 years. Type 5 represents 1999 regrowth stands. Numbers indicate specific forest sites. H.J. Andrews Experimental Forest, Oregon.

regrowth stands plus the 1999 regrowth stands (similar in age since cut) to the rest of the 1982 data set. The results were significant, indicating that the grouping was less random than would be expected by chance (Table 3).

The 1982/1999 combined data were split into various subsets and then subjected to ordination analyses in order to more fully understand the effect of time on the forest stands. The first subset consisted of two complementary groups, the first being the regrowth stands (the herb stage regrowth from 1982 and tree stage regrowth from 1999), and the other the old-growth stands. The resulting patterns showed a clear distinction between the two different ages of regrowth. The ordination diagram showed a haphazard arrangement of points for the old-growth stands, as would be expected considering the assumed stability of old-growth forest. A significant difference was found to exist within the multi-dimensional space between the regrowth stands from the two different years ($P \leq 0.01$, MRPP) (Table 3). By contrast, differences among the old-growth stand plots were found to be non-significant between years ($P = 0.13$, MRPP) (Table 3).

The combined 1982/1999 data were then split into years. Only those stands that were sampled in both 1982 and 1999 were included (Fig. 6a and b). When the stands were plotted based on the 1982 data, the regrowth stands occupied a different area of the ordination diagram than did the old-growth stands (Fig. 6a). Conversely, when the stands were subjected to ordination according to the 1999 data, the regrowth and old-growth stands occupied overlapping regions of the ordination diagram, indicating their increased similarity (Fig. 6b). MRPP analysis showed significant differences between the groups in 1982 ($P < 0.01$), and non-significant differences between the groups for 1999 ($P = 0.29$). These data further suggested that the beetle communities in the herb stage regrowth of 1982 changed significantly with respect to the communities within the same stands in 1999.

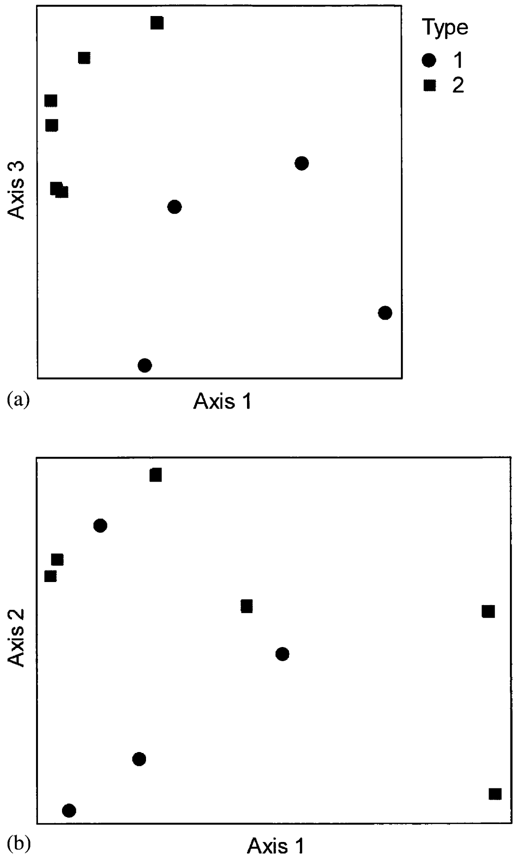

Fig. 6. Ordination of 1982/1999 beetle species data illustrating similarity between beetle communities in regrowth stands and old-growth stands in both 1982 and 1999. Types 1 and 2 indicate seral stages: (1) regrowth stands; (2) old-growth stands. (a) Ordination of 1982/1999 shared stands for data collected in 1982, (b) ordination of 1982/1999 shared stands for data collected in 1999. H.J. Andrews Experimental Forest, Oregon.

4. Discussion

4.1. Taxonomic scope

Several patterns emerged during examination of the taxonomic data. First, a general pattern regarding change in beetle abundance was seen to follow clear-cut management. These data suggested that clear-cutting was associated with a reduction in beetle abundance and that further reductions in abundance occurred through the shrub stage of succession. This initial reduction in abundance then was followed by an increase in abundance through the later seral stages, corresponding to canopy closure. The culmination of this process was the peak in abundance observed in the old-growth stands.

Second, species richness was found to be highest in the herb stage regrowth stands, and lowest in the old-growth stands. Although, the sampling indicated the presence of old-growth specialist species, including *Zacotus mathwesii* LeConte and *Epuraea obtusicollis* Reitter, the herb stage regrowth stands had a higher number of seral specialists. The herb stage regrowth stands supported a number of species specific to that age class including: *Microlestes nigrinus* Mannerheim, *Trachypachus holmbergi* Mannerheim, *Bromius obscurus* Linnaeus and *Carabus taedatus* Fabricius. Additionally, two other species, *Bolbocerus obesus* (LeConte) and *Neocyrtusa sternita* Hatch, whose distribution also included shrub stage and tree stage regrowth, were found in greatest abundance in herb stage regrowth stands. The presence of these relatively specialized species as well as others more generally distributed, but not found in old-growth stands, accounted for the higher species richness found in the herb stage regrowth stands.

Although, patterns were found regarding abundance and species richness data among beetle communities through time, the significance of those patterns was inconsistent among years. Consequently, the abundance and richness data were not sufficient for fully describing the similarities and differences in the beetle communities among the forest stands. Instead, we suggest, in answer to question one above, that the need to assess biotic responses to environmental change necessitates the use of multivariate techniques, where statistical comparisons of the species assemblages may be made based on presence/absence and relative abundance in species composition among samples.

4.2. Community considerations

Although, our study represented only two brief windows of time, the data suggested that over a period of 17 years, beetle communities in old-growth stands remained relatively stable, while those in early seral stands were changing along a trend parallel to changes in vegetation (Figs. 4 and 6). For instance, the regrowth stands classified as herb stage in 1982 were classified as tree stage in 1999. In 1999, analysis showed the tree stage regrowth stands to be similar to the tree stage regrowth stands of 1982. Furthermore, our study documented a change in beetle communities in regrowth stands over time, showing that young stands become more "old-growth" like within a relatively short period of time in regards to their beetle communities. Our study also provided evidence that the changes in the beetle communities occurred along a gradient from clear-cut, herb dominated, shrub dominated, and tree dominated regrowth stages, respectively, to old-growth forest. Our general hypothesis was that beetle communities would exhibit significant change over time, and these data do not allow us to reject that hypothesis. The differentiation of forest stands based on beetle communities was consistent with the findings of Niemelä et al. (1993) who found beetle communities to differ according to stand age. Rykken et al. (1997) also found beetle communities to differ according to stand conditions. Therefore, ground beetles collected via pitfall traps appear to provide a system useful in monitoring environmental changes both temporally and spatially on a long term basis.

There are two notable exceptions to the pattern of change over the 17-year-period. The first of these, in Fig. 4, one forest stand was found to be unique in both its direction and amount of change. This stand is the only location within the H.J. Andrews Forest watershed supporting a small, localized community of white oak (*Quercus garryanna* Dougl.), typically a valley and foothill plant community. Although, stand four was different in many regards to the other sampled stands, it was included due to its importance to the broader geographic region, and our desire for this study to be broadly representative of the lower elevations of the H.J. Andrews Forest. The second, in Fig. 5, stands 33, 34 and 35 were more closely associated with the 1982 shrub stage regrowth stands rather than the 1982 tree stage regrowth stands as would be expected. These three stands were very dry, and developed a canopy more slowly than the wetter stands. In addition, these three stands were slightly younger than the other stands in this seral stage and consequently had beetle communities resembling those of early seral stands.

The issues typically associated with biodiversity and forest management concern the distribution and abundance of species richness relative to patches of the landscape and how those patches are managed. For instance, Hansen et al. (1991) asked whether plantations managed for wood production support fewer species than do natural forests. In addition, they asked whether fragmentation of remaining natural forests is likely to reduce biodiversity even further in natural stands. Our data support the conclusions of Hansen et al. (1991), that a full suite of seral stages is critical to maintaining a high level of biodiversity. Furthermore, our study addresses their concern that more "research is needed on the temporal and spatial patterning of seral stages that is needed by native species." Our study site, the H.J. Andrews Experimental Forest, produced a mix of young seral patches for examining biodiversity across a regeneration gradient and the recent repeat measurement of these data after a 17-year-period. Given the ground beetle assemblages, as measured in our study, which is representative of Douglas-fir forests of the Pacific Northwest, it appears that 17 years encompasses a large proportion of the dynamic change which occurs in the community from cutting to exhibiting initial characteristics of old-growth. It will be interesting to see if future studies, involving short lived animals, also demonstrate that early seral stages, measured in terms of only a few years, represent the majority of the period of time in which old-growth characteristics can be detected.

In conclusion, our data suggest that forest managers should consider maintaining a diverse array of young seral stands. In terms of beetle communities, significant differences may be detected at the scale of years rather than decades. This would indicate that a number of seral stages should be perpetuated within the first 20 years of regrowth in order to maximize beetle diversity.

Acknowledgements

The authors wish to thank Greg Brenner for statistical advice and help in beetle identification, Jim LaBonte for identification verification, J.D. Lattin for his initial support of Gary Parsons during the 1982/1983 pilot study, Art McKee for assistance in the location of sample stands, Tim Schowalter for his comments on the 1999 protocol and data interpretation, and Paul Hammond who read a previous version of this manuscript. This research was supported by the National Science Foundation Program for Long Term Ecological Research (LTER) grant number DEB-96-32921. This is Oregon State University Agricultural Experiment Station Technical Paper No. 11950.

References

Biondini, M.E., Mielke, P.W., Berry, K.J., 1988. Data-dependent permutation techniques for the analysis of ecological data. Vegetatio 75, 161–168.

Borror, D.J., Triplehorn, C.A., Johnson, N.F., 1989. An Introduction to the Study of Insects. 6th ed. Saunders College Publishing, Philadelphia, PA, USA.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Digweed, S.C., Currie, C.R., Carcamo, H.A., Spence, J.R., 1995. Digging out the digging-in effect of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). Pedobiologia 39, 561–576.

Dyrness, C.T., Franklin, J.F., Moir, W.H., 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. United States/International Biological Program, Coniferous Forest Biome Project Bulletin Number 4. College of Forestry Resources, University of Washington, Seattle, WA, USA.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68.

Franklin, J.F., 1989. Toward a new forestry. Am. For. 95, 37–44.

Franklin, J.F., Forman, R.T., 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Lands. Ecol. 1, 5–18.

Greenslade, P.J.M., 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). J. Anim. Ecol. 33, 301–310.

Hammond, P.C., Miller, J.C., 1998. Comparison of the biodiversity of three forested ecosystems. Ann. Ent. Soc. Am. 91, 323–328.

Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests. Lessons from natural forests. Bio. Science 41, 382–392.

Harris, L.D., 1984. The Fragmented Forest. Island Biogeography Theory and the Preservation of Biotic Diversity. University of Chicago Press, Chicago, IL, USA.

Hatch, M.H., 1953. The Beetles of the Pacific Northwest. Part 1. Introduction and Adephaga, vol. 16. University of Washington Publication in Biology. University of Washington Press, Seattle, WA, USA.

Hatch, M.H., 1957. The Beetles of the Pacific Northwest. Part 2. Staphyliniformia, vol. 16. University of Washington Publication in Biology. University of Washington Press, Seattle, WA, USA.

Hatch, M.H., 1962. The Beetles of the Pacific Northwest. Part 3. Pselaphidae and Diversicornia. University of Washington Publication in Biology, vol. 16. University of Washington Press, Seattle, WA, USA.

Hatch, M.H., 1965. The Beetles of the Pacific Northwest. Part 4. Macrodactyles, Palpicornes, and Heteromera, vol. 16. University of Washington Publication in Biology. University of Washington Press, Seattle, WA, USA.

Hatch, M.H., 1971. The Beetles of the Pacific Northwest. Part 5. Rhipiceroidea, Sternoxi, Phytophaga, Rhynchophora, and Lemellicornia, vol. 16. University of Washington Publication in Biology. University of Washington Press, Seattle, WA, USA.

Hayes, J.P., Chan, S.S., Emmingham, W.H., Tappeiner, J.C., Kellogg, L.D., Bailey, J.D., 1997. Wildlife response to thinning young forests in the Pacific Northwest. J. Forestry 95, 28–33.

Jennings, D.T., Houseweart, M.W., Dunn, G.A., 1986. Carabid beetles (Coleoptera: Carabidae) associated with strip clear-cut and dense spruce-fir forests of Maine. Coleopt. Bull. 40, 251–263.

Kimmins, J.P., 1997. Forest Ecology, a Foundation for Sustainable Management, 2nd ed. Prentice Hall, Upper Saddle River, NJ, USA.

Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29, 1–27.

Lenski, R.E., 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. Ecol. Entomol. 7, 385–390.

Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J., Risser, P.G., 1991. The sustainable biosphere initiative: an ecological research agenda. Ecology 72, 371–412.

McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4.28 Beta. MjM Software, Gleneden Beach, OR, USA.

McKee, A., 1998. Focus on field stations: H.J. Andrews Experimental forest. Bull. Ecol. Soc. Am. 79, 241–246.

Miller, J.C., 1993. Insect natural history, multi-species interactions and biodiversity in ecosystems. Biodiv. Cons. 2, 233–241.

Niemelä, J., Spence, J.R., Spence, D.H., 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera: Carabidae) in Central Alberta. Can. Entomol. 124, 521–540.

Niemelä, J., Langor, D., Spence, J.R., 1993. Effects of clear-cut harvesting on boreal ground-beetles assemblages (Coleoptera: Carabidae) in western Canada. Conserv. Biol. 7, 551–561.

Parsons, G.L., Cassis, G., Moldenke, A.R., Lattin, J.D., Anderson, N.H., Miller, J.C., Hammond, P., Schowalter, T.D., 1991. Invertebrates of the H.J. Andrews Experimental Forest, western Cascade Mountains, Oregon. V. An Annotated List of the Insects and Other Arthropods. US Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-290.

Pimentel, R.A., 1985. Biostat II: A Multivariate Statistical Toolbox. Tutorial Manual. Sigma Soft, San Luis Obispo, CA, USA.

Refseth, D., 1980. Ecological analyses of carabid communities—potential use in biological classification for nature conservation. Conserv. Biol. 17, 131–141.

Rykken, J.J., Capen, D.E., Mahabir, S.P., 1997. Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. Conserv. Biol. 11, 522–530.

Schoonmaker, P., McKee, A., 1988. Species composition and diversity during secondary succession of coniferous forests in the Western Cascade Mountains of Oregon. For. Sci. 34, 960–979.

Schowalter, T.D., 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests of western Oregon. Can. J. For. Res. 19, 318–322.

Schowalter, T.D., 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. For. Ecol. Manage. 78, 115–125.

Spence, J.R., Buddle, C.M., Gandhi, K.J.K., Langor, D.W., Volney, W.J.A., Hammond, H.E.J., Pohl, G.R., 1999. Invertebrate biodiversity, forestry and emulation of natural disturbance: a down-to-earth perspective. In: Proceedings of the Pacific Northwest Forest and Rangeland Soil Organism Symposium. US Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-461, pp. 80–90.

Spence, J.R., Niemelä, J.K., 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. Can. Entomol. 126, 881–894.

Tabachnik, B.G., Fidell, L.S., 1989. Using Multivariate Statistics, 2nd ed. Harper & Row, New York, USA.

Waring, R.H., Schlesinger, W.H., 1985. Forest Ecosystems: Concepts and Management. Academic Press, Orlando, FL, USA.

Weaver, J.C., 1995. Indicator species and scale of observation. Conserv. Biol. 9, 939–942.

Wilson, E.O., 1992. The Diversity of Life. Belknap Press, Cambridge, MA, USA.

Work, T.T., Buddle, C.M., Korinus, L.M., Spence, J.R., 2002. Pitfall trap size and capture of three taxa of litter-dwelling arthropods: implications for biodiversity studies. Environ. Entomol. 31, 438–448.