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Abundance, species diversity, and community structure of Collembola in successional coastal temperate forests on Vancouver Island, Canada

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Abstract

The ecological implications of the conversion of old-growth temperate rainforests to managed forests have generated much discussion worldwide. This paper examines the effects of such a conversion on different aspects of the biodiversity of the soil collembolan fauna, and attempts to determine the time that will be required for the collembolan fauna to approach the abundance and community structure seen in old-growth forests. The study also investigates the potential of using different measures of species diversity and community structure as indicators of old-growth conditions in forest soils. The study was carried out in three chronosequence sites in Douglas-fir dominated stands on the dry leeward eastern side of Vancouver Island, BC, Canada. Each of the three sites contained stands representing four stages of stand development: regeneration (7–9 years), immature (35–46 years), mature (80–102 years) and old-growth (>248 years). The Collembola were extracted from litterbags containing needle litter or wood chips, and from the forest floor (LFH) layer in the late autumn of four successive years.

Overall abundance of Collembola was highest in the old-growth and lowest in the regeneration stands. Although population numbers in the immature and mature forests were significantly higher than in regeneration stands, they still had not achieved the levels observed in old-growth forests. In the forest floor, species richness was low in regeneration stands compared to later stages of stand development, but did not differ significantly among immature, mature and old-growth stands. Measures of species diversity based on Shannon's and Simpson's indices of diversity did not differ significantly according to the stage of stand development.

It was not possible to distinguish individual collembolan species that could be used as indicators of old-growth conditions. The same species occurred in most or all stand ages, with differences being determined by changes in relative and absolute abundance of the species comprising the community. However, principal component analysis of data on the Collembola of needle litterbags and the LFH layer showed that the collembolan community of the regeneration stands could be clearly differentiated from those of the forested stands. In addition, the collembolan communities of 80–102-year-old forests could still be distinguished from those of the old-growth forests. In contrast, the collembolan fauna of decomposing wood chips was very similar in all stand ages, with the exception of the regeneration stands.

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1. Introduction

Old-growth forests of the north Pacific coast of North America are renowned for their diversity, richness, and longevity. They furnish a wide variety of timber resources, and in addition, are increasingly appreciated for non-timber values such as recreation, ecotourism, edible mushrooms, and also for profound spiritual values. Although many of the concerns regarding the conversion of old-growth to second growth forests are based on social considerations (van Kooten and Bulte, 1999), serious scientific concerns regarding the long-term environmental effects of the conversion have also been raised, particularly with regard to effects on biodiversity, erosion of nutrient capital, and changes in the carbon balance (Maser, 1990; Kimmins, 1995; Trofymow et al., 1997).

Much of the biodiversity of forest ecosystems resides in the soil (Behan-Pelletier and Newton, 1999), and the importance of the biodiversity of the soil biota to the integrity and functioning of terrestrial ecosystems, is well recognised (Pankhurst, 1997; Behan-Pelletier and Newton, 1999; Wall, 1999). Indeed, several researchers (e.g. reviews by Linden et al., 1994; van Straalen, 1997, 1998) have suggested that soil arthropod communities have potential for development as biological indicators of soil health. Unfortunately, particularly in North America, we know only a little about what organisms are present in forest soils, especially at the species level. We know even less about how they respond to different forest management practices (Marshall, 1993; Perry, 1998). Thus we cannot say how forestry practices are likely to affect soil biodiversity or the long-term sustainability of the soil.

Collembola were chosen for detailed study since they are extremely abundant in forest soils (Marshall, 1993) and are one of the few soil groups for which comprehensive keys are available in Canada, allowing identifications to be made at species level.

The present study is part of a larger chronosequence project, designed to study the effects of converting old-growth to second growth forests (Trofymow et al., 1997; Trofymow and Porter, 1998). In long-lived forests such as these, where individual trees live for hundreds of years, chronosequence studies are useful for providing snapshots of ecosystem development over time, allowing us to gauge the degree to which old-growth characteristics are attained during forest succession.

The specific objectives of the present study were to:

(1) assess the effects of forest conversion on different aspects of the biodiversity of the soil collembolan fauna;
(2) estimate faunal recovery time after major disturbance; and
(3) investigate the potential of using different measures of species diversity and community structure as indicators of old-growth conditions in forest soil.

In another publication (Addison et al., 2003), we discuss the implications of the observed changes in collembolan abundance and community structure for functional relationships in forest soil.

2. Materials and methods

2.1. Study sites

The study was carried out at three replicated sites in the Very Dry Maritime subzone of the Coastal Western Hemlock Biogeoclimatic Zone (CWHxm; Klinka et al., 1991), one of the most threatened forest landscapes on eastern Vancouver Island, BC, Canada (MacKinnon and Eng, 1995). The stands were composed mainly of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), with, depending upon stand age, significant amounts of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and lesser amounts of western redcedar (*Thuja plicata* Donn), western white pine (*Pinus monticola* Dougl.) and red alder (*Alnus rubra* Bong.). The three sites studied are referred to as Victoria Watershed South (VWS: 48°34′ N; 123°39′ W), Victoria Watershed North (VWN: 48°38′ N; 123°43′ W), and Koksilah (KOK: 48°39′ N; 123°46′ W).

Each of the three sites or chronosequences contained four stand ages (ages given as of 1993): regeneration (R; 7–9 years), immature (I; 35–46 years), mature (M; 80–102 years) and old-growth (OG; >248 years). For each of the three sites, all four stand ages were located within a 5 km × 5 km area. All the stands <248 years in age (i.e. regeneration, immature and mature) originated after clearcutting, with the exception of the mature plot at Koksilah, which was of fire

origin. Detailed descriptions of the study sites and plot layout are given in Trofymow et al. (1997).

2.2. Experimental design and sampling

Four strings of litterbags were placed on the surface of the L layer of the soil in each of three subplots within each of the stand ages at each site in October 1992. All litterbags were 20 cm × 20 cm in size and made from woven polypropylene pool cover/shade cloth following methods used in the Canadian Intersite Decomposition Experiment (Trofymow and CIDET Working Group, 1998). Each string included bags with the following substrates:

1. Douglas-fir needles (10 g dry weight in a fine (0.2 mm × 0.4 mm) mesh bag).
2. Western hemlock wood chips (50 g dry weight in a fine mesh (0.2 mm × 0.4 mm) bag).
3. Western hemlock wood chips (50 g dry weight in a coarse mesh (3.0 mm × 3.0 mm) bag).

In the autumn of each of the following 4 years (1993–1996), one string of litterbags was collected from each subplot. Only litterbags from two of the three subplots were used for this study. Samples of the LFH layer (approximately 15 cm × 15 cm, down to, but not including the mineral soil), the fourth substrate sampled in this study, were also taken at each sampling time.

2.3. Methods

In the laboratory, samples were stored at 5 °C until processing, usually within one week. High gradient extraction over a period of 7 days was used to extract soil arthropods from field moist sub-samples of the wood chips and LFH material. As the amount of material in the needle litterbags was insufficient for sub-sampling, the fauna was extracted from the entire material. Moisture content was determined after drying in a forced air oven at 70 °C for 48 h. Abundance data for Collembola are reported per 100 g dry weight of organic material.

Fauna from a total of 384 samples (3 sites × 4 stand ages × 2 subplots × 4 organic substrates × 4 years) were sorted and categorised into taxonomic groupings, and over 12,000 Collembola were identified to species level. Species determinations were made using the keys of Christiansen and Bellinger (1998), Fjellberg

(1985), and other literature where appropriate. A series of reference slides was prepared, and the slides were deposited in the Soil Arthropod Collection of the Pacific Forestry Centre, Canadian Forest Service, Victoria, BC.

2.4. Data analyses

The discussions and recommendations of Ludwig and Reynolds (1988) were used to choose and compute diversity indices. Hill's numbers (N0, N1, N2; Hill, 1973) were calculated to express the different aspects of species diversity. Since all three of these indices are expressed in the same units (number of species), the results are easily interpreted and compared. Thus N0, the mean number of species in a sample, represents species richness, while the indices N1 ($e^{\text{Shannon's index}}$) and N2 (1/Simpson's index) incorporate both species richness and species equitability and respectively, express the mean number of abundant, and very abundant species in the samples.

$$\text{Shannon's index H} = -\sum_{i=1}^{S} \left[\left(\frac{ni}{n} \right) \ln \left(\frac{ni}{n} \right) \right]$$

$$\text{Simpson's index } \lambda = \sum_{i=1}^{S} \frac{ni(ni-1)}{n(n-1)}$$

where ni is the number of individuals in the ith species and n the total number of individuals for all species in the sample.

Analysis of variance (ANOVA, Minitab® 12 for Windows) tests were used to identify differences in the abundance and the species diversity of Collembola due to substrate, stand age, year of sampling and site. Site was treated as a blocking factor. Since initial tests showed that the substrate × year interaction term was significant ($P = 0.005$), subsequent ANOVA tests were carried out separately for each of the substrates. Thus, for each substrate the model used tested for main effects and the stand age × year interaction term. Mesh size (coarse versus fine) was included as an additional factor in the analysis of the wood chip data. Within a single substrate, none of the interaction terms was significant, so only main effects are presented in this paper. The Bonferroni pairwise procedure was used to adjust P values to allow multiple comparison of means (Minitab® 12 for Windows).

Differences in treatment effects discussed below were all significant at $P \leq 0.05$. For each substrate, collembolan data for the two subplots were combined before application of the statistical analyses, providing a single value per substrate per plot. Before being used in statistical tests, population data were transformed using the logarithmic transformation, $\log_{10}(x+1)$ where x was the number of individuals per 100 g dry weight of substrate. In the text, derived means are presented.

Principal component analyses (PCA) were also performed using Minitab® 12 for Windows. All the PCA analyses presented were based on $\log_{10}(n+1)$ transformation of the species abundance data (numbers per 100 g dry weight) of the 40 most abundant species, pooled across years. In order to facilitate discussion, ellipses were used to emphasise groupings within the plots of the ordination data, but these have no statistical significance.

3. Results

3.1. Abundance and species diversity of Collembola of the forest floor (LFH layer)

Overall, Collembola were most abundant in the old-growth plots and least abundant in the regeneration plots (Table 1). Although there were significantly more Collembola in the immature and mature stages than in the regeneration plots, abundance was still significantly lower than levels seen in old-growth stands. This general pattern was maintained each year from 1993 to 1996 (Fig. 1). Species richness (N0) was also significantly reduced in regeneration stands compared with old-growth (Table 2), but species richness in

the immature and mature stands did not differ significantly from either the regeneration or old-growth plots. The age of the stand had no significant effect on the other two measures of species diversity (N1 and N2).

The year of sampling had a dramatic impact on both collembolan abundance and species diversity. Numbers of Collembola in all stand ages in 1994 were significantly reduced compared with the other years (Table 1). Mean values for all three species diversity indices were highest in 1993, and declined significantly in 1994. Although values for N0 had recovered to 1993 values by 1996, values for N1 and N2 remained low (Table 2).

3.2. Abundance and species diversity of Collembola of needle litterbags

The mean number of Collembola extracted from needle litter bags placed in the regeneration plots did not differ significantly from levels found in the litterbags of the mature or old-growth forest, although it was significantly lower than in needle litterbags placed in the immature stands (Table 1). The effect of the year of sampling was also significant, with collembolan numbers increasing in litterbags in all stand ages in the last year of the experiment (Fig. 1).

Analyses of the data on species diversity of the Collembola inhabiting needle litterbags indicated that only the stand age effect was significant. For all three indices, mean values were significantly higher in the old-growth litterbags than in those taken from other stand ages (Table 3). There was no evidence that collembolan species diversity changed over the 4 years that the needle litterbags were in the field.

Table 1
Effect of forest stand age and year of sampling on abundance of Collembola (three-way Randomised Block ANOVA; site × stand age × year of sampling)

Substrate	Effect of stand age					Effect of year of sampling				
	OG	R	I	M	ANOVA P value	1993	1994	1995	1996	ANOVA P value
LFH	763.8 c	102.1 a	338.8 b	313.3 b	<0.001	383.7 b	119.1 a	485.3 b	458.1 b	<0.001
Needle litter	1130.2 ab	549.5 a	1236.9 b	803.5 ab	0.021	626.6 a	663.7 a	653.1 a	2280.3 b	<0.001
Wood chips	167.1 b	44.5 a	173.4 b	76.8 ab	<0.001	65.0 ab	37.1 a	117.8 b	347.5 c	<0.001

Numbers are derived means per 100 g dry weight substrate. Within the same row, means followed by the same letter do not differ significantly from one another (Bonferroni $P < 0.05$). Interaction terms were not significant. Site effects not shown. OG is old-growth, R is regeneration, I is immature, M is mature.

Table 2
Effect of forest stand age and year of sampling on species diversity indices (Hill, 1973) for Collembola in the LFH layer

Diversity index	Effect of stand age					Effect of year of sampling				
	OG	R	I	M	P value	1993	1994	1995	1996	P value
N0	15.8 b	8.8 a	12.8 ab	11.2 ab	0.001	15.1 a	8.2 b	11.1 ab	14.2 a	0.001
N1	7.6	5.7	7.1	5.9	0.220 ns	9.3 a	4.6 b	5.8 b	6.6 ab	0.001
N2	5.7	5.3	5.9	4.4	0.482 ns	8.1 a	3.8 b	4.6 b	4.9 b	0.001

Non-significant (ns). Within the same row, means followed by the same letter do not differ significantly from one another (Bonferroni $P < 0.05$). Interaction terms were not significant. OG is old-growth, R is regeneration, I is immature, M is mature.

Table 3
Effect of forest stand age and year of sampling on species diversity indices for Collembola in needle litterbags

Diversity index	Effect of stand age					Effect of year of sampling				
	OG	R	I	M	P value	1993	1994	1995	1996	P value
N0	17.1 b	8.6 a	12.4 a	11.9 a	0.001	12.5	13.1	11.0	13.3	0.404 ns
N1	9.6 b	3.8 a	5.2 a	5.6 a	0.001	5.6	7.0	5.9	5.7	0.461 ns
N2	7.4 b	3.1 a	3.9 a	4.1 a	0.001	4.0	5.6	4.6	5.3	0.279 ns

Non-significant (ns). Within the same row, means followed by the same letter do not differ significantly from one another (Bonferroni $P < 0.05$). Interaction terms were not significant. OG is old-growth, R is regeneration, I is immature, M is mature.

3.3. Abundance and species diversity of Collembola of the wood chip litterbags

Preliminary analyses indicated that numbers of Collembola in litterbags containing woody materials were very low, particularly in the first 2 years of the study, and that there was no significant effect of litterbag mesh size on collembolan numbers. Thus for each stand age–year–site combination, data on collembolan fauna of the fine-mesh and the coarse-mesh bags were pooled.

There were significantly fewer Collembola in the litterbags of woody material placed in the regeneration sites than in those of immature and old-growth plots (Table 1). Numbers of Collembola in the wood

litterbags were low for the first 2 years but increased dramatically in all stand ages over the next 2 years (Fig. 1).

As many of the wood chip litterbags contained only a few species of Collembola, in order to calculate diversity indices, data from the 4 years and two mesh sizes were combined to produce a single value for each site-stand age combination. Each "sample" used in this analysis was therefore eight times the size of the samples used in the needle litter and LFH analyses. The effect of stand age on the diversity indices N0 and N2 was not significant and although the ANOVA showed a significant effect of stand age on N1, subsequent application of the pairwise comparison failed to identify any significant differences (Table 4).

Table 4
Effect of forest stand age on species diversity indices for Collembola in wood chips

Diversity index	Old-growth	Regeneration	Immature	Mature	ANOVA P value (stand age effect)
N0	22.5	15.2	20.2	20.2	0.094 ns
N1	11.6	7.3	8.0	10.9	0.049
N2	8.1	4.7	5.1	8.8	0.057 ns

Non-significant (ns). Data for the two mesh sizes and 4 years have been pooled. The Bonferroni pairwise comparison of means detected no significant differences among the values of N1 for the different stand ages.
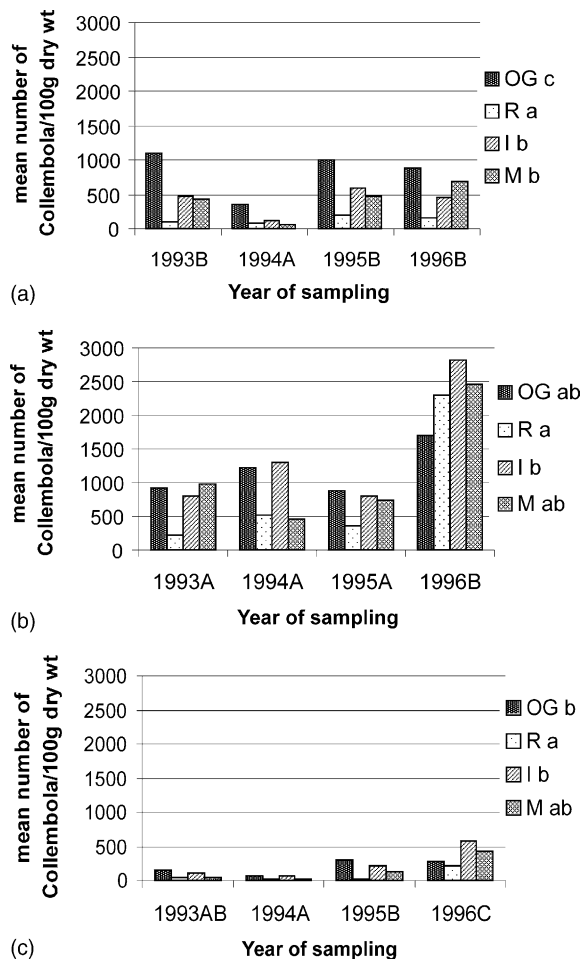
Fig. 1. Effect of forest stand age on mean numbers of Collembola (per 100 g dry weight) in: (a) the LFH layer; (b) needle litter; (c) wood chips. Derived means are shown. In the legend, the mean numbers of Collembola in stand ages followed by the same lower case letters are not significantly different. On the X-axis, the mean number of Collembola in years followed by the same letters in upper case are not significantly different. OG is old-growth, R is regeneration, I is immature, and M is mature.

3.4. Collembolan species related to stand age

Seventy-five species or morphospecies of Collembola were identified in this study (Appendix A). Taxonomic authorities and the species codes used in different analyses and figures are also provided in Appendix A.

Considering all the substrates together (wood chips, needle litter and LHF), there was very little differ-

ence between the total number of species collected from materials in the regeneration sites (54 species) and numbers of species collected in older stands (58–59 species) (Table 5). Only *Schaefferia cheoha*, *Micranurida spirillifera* and *Arrhopalites hirtus* were found exclusively in old-growth samples. None of the collected species was present solely in regeneration plots.

3.5. Collembolan community analyses

Principal component analysis was used to provide an ordination of the different site–stand age–substrate combinations, based on the collembolan species composition of the samples. For the Collembola of the LHF layer, the resulting ordination diagram (Fig. 2) shows that regeneration communities all have low loadings on PC1, while at the opposite end of the scale, all the old-growth stands have high loading for this factor. The immature and mature sites are found, intermixed, between the two extremes. PC2 is related to site location, with all stages of the chronosequence at the Koksilah site occurring at the bottom of the plot (low loadings for PC2), while the two Victoria Watershed sites occupy the centre and upper portions of the diagram. All the regeneration plots have similar loadings on both axes, indicating similar communities. In contrast, the more mature the stands, the greater is the divergence between the collembolan communities of the Koksilah site on one hand, and the two Victoria Watershed sites on the other. The collembolan community of the Koksilah old-growth is profoundly different than those of Victoria Watershed North and South.

A plot of the species scores associated with the site and stand age plot is presented in Fig. 3. As in the previous diagram, species centroids with low loadings on Species Score Axis 1 (e.g. *Tetracanthella pacifica*, *Xenyllodes wapiti*, *Hymenaphorura cocklei* and *Megalothorax minimus*) are associated with regeneration plots, those with high loading on this factor, with old-growth (e.g. *Paranura colorata*, *Mespahorura yosii* and *Folsomia* sp. *nivalis* grp.). Several species (e.g. *Onychiurus* sp. ?*reluctus*, *Heteraphorura* sp. *subtenuis* grp. and *Folsomia* sp. *stella* grp.) were strongly influenced by site factors, with centroids identified with the Koksilah sites.

The relationship between substrate type and stand age is explored in Fig. 4. The collembolan

Table 5
Number of species of Collembola extracted from samples (wood, litter and LFH) in different stand ages

Number of species	Old-growth	Regeneration	Immature	Mature
Total (all substrates)	59	54	58	58
Wood (coarse mesh)	40	24	34	34
Wood (fine mesh)	36	30	35	35
Needle litter	44	37	38	38
LFH	49	36	46	43

Data for different sites and times have been pooled.
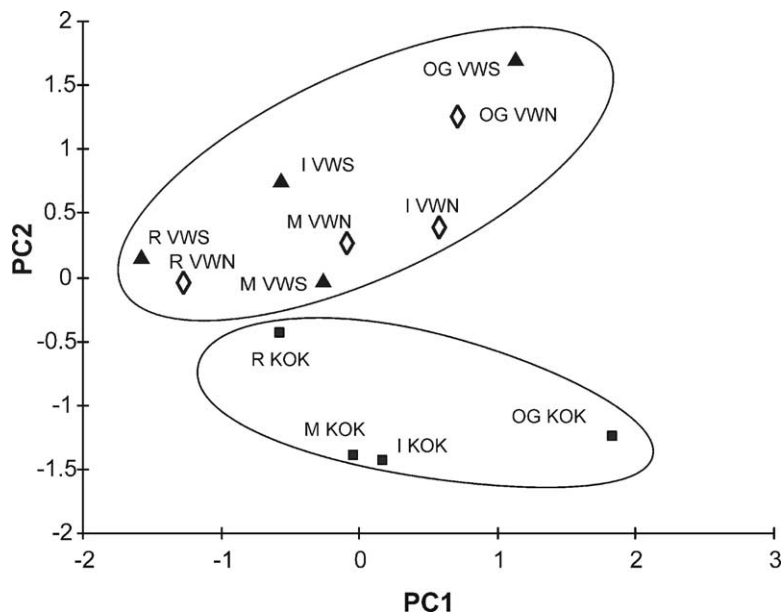
Fig. 2. Distribution of site–stand age combinations based on PCA of collembolan species of the LFH layer ($\log_{10}(n + 1)$ transformation of numbers per 100 g dry weight). OG is old-growth, R is regeneration, I is immature, and M is mature. VWS is Victoria Watershed South, VWN is Victoria Watershed North, KOK is Koksilah. Ellipses are used to emphasise the groupings according to site, but have no statistical significance.

communities of the regeneration plots were very similar to one another, regardless of substrate type. All the collembolan communities inhabiting wood chips from plots with a forest canopy cluster together, regardless of mesh size or whether the bags were placed in immature, mature or old-growth forests. The communities of the mature and immature LFH samples were very similar to each other, as were the communities decomposing needle litter at those two sites. However, the analysis showed that the remaining old-growth samples (needle litter and LFH) had collembolan communities that could be clearly differentiated from those of younger forests.

4. Discussion

4.1. Changes in collembolan abundance, diversity, and community structure in relation to stand age

Several studies have shown a decline in collembolan abundance in response to clearcutting, at least in the short-term (i.e. <20 years post-harvest) (e.g. Vlug and Borden, 1973; Huhta, 1976; Bird and Chatarpaul, 1986; Hoekstra et al., 1995; Donegan et al., 2001). However these studies do not address the question of how long it takes for the forest soil community to recover, and whether different species or species groups
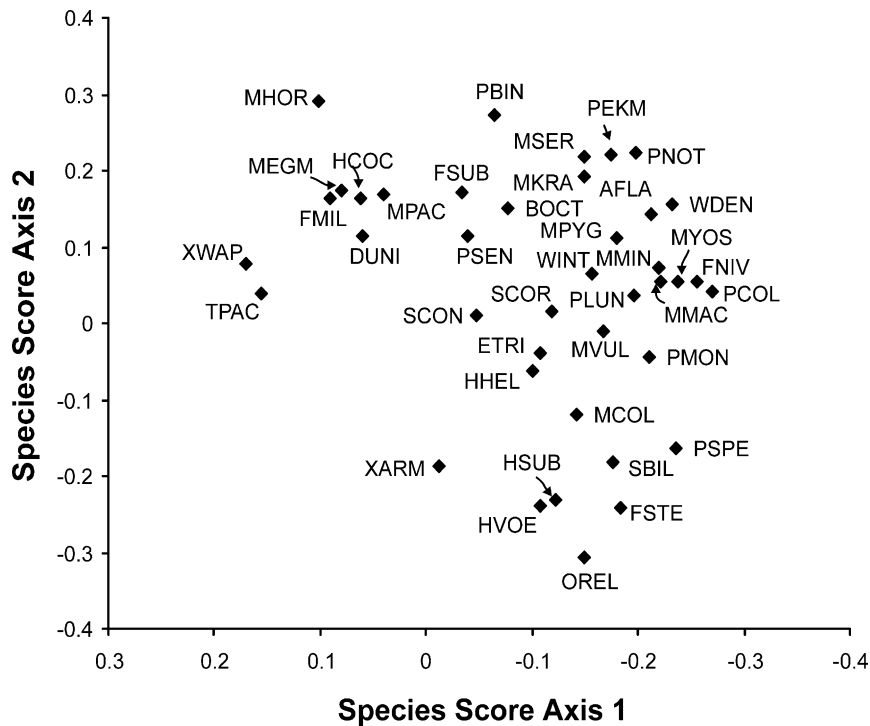
Fig. 3. Species scores for PCA analysis of Collembola in the LFH layer. Species codes are given in Appendix A, and with the exception of *Megalothorax minimus* (MEGM), are composed of the first letter of the genus and the first three letters of the species name.

were affected differentially by clearcutting, and if so, to what extent.

The present study showed that even 80–102 years post-disturbance, collembolan numbers in the LFH layer of the CWHxm forest were still significantly lower than in old-growth forests. Setälä and Marshall (1994) described this same general pattern of abundance for Collembola in decomposing stumps in the same forest type. Fons and Klinka (1998), working on a set of chronosequences in the closely allied Very Wet Maritime subzone of the same type of forest type (CWHvm) reached a similar conclusion. In their study, collembolan numbers 60 years post-disturbance had not reached levels seen in the old-growth. Thus it appears that in these coastal rainforests, time periods in excess of 60–100 years will be required for collembolan abundance in the forest floor to return to pre-disturbance levels.

The results of the analysis of collembolan community structure in relation to forest age tend to agree with the time-frame for recovery suggested by the abun-

dance data. Even 80–102 years after stand initiation, the collembolan communities of both the forest floor and decomposing needle litter could still be clearly distinguished from those found in the same substrates located in old-growth forests (Fig. 4). For wood chips however, community structure of the collembolan fauna was related to whether or not the plot had a forest canopy (i.e I, M and OG sites) or whether the litterbags were located in regeneration plots.

The relationship between various indices of collembolan species diversity and forest stand age was less clear. In the LFH, only species richness (N0) showed a statistically significant response to stand age, but even then detected only significant differences between the extremes of stand age, i.e. regeneration and old-growth plots. On the other hand, the collembolan fauna in the needle litterbags placed in old-growth stands showed higher species richness (N0) and species diversity (N1 and N2) than the bags placed in any of the other forest stand ages. Thus for needle litter and the forest floor, species diversity indices tended to detect differences
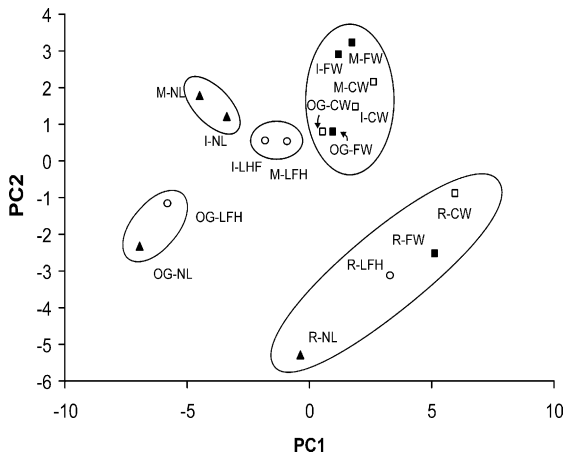
Fig. 4. Distribution of substrate-stand age combinations based on PCA of collembolan species ($\log_{10}(n+1)$ transformation of numbers per 100 g dry weight). OG is old-growth, R is regeneration, I is immature, M is mature. NL (▲) refers to needle litter, CW (□) is wood in coarse mesh litterbags, FW (■) refers to wood in fine mesh litterbags and LFH (○) refers to forest floor material. Ellipses are used to emphasise the groupings according to substrate–stand age combinations, but have no statistical significance.

between the faunas of old-growth forests on one hand, and regenerating forests (all stages or just a particular stage), on the other. None of these three measurements of species diversity detected significant differences in the collembolan fauna of wood chips placed in different stand ages.

Other attempts to use species diversity indices to measure the response of soil invertebrates to various kinds of disturbance have also met with mixed results (van Straalen, 1998). Bird et al. (2000) found that the species richness of soil invertebrates responded to forest fertilisation treatment, while Shannon's index of Diversity did not. Several studies have shown that diversity of soil invertebrates (particularly of the more mobile macroarthropods) actually increased following clearcutting (Addison and Barber, 1997; Brumwell et al., 1998). In other cases, collembolan species diversity was shown to be relatively insensitive to clearcutting, at least in the short-term (Addison and Barber, 1997; Siira-Pietikäinen et al., 2001).

None of the analyses demonstrated statistically (or biologically) significant differences between the collembolan communities of immature and mature forests, suggesting that the characteristics used to differentiate these two stand ages were not important to Collembola. Setälä and Marshall (1994) reached a similar conclusion with respect to collembolan communities of decaying stumps at these same sites.

4.2. Annual variability in measurements of collembolan abundance and species diversity

Collembolan abundance and species diversity were both sensitive to interannual effects. In 1994 both abundance and species diversity values for Collembola in the LFH layer declined to ∼50% of the values obtained the previous year, although there was no change in the pattern of response to forest age. Examination of the records of the nearest climate station for the area did not provide any obvious explanation for the observed declines. In addition, corresponding drops in collembolan abundance or species diversity were not observed in the litterbag materials from the identical sampling locations, suggesting that the enclosure of materials in litterbags mitigated the effect of the stress. Yet whatever the reasons for the observed declines in abundance and species diversity in 1994, the results underscore the fact that, even in the forest floor of undisturbed old-growth forests, large fluctuations in both collembolan numbers and species diversity can be expected.

4.3. Collembolan species or communities indicative of old-growth conditions

A serious environmental concern regarding clearcutting is that biodiversity will be decreased, and that species will be extirpated (Carey, 1998; Moldenke and Lattin, 1990). Thus one of the principal objectives addressed in this study was to look for species that could be considered indicative of old-growth conditions.

Even though clear differences between the collembolan communities of the different ages of forested stands could be identified (Fig. 4), these differences mainly involved changes in the relative and absolute abundance of the constituent species, rather than the elimination or addition of species to the fauna. Although three species (*M. spirillifera*, *A. hirtus* and *S. cheoha*) were found only in old-growth samples in the present study, none of them can be considered true old-growth specialists. In previous studies (Setälä and

Marshall, 1994; Setälä et al., 1995), *M. spirillifera* and *A. hirtus* were both found in decomposing stumps in all stand ages, and all three of these species also occur in other ecozones in Canada (Skidmore, 1995). Only four individuals of *S. cheoha* were collected in the present study, and although all were in samples taken from the old-growth forests, Setälä and Marshall (1994) reported two specimens of this species in decaying stumps in the mature forest at VWS. *Schaefferia cheoha* differs from another described species, *S. duodecimocellata* in that the former has three to four dorsal dental setae, and the latter five such setae. Fjellberg (1985) reported that specimens from Alaska and Washington had a variable number of dorsal dental setae (three to seven), and applied the older name of *S. duodecimocellata* to his specimens. Since specimens collected in the present study had three to four dental setae, they are reported here as *S. cheoha*. However, it is possible that the two species are in fact synonymous (Fjellberg, 1985). *Schaefferia duodecimocellata* is reported from Alaska, and from Interior Douglas-fir and Engelmann Spruce-Subalpine Fir sites in BC (Addison, unpublished data). In the latter case, the species was most abundant in the mineral soil, a habitat that was not sampled in the present study. Thus additional research will be required to determine the true distribution and taxonomic status of this species before it can be considered an old-growth specialist.

Another six species of Collembola were found in old-growth but not regeneration samples, but all of these also occurred in immature or mature samples, or both. In the present study, *P. voetglini* (formerly known only from epiphytes on *Pseudotsuga* in Oregon, USA) was found in low numbers in all stand ages except the regeneration stands, raising the possibility that this species normally inhabits the bark or canopy of trees over a certain minimum size.

The distribution of *H. cocklei* also illustrates the problems of identifying "indicator species" using only limited data, especially when the fauna is poorly understood. On the basis of its distribution in the samples collected in the present study (LFH, wood and needle litter) we could conclude that this species was typical of early successional stands in coastal temperate forests. Conversely, working at the same sites, Setälä et al. (1995), concluded that, based on their study of the collembolan fauna of stumps, *H. cocklei* preferred

stumps in the old-growth. Yet, examination of literature indicates that *H. cocklei* is considered a winter and/or high altitude species, found all along the coast of western North America from California to Alaska (Addison and Otvos, unpublished data; Christiansen and Bellinger, 1998; Skidmore, 1995), and its distribution appears to be unrelated to forest stand age.

4.4. Factors threatening the integrity of forest soil invertebrate communities

This study was unable to identify any soil collembolan species that absolutely required old-growth for survival. This is not surprising as research in other disciplines has generally found only a few species of plants and vertebrates that were unique to forest >250 years old (Carey, 1998). However, research has generally shown that several species are associated with particular elements of old-growth (e.g. large decaying logs), or habitats most likely to be found in old-growth environments, such the suspended soils and moss mats of ancient forest canopies (Carey, 1998; Winchester, 1998). These specialised habitats were not included in the present study. Although forest management strategies can, and frequently are modified to incorporate certain elements of old-growth (e.g. snags, coarse woody debris), other characteristics, such as suspended soils are difficult or impossible to emulate. Studies in the closely allied Very Wet Maritime Coastal Western Hemlock subzone (CWHvm) have indicated that suspended soils did not develop in trees <200–250 years old (Winchester, 1998). In addition, at least some elements of the mite fauna of these forests were unique to the canopy (Behan-Pelletier and Winchester, 1998; Winchester et al., 1999). Whether this applies to the collembolan fauna is not known.

As many soil invertebrates have limited dispersal abilities, there is increasing concern that the forest fragmentation resulting from forest harvesting activities may limit the ability of some invertebrate species to maintain viable populations on the landscape (Moldenke and Lattin, 1990; Spence et al., 1996). The experimental design used in this study required that all four stages of stand development be present within relatively close proximity of one another (within a 5 km × 5 km area). Under these conditions, there was no evidence to suggest collembolan species were being eliminated. Unfortunately,

this close juxtapositioning of forest age classes is not always reflected in commercial logging practices.

Whereas it is possible to modify harvesting practices so as to minimise direct impacts of logging on soil invertebrates, another potentially greater threat to the survival of indigenous soil invertebrate communities is posed by the invasion of exotic species. There are increasing reports of the occurrence of exotic earthworm species in coastal forests (e.g. Panesar et al., 2000; Kranabetter and Banner, 2000; Marshall and Addison, unpublished data), particularly in clearcuts and along watercourses. At the VWS site, the invasive earthworm species *Lumbricus rubellus* Hoffmeister was found in a riparian area beside the study site, while *Aporrectodea tuberculata* (Eisen), another exotic species of earthworm, was found in the mature stand at that site. Although soils at both the immature and old-growth stands at the VWS site had a well-developed LFH layer (5–6 cm in depth), the soil in the mature stand had only a 2 cm L layer (Trofymow et al., 1997). As many soil invertebrate decomposer species in coastal rainforests are associated with a well-developed LFH layer, it is likely that the invasion of exotic earthworm species, capable of profoundly changing soil characteristics, will pose a substantial threat to the integrity of native invertebrate communities.

5. Conclusions

The abundance and community structure of Collembola in old-growth forests differed significantly from those of younger forests, and could still be differentiated from those of mature forests 80–102 years after clearcutting. Community structure, as revealed by principal component analysis was a sensitive indicator of the degree of faunal recovery over time. Species diversity indices tended to be less sensitive.

In spite of the clear differences in the collembolan community structures of different forest successional stages, the same species of Collembola tended to occur in all stand ages, with differences in the fauna being due to changes in relative and absolute abundance of the species comprising the community. This study was unable to identify any soil collembolan species that could be considered as absolutely requiring old-growth for survival. Given that virtually all the species in the old-growth were present in earlier forest

successional stages, it is likely that given the appropriate environmental conditions and a favourable configuration of stand ages on the landscape, the structure of the collembolan communities of younger stands will in time approach those of the old-growth.

Acknowledgements

Appendix A. List of Collembola species: class Collembola

Families and genera follow Bellinger, P.F., Christiansen, K.A. and Janssens, F. 1996–2002. Checklist of the Collembola of the World. http://www.collembola.org. The four-letter codes are the species abbreviations used in Fig. 3.

Family Hypogastruridae Börner, 1906	
Ceratophysella sp.	
Hypogastrura sp. nr. *helena* Christiansen and Bellinger, 1980	HHEL
Hypogastrura macrotuberculata Hammer, 1953	
Microgastrura minutissima (Mills, 1934)	MMIN
Mitchellania krafti (Scott, 1962)	MKRA
Mitchellania horrida (Yosii, 1960)	MHOR
Mitchellania vulgaris (Yosii, 1960)	MVUL
Schaefferia cheoha Wray, 1963	
Willemia denisi Mills, 1932	WDEN
Willemia intermedia Mills, 1934	WINT
Xenylla humicola (O. Fabricius, 1780)	XHUM
Family Onychiuridae Börner, 1901	
Allonychiurus flavescens grp. (Kinoshita, 1916)	AFLA

Appendix A (*Continued*)

Deuteraphorura lusa (Christiansen and Bellinger, 1980)	
Heteraphorura sp. (*subtenuis* grp. (Folsom, 1917))	HSUB
Hymenaphorura cocklei (Folsom, 1908)	HCOC
Lophognathella choreutes Börner, 1908	
Onychiurus dentatus (Folsom, 1902)	
Onychiurus sp. ?*reluctus* Christiansen, 1961	OREL
Protaphorura sp.	PSPE
Protaphorura voegtlini (Christiansen and Bellinger, 1980)	PVOE
Family Tullbergiidae Bagnall, 1935	
Mesaphorura macrochaeta Rusek, 1976	MMAC
Mesaphorura pacifica Rusek, 1976	MPAC
Mesaphorura ruseki (Christinansen and Bellinger, 1980)	
Mesaphorura yosii Rusek, 1967	MYOS
Multivesicula columbica Rusek, 1982	MCOL
Family Neanuridae, Börner, 1901	
Friesea alaskella Fjellberg, 1985	
Friesea cera Christiansen and Bellinger, 1973	
Friesea grandis Mills, 1934	
Friesea millsi Christiansen and Bellinger, 1973	FMIL
Micranurida pygmaea Börner, 1901	MPYG
Micranurida spirillifera Hammer, 1953	
Morulodes serratus (Folsom, 1916)	MSER
Paranura colorata Mills, 1934	PCOL
Pseudachorutes sp. 1 (cf. *corticolous* Schäffer, 1896)	
Pseudachorutes sp. 2 (cf. *lunatus* Folsom, 1916)	PLUN
Pseudachorutes sp. nr. *saxatilis* MacNamara, 1920	
Family Odontellidae Massoud, 1967	
Superodontella biloba (Christiansen and Bellinger, 1980)	SBIL
Superodontella cornifer (Mills, 1934)	SCOR
Xenyllodes armatus Axelson, 1903	XARM
Xenyllodes wapiti Fjellberg, 1985	XWAP

Appendix A (*Continued*)

Family Entomobryidae Schött, 1891	
Entomobrya triangularis Schött, 1896	ETRI
Pseudosinella octopunctata Börner, 1901	
Sinella binoculata (Schött, 1896)	
Sinella sp. ?*sexoculata* (Schött, 1896)	
Family isotomidae Schött, 1891	
Anurophorus sp. nr. *septentrionalis* Palissa, 1966	
Boernerella octogenaria Mills and Schmidt, 1957	BOCT
Cryptopygus sp. 1	
Desoria sp. 1	
Desoria sp. 3	
Desoria sp. 4	
Desoria sp. 5 (?*nigrifrons* Folsom, 1937)	
Desoria sp. ?*uniens* (Christiansen and Bellinger, 1980)	DUNI
Folsomia sp. ?*macroseta* Ford, 1962	
Folsomia sp. *nivalis* grp. Packard, 1873	FNIV
Folsomia sp. *stella* grp. Christiansen and Tucker, 1977	FSTE
Metisotoma grandiceps (Reuter, 1891)	
Micrisotoma achromata Bellinger, 1952	
Parisotoma ekmani (Fjellberg, 1977)	PEKM
Parisotoma notabilis (Schäffer, 1896)	PNOT
Proisotoma minima (Absolon, 1901)	
Pseudanurophorus binoculatus (Kseneman, 1934)	PBIN
Pseudisotoma monochaeta (Kos, 1942)	PMON
Pseudisotoma sensibilis (Tullberg, 1876)	PSEN
Tetracanthella pacifica Rusek and Marshall, 1976	TPAC
Vertagopus sp.	
Family Tomoceridae Schäffer, 1896	
Plutomurus brevimucronatus (Denis, 1928)	
Pogognathellus flavescens (Tullberg, 1871)	
Tomocerina lamellifera (Mills, 1934)	

Appendix A (*Continued*)

Family Arrhopalitidae Richards, 1967
 Arrhopalites sp. ? *clarus* Christiansen,
  1966
 Arrhopalites sp. ? *diversus* Mills, 1934
 Arrhopalites hirtus Christiansen, 1966

Family Dicyrtomidae Börner 1906
 Ptenothrix maculosa (Schött, 1891)

Family Katiannidae Börner 1913
 Sminthurinus conchyliatus Snider,   SCON
  1978

Family Sminthurididae Börner 1906
 Sphaeridia pumilis (Krausbauer, 1898)

Family Neelidae Folsom, 1896
 Megalothorax minimus Willem, 1900   MEGM

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