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Biotic and Abiotic Factors Affecting the Structures of Ground Invertebrate Communities in Japanese Cedar Dominant Forests

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Abstract

The relationships between the structures of ground invertebrate communities, forest structure, and abiotic and forest floor biotic factors in cedar dominant forests (*Cryptomeria japonica*) on Sado island, Japan were investigated. Three primary forests (one primary pure cedar forest and two primary coniferous-broadleaved mixed forests) and three plantation forests were chosen for this study. The diversity of invertebrate communities in the primary forests was higher than in the plantation forests. The primary forests also had a steeper slope angle, higher soil water content, higher photon flux density and canopy openness, and a thinner litter layer than the plantation forests. The structures of invertebrate communities strongly correlate with slope angle, elevation, light conditions, litter layer depth, and understory species composition. In particular, light conditions and understory species composition were revealed as having a strong influence on the structures of invertebrate communities. The structures of ground invertebrate communities seem to be indirectly affected by light conditions through forest floor microclimates. Understory species seem to provide invertebrates with a food resource, sufficient protection against extreme microclimates and shelter from predators. The ground invertebrate community in one of the plantation forests was relatively similar to that in the primary forests, because as it has been managed regularly, it has a similar forest structure and light conditions, and is situated closer to some primary forests compared to the other plantation forests. Thus, this supports the hypothesis that differences in light conditions and understory species composition are the main factors affecting the diversity of invertebrate communities in primary and plantation forests.

Keywords; ground invertebrate community; cedar dominant forest; light conditions; understory species composition

Introduction

It is known that there is a relationship between forest structure and the composition of invertebrate species living in forests. For example, Dabrowska-Prot (1999) reported that forest habitat degradation in deforested areas leads to a drop in quantitative and qualitative fauna richness. Nakamura *et al.* (1970) reported that the soil invertebrate fauna of primary mixed stands of broad-leaved and coniferous trees were richer than those found in fir and spruce plantations. Furthermore, Watanabe and Shidei (1963) reported that the soil invertebrates of primary forests (fir, red pine and mixed broad leaf forests) were more abundant than those in Japanese cedar plantations. However, the effect of abiotic and vegetative factors on invertebrate communities has not been studied in detail.

Abiotic factors are known to directly influence invertebrate communities, and they also have an indirect effect through the vegetation composition (Nakamura *et al.* 1970). Understory vegetation directly influences invertebrates since it provides them with not only a food resource but also sufficient protection against extreme microclimates and shelter from predators (Dabrowska-Prot 1999; Nichols and Burrows 1985; Uetz 1979). Therefore, it can be hypothesized that invertebrate communities are affected by plant species composition and forest structure, as well as abiotic factors such as light conditions, slope angle and soil water content.

In this paper, the relationship between ground invertebrate communities, forest structure, abiotic and forest floor biotic factors is investigated in detail in cedar dominant forests. Such forests are indigenous to and relatively common in Japan. Primary forests consisting of Japanese cedar, *Cryptomeria japonica*, are distributed discontinuously from Aomori Prefecture to Yakushima Island, Kagoshima Prefecture (Takeoka 1970), while plantations of this species cover 12% of the land area of Japan. The Japanese cedar adapts well to temperate and moist climates (Tsumura and Ohba 1993). There are several reports that document the fauna of primary cedar forests such as the forest birds (Eguchi *et al.* 1989, 1992) and Sika deer, *Cervus nippon yakushimae* (Takatsuki 1990) that were investigated on Yakushima. Furthermore, Yamamoto *et al.* (1994) reported that the abundance and diversity of forest floor invertebrates in naturally regenerated cedar forests were greater than those in cedar plantations.

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However, there are limited studies that document the invertebrate communities of primary cedar forests.

This paper investigates and statistically analyzes the environmental conditions that influence ground invertebrate communities. The following are considered: (1) the relationships between the structures of ground invertebrates and forest structure (2) the relationships between abiotic and biotic factors and forest structure, and (3) how abiotic and biotic factors control ground invertebrate communities.

Materials and methods

Study sites

Investigations were conducted in the Niigata University Forest in Sado and the neighboring Osado Mountains in northern Sado Island, Japan. Sado Island is 855 km^2 in area and located at 138 °E 38 °N. In the Osado Mountains, where fog frequently rises due to the moist sea winds, the primary cedar (*Cr. japonica*) forest appears along a cloud belt. In the Niigata University Forest, primary pure cedar stands and cedar-deciduous broadleaved mixed stands cover an area of 100 ha and 200 ha, respectively.

For comparisons of ground invertebrate communities, one primary pure cedar forest (PR-P), two primary coniferous-broadleaved mixed forests (PR-M) and three plantation forests (PL) were chosen. In each site, two 10×10 m study plots were constructed. The distance between the two plots was less than 200 m. Three study sites (PR-P, PR-M1, PR-M2) were established in the primary forests on the mountain slopes (Table1):

PR-P: PR-P is located in the fog belt. The elevations of the two study plots were 860 m and 880 m. The canopy layer, which is relatively open because of gap formation as a result of old cedars, is composed of *Cr. japonica*, while *Hydrangea serrata var. megacarpa* and some shrub species dominate the understory.

PR-M1: PR-M1 is also located in the fog belt. The elevations of the two study plots were 820 m. The canopy layer is composed of *Cr. japonica* and *Pterocarya rhoifolia*, while *Arachniodes standishii*, *Hydrangea serrata* and some shrub species dominate the understory.

PR-M2: The elevations of the two study plots were 700 m and 710 m. The canopy layer is composed of *Cr. japonica* and *Cercidiphyllum japonicum*, while *Elatostema umbellatum var. majus*, *Hydra. s. var. megacarpa*, *Diplazium wichurae* and some shrub species dominate the understory.

Three study sites were also established in the cedar plantation forests (Table1). One plantation forest is situated in Niigata University Forest:

PL1: The elevations of the two study plots were 340 m and 380 m. PL1 is situated in the Niigata University Forest. *Hydra. s. var. megacarpa*, *Selaginella remotifolia*, *Rubus palmatus* and some shrub species dominate the understory. PL1 is relatively closed to some primary forests appearing on middle mountain slopes.

PL2: The elevations of the two study plots were 170 m. *Hydra. s. var. megacarpa*, *X. strumarium*, *R. palmatus* and some shrub species dominate the understory. In PL2, tree density is high, and the canopy layer is almost closed, because this stand has not been managed regularly.

PL3: The elevations of two study plots were 100 m. *Stegnogramma pozoi*, *Caculia adenostyloides*, *R. palmatus* and some shrub species dominate the understory. Tree density is high, and the canopy layer is almost closed, because this stand also has not been managed regularly.

Sampling

Invertebrates were collected at each study plot one for a day using 25 pitfall traps arranged on an 8×8 m grid. Plastic cups with a top diameter of 66 mm and a depth of 74 mm were used as the traps. The survey was carried out on June 24-28, August 9-14, and October 9-15, 2001. However, the survey was carried out for two days as for PR-P and PR-M1 in October, and could not be carried out in PR-M1 in June because of heavy rainfall.

Abiotic and forest floor biotic factors

A survey of abiotic (slope angle, elevation, PFD (Photon Flux Density), canopy openness and soil water content) and biotic factors (litter layer depth and understory vegetation) was conducted in each plot.

Hemispherical photographs were taken with a fish-eye lens camera (PENTAX MZ-M, SIGMA 8 mm F4 EX Circular Fisheye) from August to September 2001. In each plot, five photographs from a height of 30 cm and those from a height of 2 m above the ground were taken. Annual PFD and canopy openness were calculated using the Winphot 5.0 program (Ter Steege 1997). The mean PFD of the five photos was used as the representative value of each study plot.

Soil samples were collected using a 100 cc cylinder in August 2001 to measure soil water content. Soil water content was then calculated as follows:

$$(W_W - W_D) / W_W \times 100\ (\%),$$

where W_W is the wet weight of the soil sample, and W_D is the dry weight of the soil sample after being dried for 24 hours at 60°C.

Litter layer depth was measured repeatedly five times at each plot in June, August, and October 2001, and the averages in each season were used for analysis. For the data of understory vegetation, five 1×1 m understory plots were set at each study plot. The coverage (%) of each species under heights of 1.3 m was investigated from August to September 2001.

Data analysis

All invertebrates were classified to family (Coleoptera) or order (other taxa). The total number of individuals in each taxon collected during the three trappings was used. *Silphidae* and other Coleoptera larvae were distinguished from adult beetles. Order and family richness (N^*) were corrected using the first-order jackknife estimator (Burnham and Overton 1979):

Table 1. Study sites

Site		Slope angle (°)	Elevation (m)	Dominant tree species	Dominant understory Species
Primary pure cedar forest (PR-P)	1	15	880	*Cry*	*Hydra, Vib, Pla*
	2	25	860	*Cry*	*Hydra*
Primary coniferous-broadleaved mixed forest (PR-M1)	1	27	820	*Cry*	*Hydra, Ela, Ara*
	2	22	820	*Cry*	*Ara, Hydra, Dip*
Primary coniferous-broadleaved mixed forest (PR-M2)	1	27	710	*Cer, Cry*	*Ela, Hydra, Dip, Ara*
	2	33	700	*Cer, Cry*	*Ela, Thu, Dip, Hydra, Filicopsida sp., Ara*
Cedar forest plantation (PL1)	1	21	380	*Cry*	*Hydra, Rub, Chl, Zan, Teu, Steg*
	2	6	340	*Cry*	*Hydra, Sel, Boe, Gly, Steg, Hydro*
Cedar forest plantation (PL2)	1	7	170	*Cry*	*Xan, Rub, Ace, Steg, Mel, Dis, Dap*
	2	11	170	*Cry*	*Hydra, Hou, Rub, Steg*
Cedar forest plantation (PL3)	1	16	100	*Cry*	*Steg, Rub, Dis, Wis, Ace*
	2	5	100	*Cry*	*Steg, Stel, Cac, Hou, Per, Carex sp., Xan*

Cry, Cryptomeria japonica; Cer, Cercidiphyllum japonicum; Hydra, Hydrangea serrata var. megacarpa; Vib, Viburnum furcatum; Pla, Plagiogyria matsumureana; Ela, Elatostema umbellatum var. majus; Ara, Arachniodes standishii; Dip, Diplazium wichurae; Thu, Thujopsis dolabrata var. hondai; Rub, Rubus palmatus; Chl, Chloranthus japonicus; Zan, Zanthoxylum piperitum; Teu, Teucrium viscidum var. miquelianum; Steg, Stegnogramma pozoi; Sel, Selaginella remotifolia; Boe, Boehmeria platanifolia; Gly, Glycine max ssp. soja; Hydro, Hydrocotyle sibthorpioides; Xan, Xanthium strumarium; Ace, Acer rufinerve; Mel, Melothria japonica; Dis, Disporum smilacinum; Dap, Daphniphyllum macropodum var. humile; Hou, Houttuynia cordata; Wis, Wisteria floribunda; Stel, Stellaria diversiflora; Cac, Caculia adenostyloides; Per, Persicaria thunbergii. The dominant tree species and dominant understory species were determined by Dominant component analysis (Ohsawa 1984).

$$N^*=S+\{(t-1)/t\}\,f_1,$$

where S is the total number of orders or families, t is the total number of traps (25×3=75), and f_1 is the number of orders or families of which only one individual was recorded in a plot. Usually, f_1 indicates the number of the orders or families that were recorded only in one trap. However, we didn't distinguish the individuals collected during the 25 traps in each trial, therefore the number above was defined for f_1.

To compare the diversity of invertebrate community between study plots, the Shannon-Wiener index (H') and homogeneity factor index (J') were used:

$$H' = -\Sigma p_i \ln p_i\,,$$
$$J' = H' / \ln S$$

where p_i is the relative abundance of taxon i in a study plot.

The number of individuals in each taxon (n) was transformed into $\log_{10}(n+1)$, and disposed using the detrended correspondence analysis (DCA) method (Hill and Gauch 1980) to examine similarities in the ground invertebrate communities of different study plots. The coverage of each species in the understory was analyzed using DCA to examine similarities in the understory of different study plots.

To examine the relationship between the structures of invertebrate communities, environmental conditions and understory, Spearman's rank correlation coefficients were calculated. Axis 1 and Axis 2 of the DCA for all the invertebrates, Coleoptera and the understory was used.

Results

Relationship between ground invertebrate communities and forest structure

The primary forests showed higher species diversity of the ground invertebrate communities than the plantations (Table 2). The total number of invertebrates collected was 7272 individuals covering 26 orders (Coleoptera: 1033 individuals of 13 families) (Fig.1, Appendix 1). In PR-P and PR-M1, Collembola was abundant, especially in October. In PR-M2, Orthoptera was abundant. In the plantation forests, Amphipoda and Coleoptera were abundant. *Carabidae*, which accounted for 66% of the total number of Coleoptera, was collected mainly in the plantation forests.

The results of t-test between the primary and plantation forests showed that the N^* of invertebrates and J' and H' of Coleoptera in the primary forests were higher than in the plantation forests ($p<0.01$). PL1 showed the highest diversity of the plantation forests, and was similar to the primary forests. The N^* of the invertebrates showed that PR=PL1>PL2, PL3. The N^*, J' and H' of the Coleoptera approximately showed that PR=PL1>PL2, PL3. The J' and H' of the invertebrates showed that PR-M2>PL1>PR-M1=PL2, PL3>PR-P. The J' and H' of the invertebrates were relatively low in PR-P and PR-M1, because the number of Collembola was very abundant there. Excluding Collembola from the analyses, diversity indices in the primary forests were higher than those in the plantation forests.

In the DCA for all the invertebrates (Fig.2a) and Coleoptera (Fig.2b), the primary forests and plantation forests were clearly grouped according to Axis 1. This is because Orthoptera, Polydesmida, Collembola, *Silphidae* and *Scarabaeidae* were abundant in the primary forests, while Amphipoda, Coleoptera and

Table 2. Estimated number (N^*), homogeneity factor index (J') and diversity (H') of all the invertebrates and Coleoptera in each site.

		All the invertebrates			Coleoptera		
		N^*	J'	H'	N^*	J'	H'
PR-P	1	18.97	0.49	1.39	10.96	0.90	1.86
	2	19.96	0.60	1.69	9.96	0.91	1.77
PR-M 1	1	24.89	0.60	1.69	10.99	0.51	1.16
	2	17.99	0.64	1.80	10.93	0.88	1.57
PR-M 2	1	18.99	0.74	2.13	8.95	0.83	1.34
	2	20.96	0.74	2.15	8.99	0.83	1.72
PL 1	1	17.00	0.75	2.11	8.95	0.81	1.31
	2	18.99	0.68	1.96	12.95	0.55	1.20
PL 2	1	14.99	0.67	1.77	5.97	0.17	0.24
	2	13.99	0.69	1.78	3.97	0.10	0.07
PL 3	1	14.97	0.72	1.85	6.96	0.21	0.29
	2	13.99	0.61	1.57	6.96	0.25	0.35

Richness is the number of orders for the invertebrates, and the number of families for the Coleoptera. Diversity (H') was calculated using the Shannon-Wiener index. Study site abbreviations are the same as in Fig. 1.

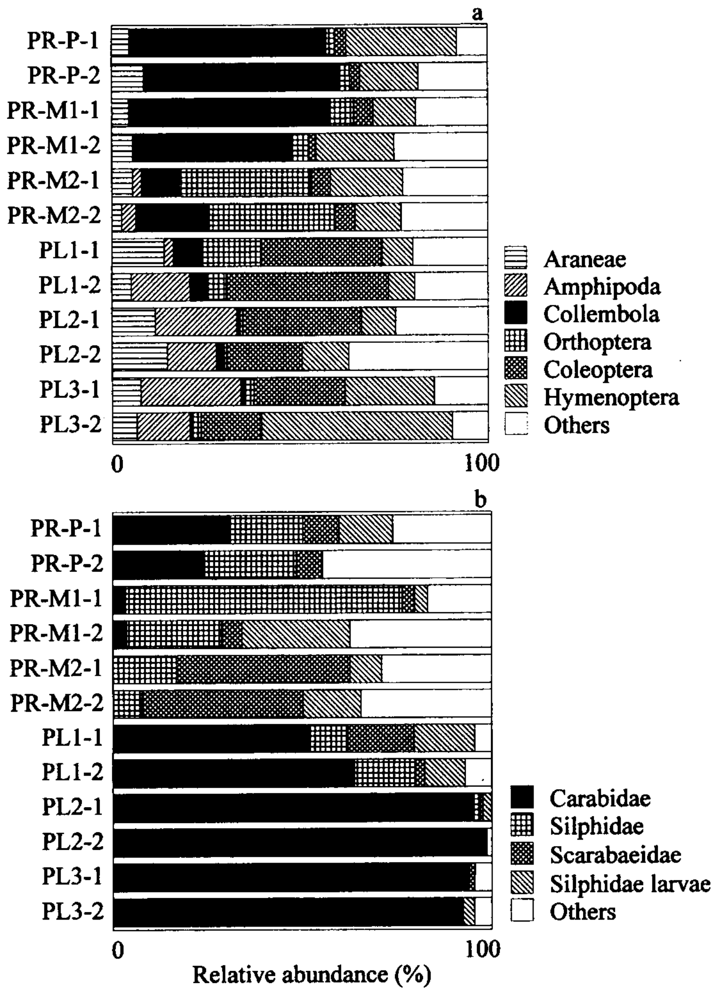

Fig. 1. Relative frequency of invertebrates per day. (a) all the invertebrates (unit: order), (b) Coleoptera (unit: family). PR-P, primary pure cedar forest; PR-M1, primary coniferous-broadleaved mixed forest 1; PR-M2, primary coniferous-broadleaved mixed forest 2; PL1, cedar forest plantation 1; PL2, cedar forest plantation 2; PL3, cedar forest plantation 3.

Carabidae were abundant in the plantation forests. The Axis 2 of the DCA for all the invertebrates and that for Coleoptera did not distinguish the forest structures. In plantation forests, the similarities between PL2 and PL3 were high, while PL1 showed a relatively high similarity to the primary forests.

Relationship between abiotic factors and forest floor biotic factors, and forest structure

The abiotic factors of primary forests showed steeper slope angle, higher soil water content, higher PFD and canopy openness, and a thinner litter layer compare to the plantation forests (Tables 1 and 3). The results of t-test showed that values of slope angle ($p<0.01$), soil water content ($p<0.01$), PFD at 2 m ($p<0.01$), and canopy openness at 2 m ($p<0.05$) in the primary forests were higher than those in the plantation forests.

DCA analysis showed that understory species composition differed clearly between primary forests and plantation forests (Fig.3). The primary forests and plantation forests were grouped according to the score of Axis 1 of the DCA. This is because *E. u. var. majus*, *A. standishii*, and *Dip. wichurae* dominated the primary forests, and *X. strumarium*, *R. palmatus*, and *Houttuynia cordata* dominated the plantation forests. Compared to the plantation stands, the similarities among primary forests were very high. PL1 showed a relatively high similarity to the primary forests.

Relationship between biotic and abiotic factors, and ground invertebrate communities

Spearman's rank correlation coefficients showed that the structures of invertebrate communities correlate strongly with understory species composition, slope angle, and PFD (Table 4a). Furthermore, the number of Araneae present correlated strongly with litter layer depth in June ($p<0.01$) and August ($p<0.01$) positively. The presence of Polydesmida and Collembola correlated strongly with the score of Axis 1 of the DCA for the understory ($p<0.001$). Orthoptera correlated strongly with the PFD at 2 m ($p<0.01$) positively, litter layer depth in June ($p<0.01$) and October ($p<0.001$) negatively, and Axis 1 for the understory ($p<0.001$). Coleoptera correlated strongly with Axis 1 for the understory ($p<0.01$), while *Scarabaeidae* correlated strongly with canopy openness at 30 cm ($p<0.01$)

positively. Understory correlated strongly with elevation, soil water content, and light conditions.

Analysis of the Spearman's rank correlation coefficients among environmental conditions showed the strong correlation between PFD and canopy openness, and that between elevation and soil water content ($p<0.001$) positively (Table 4b).

Discussion

The diversity of invertebrate communities in the primary forests was higher than in plantation forests. Some previous studies have suggested that the biological communities of plantation forests are poorer than primary forest (Watanabe and Shidei 1963; Nakamura *et al.* 1970; Dabrowska-Prot 1999). However, in PR-P and PR-M1, the J' and H' values of the invertebrates were low, since the number of Collembola was very abundant. From the viewpoint of biomass, the proportion of Collembola within the invertebrates was low, since its bodysize is very small. Excluding Collembola, the invertebrate communities in the primary forests were more diverse than in the plantation forests.

Compared to the plantation forests, PFD and canopy openness in the primary forests were higher (Table 3). Because climax forests such as the primary forests sampled in this study have some gaps and a mosaic pattern in their spatial architecture. It can be suggested that the strong positive correlation observed between elevation and soil water content was caused by the presence of the fog belt where it is moist in high altitude areas (Table 4b). Understory correlated strongly with elevation, soil water content, and light conditions. Vegetation such as the fiddlehead fern, which is distributed throughout humid environments, dominated the primary forests because of their high soil water content. This seems to have resulted in the observed differences in understory between the primary forests and plantation forests. Thus, it can be suggested that soil water content and light conditions have a direct influence on forest floor biotic factors. In this study, elevation seems to have a different influence on some abiotic factors in primary forests and plantation forests. Cedar plantation forests could not be found at the same altitude as the primary forests because cedar plantations are not successful in upper mountainous regions because of heavy snow disturbance. So we couldn't separate the influence of elevation in this study.

It can be suggested that light conditions and understory species composition most strongly influence the structures of invertebrate communities among strongly correlated factors. Light conditions are affected by forest structure and influence forest floor microclimates, such as temperature and humidity (Watts and Gibbs 2002). The structures of ground invertebrate communities seem therefore to be indirectly affected by light conditions. In this study, Coleoptera and the understory strongly correlated with light conditions. Fahy and Gormally (1998) pointed out that light plays a major role in the determination of plant and ground beetle communities. Axis 1 of the DCA for understory species composition correlated strongly with Polydesmida, Collembola, Orthoptera, and Coleoptera. The understory provides invertebrates with not only a food resource but also sufficient protection against extreme microclimate conditions, and shelter from predators (Dabrowska-Prot 1999; Nichols and Burrows 1985; Uetz 1979). Thus, the understory seems to directly influence the structures of ground invertebrate communities. In particular, the Coleoptera, which is largely composed of carnivores, strongly correlated with vegetation. Coleoptera is affected by vegetation through its role as a food resource (Fahy and Gormally 1998), for example, for polyphagous beetles and phytophagous invertebrates, which then become the prey of carnivores.

The ground invertebrate community in PL1, where Collembola and Orthoptera were relatively abundant, was relatively similar to that in the primary forests. Moreover the diversity in PL1 was higher than that in PL2 and PL3. This is partly because PL1 has been managed adequately. Therefore, the forest structure and light conditions in PL1 are more similar to the primary forests than those in PL2 and PL3 (Table 3). Furuta (1983) and Yamamoto *et al.* (1994) reported that the cedar plantation forests adjacent to primary cedar forests had abundant and diversified forest floor invertebrate fauna, since there were various niches for invertebrates such as *Carabidae*. PL1 might be such a case, since it is situated close to some primary forests. These factors seem to have caused the similarities in ground invertebrate communities between this plantation and the primary forests.

This study was an individual case study. However, the causal relationship between ground invertebrate communities and light conditions, soil water content, and forest floor biotic factors, was demonstrated. Such studies, promote a better understanding of the ecosystem of primary and plantation cedar forests, which are relatively common in Japan.

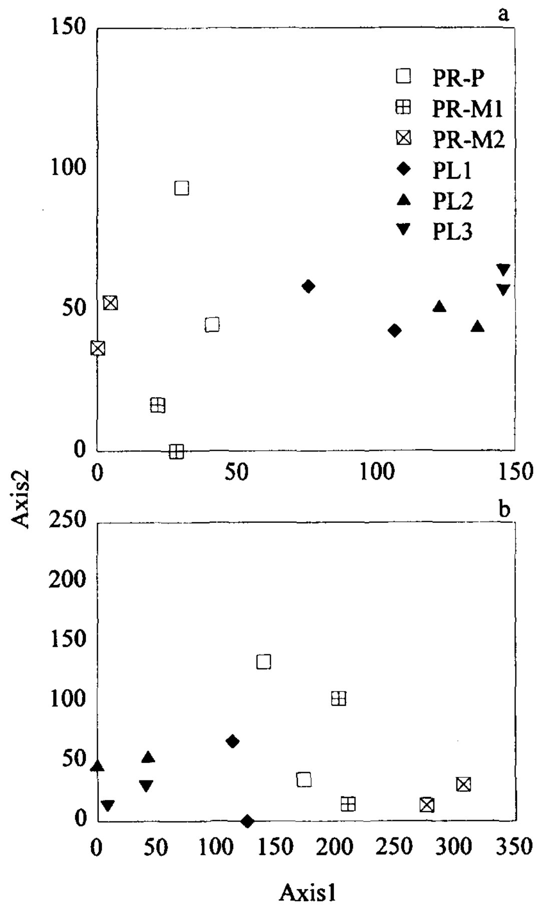

Fig. 2. DCA ordination for (a) all the invertebrates, (b) Coleoptera. The eigenvalue of each axis is: (a) Axis 1 : 0.219, Axis 2 : 0.064, (b) Axis 1 : 0.451, Axis 2 : 0.131. Abbreviations of the study sites are as in Fig. 1.

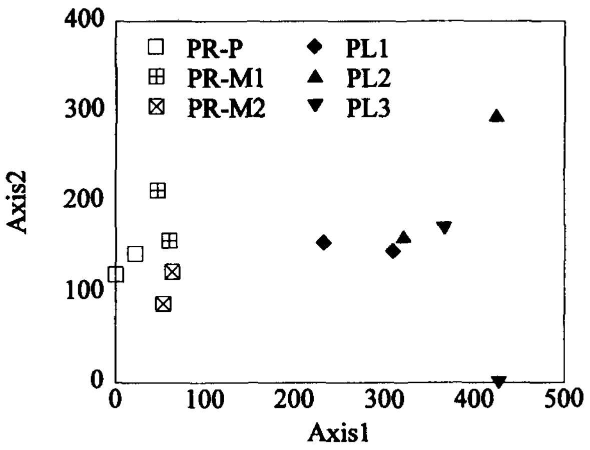

Fig. 3. DCA ordination for the understory. The eigenvalue of each axis is: Axis 1 : 0.761, Axis 2 : 0.447. Abbreviations of the study sites are as in Fig. 1.

Table 3. Environmental conditions (Mean±SE).

Site		PFD at 2m (mol/m²/day)	PFD at 30cm (mol/m²/day)	Canopy openness at 2m (%)	Canopy openness at 30cm (%)	Soil water content (%)	Litter layer depth (Jun) (cm)	Litter layer depth (Aug) (cm)	Litter layer depth (Oct) (cm)
PR-P	1	13.21±0.90	9.54±1.25	30.93±3.24	21.70±1.25	68.8	5.0±0.55	5.2±0.66	6.6±0.40
	2	14.76±1.05	10.37±1.74	30.69±2.02	21.29±2.65	79.2	6.6±0.68	4.0±0.71	5.8±0.66
PR-M 1	1	10.74±1.54	9.44±0.80	21.19±1.86	18.07±0.72	70.2	3.8±0.73	3.2±1.24	6.4±0.87
	2	11.93±2.70	8.30±1.71	25.18±2.49	14.16±0.84	74.0	6.4±0.60	4.4±0.51	6.0±1.00
PR-M 2	1	16.16±1.56	11.36±1.03	28.38±2.09	22.58±2.12	31.0	2.8±0.37	1.8±0.58	3.4±0.51
	2	15.11±0.38	14.48±0.53	28.95±0.73	26.96±0.38	42.2	2.8±0.20	2.6±0.93	3.0±0.71
PL 1	1	10.13±0.40	9.42±1.15	22.32±0.56	21.73±1.27	38.3	5.8±0.80	5.8±0.37	5.6±0.68
	2	12.76±0.56	12.45±0.43	28.37±1.32	27.48±1.43	32.1	4.8±0.58	2.0±0.89	5.8±1.83
PL 2	1	9.10±0.25	8.84±0.18	20.71±0.59	18.92±0.53	23.3	7.4±1.36	7.2±0.86	7.6±0.75
	2	7.32±0.19	7.57±0.23	17.44±0.43	17.18±0.44	24.4	7.2±1.02	6.4±1.54	7.0±1.05
PL 3	1	9.38±0.35	6.32±0.21	20.60±0.82	14.49±0.18	21.6	6.8±1.36	5.0±0.84	7.2±0.73
	2	9.15±0.30	7.56±0.60	21.29±0.84	16.85±1.06	25.8	3.4±0.68	5.2±1.11	6.6±0.75

Study site abbreviations are the same as in Fig. 1.

Table 4a. Spearman's rank correlation coefficients between each Axis1 and Axis2 of the DCA for all the invertebrates, the Coleoptera and the understory, and each Axis1 and Axis2 of the DCA for the understory and environmental conditions.

	DCA for all the invertebrates		DCA for the Coleoptera		DCA for the understory	
	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2
Axis 1 of the DCA for the understory	0.769 **	0.154	-0.720 **	-0.273		
Axis 2 of the DCA for the understory	0.203	-0.245	-0.315	0.049		
Slope angle	-0.858 ***	-0.133	0.785 **	0.074	-0.634 *	-0.105
Elevation	-0.763 **	-0.299	0.721 **	0.359	-0.956 ***	-0.193
PFD at 2m	-0.811 **	-0.133	0.860 ***	-0.238	-0.734 **	-0.532
PFD at 30cm	-0.685 *	-0.217	0.734 **	-0.070	-0.559	-0.469
Canopy openness at 2m	-0.608 *	0.021	0.699 *	-0.014	-0.769 **	-0.636 *
Canopy openness at 30cm	-0.392	-0.035	0.420	-0.056	-0.252	-0.483
Soil water content	-0.671 *	-0.182	0.692 *	0.266	-0.874 ***	-0.231
Litter layer depth (Jun)	0.508	0.263	-0.627 *	0.224	0.224	0.771 **
Litter layer depth (Aug)	0.659 *	0.319	-0.729 **	0.557	0.396	0.385
Litter layer depth (Oct)	0.747 **	0.046	-0.751 **	0.249	0.495	0.516

***:$p<0.001$, **:$p<0.01$, *:$p<0.05$

Table 4b. Spearman's rank correlation coefficients among abiotic factors and litter layer depth.

	Slope angle	Elevation	PFD at 2m	PFD at 30cm	Canopy openness at 2m	Canopy openness at 30cm	Soil water content	Litter layer depth (Jun)	Litter layer depth (Aug)
Elevation	0.583 *								
PFD at 2m	0.652 *	0.693 *							
PFD at 30cm	0.473	0.562	0.825 ***						
Canopy openness at 2m	0.368	0.738 **	0.881 ***	0.755 **					
Canopy openness at 30cm	0.207	0.257	0.608 *	0.888 ***	0.587 *				
Soil water content	0.536	0.882 ***	0.594 *	0.483	0.671 *	0.147			
Litter layer depth (Jun)	-0.381	-0.229	-0.627 *	-0.553	-0.501	-0.480	-0.277		
Litter layer depth (Aug)	-0.551	-0.368	-0.806 **	-0.680 *	-0.515	-0.459	-0.389	0.698 *	
Litter layer depth (Oct)	-0.626 *	-0.439	-0.786 **	-0.758 **	-0.653 *	-0.667 *	-0.530	0.689 *	0.696 *

***: $p<0.001$, **: $p<0.01$, *: $p<0.05$

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Appendix 1a. Number of whole invertebrate individuals caught per day (unit : order).

	PR-P		PR-M 1		PR-M 2		PL 1		PL 2		PL 3		Season		
Group	1	2	1	2	1	2	1	2	1	2	1	2	Jun	Aug	Oct
GASTROPODA															
Archaeogastropoda	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1
ANNELIDA															
Haplotaxida	2.5	1.5	2	0.5	2	3	0	1	0	2	19	14	36	3	8.5
Tubificida	2	8.5	8.5	6	4	5	1	0	0	0	1	0	5	2	29
ARACHNIDA															
Pseudoscorpiones	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0.5
Opiliones	1.5	1	2	0.5	5	5	3	7	0	2	0	1	5	22	1
Acari	1.5	3	3	10	1	2	3	2	3	3	0	0	6	12	13.5
Araneae	28.5	35.5	23	35	17	9	47	28	44	53	20	25	129	176	60
CRUSTACEA															
Decapoda	0	0	0	0	0	0	0	0	1	0	0	2	1	1	1
Isopoda	20.5	34.5	14	43.5	16	20	17	22	79	123	9	15	75	205	133.5
Amphipoda	0	0	0	0	7	13	8	84	83	47	70	54	139	202	25
DIPLOPODA															
Glomerida	0	1	2.5	0.5	9	4	0	0	0	0	0	0	1	4	12
Polydesmida	13.5	13.5	49.5	71.5	8	13	10	9	2	3	5	0	37	35	126
CHILOPODA															
Lithobiomorpha	2	4	0	1	1	0	8	1	0	0	0	1	9	9	0
Scolopendromorpha	0.5	0	0	0	0	0	1	1	0	0	0	0	0	1	1.5
Geophilomorpha	0	2	0	0	0	0	0	0	0	0	0	0	1	1	0
INSECTA															
Collembola	323	221.5	278.5	270.5	31	68	26	26	2	7	3	3	106	209	944.5
Thysanura	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Orthoptera	15	12	31.5	27.5	108	116	53	26	4	3	6	8	30	166	214
Psocoptera	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0
Hemiptera	0.5	1	1.5	1	0	2	2	23	3	0	1	0	11	19	5
Neuroptera	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Coleoptera	18	11.5	27	12.5	16	19	110	235	122	73	64	62	353	285	132
Coleoptera larvae	3	3	2.5	15.5	8	7	21	34	3	0	2	3	5	86	11
Diptera larvae	3	6	11.5	2.5	14	17	1	3	3	0	0	1	6	7	49
Lepidoptera larvae	0.5	0	2.5	7.5	1	0	0	2	1	1	1	0	2	7	7.5
Hymenoptera	182	66.5	59.5	133	60	43	28	38	35	45	63	195	247	527	174
Total	617.5	426	519.5	638.5	309	349	340	543	385	363	264	384	1205	1984	1949.5

Study site abbreviations are the same in Fig. 1.

Appendix 1b. The number of individuals per day of Coleoptera (unit : family).

Group	PR-P		PR-M 1		PR-M 2		PL 1		PL 2		PL 3		Season		
	1	2	1	2	1	2	1	2	1	2	1	2	Jun	Aug	Oct
Cicindelidae	0	0	1	0	0	0	0	3	0	0	0	0	1	3	0
Carabidae	6.5	3.5	1	1	0	0	68	171	119	72	62	60	300	148	116
Hydrophilidae	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0.5
Catopidae	0	0	0	0	1	1	0	2	0	0	0	0	0	3	1
Silphidae	4	3.5	21.5	7	4	2	13	43	2	0	0	0	25	73	2
Scaphidiidae	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Staphylinidae	2	2	1	3	0	3	6	8	0	1	1	2	14	11	4
Lucanidae	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Scarabaeidae	2	1	1	1.5	11	11	23	7	1	0	1	0	8	46	5.5
Tenebrionidae	0.5	0.5	0.5	0	0	0	0	0	0	0	0	0	0	0	1.5
Meloidae	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Chrysomelidae	2	0	0.5	0	0	0	0	0	0	0	0	0	2	0	0.5
Curculinidae	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1
Coleoptera larvae*	0	3	1.5	7.5	6	3	0	5	0	0	2	1	5	13	11
Silphidae larvae	3	0	1	8	2	4	21	29	3	0	0	2	0	73	0
Total	21	14.5	29.5	28	24	26	131	269	125	73	66	65	358	371	143

* Shilphidae larvae are not included in these values. Abbreviations of the stude sites are the same as Fig. 1.