Patterns of terricolous and field layer invertebrates along a boreal mire-forest gradient

Ola Atlegrim* & Kjell Sjöberg

Atlegrim, O. & Sjöberg, K. 2003: Patterns of terricolous and field layer invertebrates along a boreal mire-forest gradient. — Entomol. Fennica 14: 227–236.

In a study area ca. 5 km N of Umeå, Sweden, we tested the relationship between abundance and biomass of terricolous and field layer invertebrate taxa along a light gradient (consisting of four different forest habitats of boreal coniferous forests, each represented by one stand). In 1984, five sampling locations, each having 6 pitfall traps and 3 sweep-net samples, were randomly allocated in each stand. In total, 4879 terricolous invertebrates with a biomass of 63 490 mg and 1894 field-layer invertebrates with a biomass of 17 143 mg were caught. Mean values for each sampling location were used to analyse the pattern of invertebrate groups along the gradient using Spearman rank correlation ($n = 20$). There was a decrease in both abundance and biomass from shaded to sunny forests of Diptera (both terricolous and field layer), Hymenoptera (terricolous), Collembola (field layer) and Lepidoptera larvae (field layer), and for the abundance of terricolous Coleoptera and field layer Hymenoptera. An increase in both abundance and biomass from shaded to sunny forests was found for terricolous Collembola, Homoptera and Acari, and the abundance of terricolous Formicidae and Coleoptera larvae, and the biomass of field layer Hymenoptera larvae and total invertebrates. Diptera, Coleoptera and, especially, Lepidoptera larvae have earlier been shown to be important prey for several bird species breeding in the boreal forest and the high number and biomass of these taxa in the shaded forest habitats may indicate that preserving buffer zones and fragments of wet, shaded forest, currently done in forest management at final felling, is a good strategy.

*Ola Atlegrim & Kjell Sjöberg, Department of Animal Ecology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden; (*E-mail: ola.atlegrim@szooek.slu.se)*

Received 20 August 2002, accepted 12 September 2003

1. Introduction

An increasing number of studies have revealed that the occurrence of terricolous and field-layer invertebrates in Fennoscandian boreal forests varies considerably in both abundance and biomass, and that this may be explained by factors such as substrate availability, climate, frequency of specific micro-habitats, environmental requirements of different species, etc. (e.g. Forslund 1945, Huhta 1965, Huhta *et al.* 1967, 1986, Stuen 1983, Kastdalen & Wegge 1985, Kastdalen 1986, Biström & Väisänen 1988, Spidsö & Stuen 1988, Stuen & Spidsö 1988, Niemelä *et al.* 1988, 1990, 1992, 1993, 1994, Niemelä 1990, Punttila *et al.* 1991, Halme & Niemelä 1993, Pajunen *et al.* 1995). Also biotic interactions and/or relationships between species play an important role (e.g. Atlegrim 1989, 1991, Niemelä 1990, Niemelä *et al.* 1992). The frequency and intensity of disturbances are also important since they influence abiotic factors, such as solar radiation, moisture conditions, etc., which, in turn, influence the occurrence of invertebrates (e.g. Niemelä *et al.* 1993, Muona & Rutanen 1994, Atlegrim & Sjöberg 1995b, 1996).

Today, clear-cutting, followed by planting, is the main disturbance creating young stands, resulting in single-layered, even-aged and monocultural stands, quite different from the multilayered, mixed and uneven aged stands created by natural disturbance regimes (Hämet-Ahti 1983, Haila 1994, Esseen *et al.* 1997). Clear-cutting drastically changes abiotic conditions (Geiger 1961, Heliövaara & Väisänen 1984) which, in turn, affect the terricolous and field-layer invertebrate fauna (e.g. Punttila *et al.* 1991, Niemelä *et al.* 1993, Atlegrim & Sjöberg 1995b). Re-evaluating earlier studies (see above) with respect to abiotic factors, it is evident that many invertebrates show patterns at the taxonomic level of orders and/or families — particularly in relation to sunlight and moisture conditions.

Considering the intermediate trophic position of many terricolous and field-layer invertebrates, and that they contain many functional groups, patterns of invertebrates may be of considerable importance for the forest community as a whole. Such patterns may, for example, be important for habitat quality with respect to food availability for birds (Atlegrim & Sjöberg 1995a, b). Revealing and understanding the patterns of invertebrate occurrence in different types of boreal forests with separate abiotic factors also has implications for forest management, e.g. understanding which habitats are most important to protect and/or manage.

The aim of this study was to test if the abundance and biomass of terricolous and field layer invertebrate taxa were related to a light gradient. The light gradient consisted of four different forest habitat types which frequently occur in Fennoscandian boreal forests. The study was conducted in June, corresponding to the breeding season of many bird species, because we wanted to relate the occurrence of invertebrates in the light gradient to the diet of several birds (see Atlegrim & Sjöberg 1995b) and see if habitat quality with respect to food availability for bird species varied within the gradient. The results are discussed in relation to and compared with earlier studies of terricolous and field layer invertebrate occurrence in Fennoscandian boreal coniferous forests.

2. Study area

The study area of ca. 20 ha is located in the Middle Boreal Zone (Ahti *et al.* 1968), 5 km N of Umeå, Sweden (long. 63°55´N, lat. 20°22´E). It is characterised by a mosaic of dominant heath-forest stands of pine (*Pinus sylvestris* L.) and spruce (*Picea abies* L.) intermingled with small open mires fringed by narrow, wet, mire forests. Within this mosaic we selected one stand of spruce mire, mesic spruce, pine bog and pine heath forest (Table 1). These four habitats constitute forests which commonly occur in northern Swedish boreal forests. The bilberry, *Vaccinium myrtillus* L., dominated the field layer in all the studied habitats (Table 1). The spruce-mire and pine-bog forests generally have the wettest conditions followed by the mesic spruce forest, the pine heath forest is driest. However, in our study, the upper ground layer dried out in the pine-bog forest, probably due to rather sparse tree cover. Therefore, this habitat was considered to be drier compared with both the spruce-mire and mesic spruce forests. Light conditions were measured and found to differ significantly between the habitats (for methodology, see below). The forest habitats, therefore, represent a gradient with respect to sunlight reaching the field layer from the most shaded spruce mire forest to the most sunny pine-heath forest (Table 1).

3. Methods

3.1. Invertebrate sampling

Five sampling locations were randomly assigned within each of the four forest types, and six pitfall traps were placed in a randomised order at each sampling location, making up a total of 36 traps per forest type. Pitfall traps were plastic jars with depth 7 cm and diameter 7 cm. They were half-filled with 50% ethylene glycol and detergent. The traps were out from 2–28 June 1984, corresponding to the breeding season for most birds.

We used pitfall-trap data as a measure of relative occurrence of terricolous invertebrate taxa (at the family level) in order to relate their occurrence to the light gradient, not as a measure of numerical species composition. Topping and Sunderland (1992) showed that there was a high correspondence between spider densities as measured by density samples and pitfall traps for the time of season corresponding to our study. Törmälä (1982) found that the pitfall-trapping method gave fairly reliable results on relative occurrence of both spiders and other invertebrate taxa. This has also been shown for beetles in forest habitats (Niemelä *et al.* 1988). Activity of prey might be an important factor for detection by birds, and since pitfall data is a combination of both invertebrate abundance and their activity, pitfall traps may better reflect the availability of prey for birds, compared to other sampling methods.

Three sweep-net (diameter 0.25 m) samples were taken at each sampling location on June 13. Each sample consisted of 20 moving sweeps in the field layer. Sweep-net sampling can be influenced by weather conditions, so the sampling was conducted when the weather was warm and sunny. In earlier studies we have found a close correspondence between the number of herbivorous insect larvae visually counted within 10-dm^2 rings laid out in the field layer and data from sweep-net sampling (Atlegrim & Sjöberg 1996). Thus, sweep-net sampling gives an accurate measure of the occurrence of invertebrates in the field layer. Invertebrates were preserved in 70% ethanol. All invertebrates were determined to order and in some cases taxa were divided further into families and/or divided into adults (imago) and young (larvae). The individuals of each taxonomic group were counted and weighed (to the nearest 0.001 g) for each pitfall trap and sweep-net sample.

3.2. Light availability in the field layer

A Sky-sensor (type SKR 110) was used to measure the ratio of light intensity between 660 and 730 nm in micro Einstein × cm^{-2}. The values were obtained by placing the sensor beside the top leaves of the field layer. The values obtained in the forest stands were compared with values measured in full sunlight and the data for the stands is presented as the percentage of full sunlight reaching the field layer. At ten randomly chosen plots in each stand three values were measured. A mean value for each plot ($n = 3$) was calculated giving ten values for each stand. The ten values for each forest habitat were used to test differences in shading (% of full sunlight reaching the field layer) between the habitats with Tukey test ($n = 10$ in each comparison; $p < 0.05$; Zar [1984]). The four forest habitats differed significantly (Table 1) and thus did represent a light gradient.

Table 1. Characteristics of the studied forest stands. For measurement of shading, see text. The forest stands differed significantly from each other with respect to shading of the field layer (Tukey test; $n = 10$; $p < 0.05$).

Species/Factor	Spruce mire	Mesic spruce	Pine bog	Pine heath
Tree composition (%)				
Pinus sylvestris L.	1	0	51	93
Picea abies (L.)	93	100	48	6
Betula spp.	6	0.1	1	1
Vegetation type	Spruce mire *Vaccinium myrtillus* type [1]	Spruce heath forest of *Vaccinium myrtillus* -type [2]	Mixture of “true dwarf-shrub pine bog” and spruce mire of *Vaccinium myrtillus* type [1]	Dry pine heath forest of *Empetrum-Myrtillus* -type [2]
Moisture	wet	mesic	wet	dry
Shading (% of full sunlight reaching the field layer	70	79	91	96
Dominating field-layer species	*V. myrtillus*	*V. myrtillus*	*V. myrtillus*	*V. myrtillus*
Co-dominating field layer species	*V. vitis-idaea* *Rubus chamaemorus*	*V. vitis-idaea*	*V. vitis-idaea*	*V. vitis-idaea*

[1] Terminology follows Eurola *et al.* (1984); [2] terminology follows Kalela (1961).

3.3. Statistical analysis

A mean value for each sampling location was calculated based on the six pitfall traps and three sweep-net samples. Mean values were calculated for the abundance and biomass of each taxonomic group, the total abundance and biomass for invertebrates in the field layer (sweep-net samples), and, the total abundance and biomass with and without ants for terricolous invertebrates (pitfall traps). The four forest habitats constituted a gradient with respect to light conditions in the following order, from the most shaded to most sunny: (1) spruce-mire, (2) mesic spruce, (3) pine-bog and (4) pine-heath forest. We used the mean values for each sampling location in each forest habitat ($n = 5$ for each habitat; total $n = 20$) to determine how the abundance and biomass of different taxonomic groups were related to the light gradient using Spearman rank correlation (Zar 1984), since the assumptions for a parametric test (normality and homoscedasticity) could not be fulfilled.

4. Results

A total of 4879 terricolous invertebrates with a biomass of 63 490 mg including representatives from nine invertebrate groups were caught in the pitfall traps (Table 2). Within the field layer, we found representatives from 12 invertebrate groups with a total of 1894 individuals and a biomass of 17 143 mg (Table 3). Among the terricolous groups Collembola, Diptera, Hymenoptera, Formicidae, Coleoptera and Aranea dominated with respect to abundance, while Diptera, Formicidae, Coleoptera and Aranea dominated with respect to biomass (Table 2). The field layer was dominated with respect to abundance by Lepidoptera larvae, Nematocera, Diptera, Hymenoptera and Aranea while Lepidoptera larvae together with Hymenoptera larvae, Coleoptera and Araneae dominated with respect to biomass (Table 3).

We found several significant relationships between the occurrence of invertebrate groups and the light gradient. The abundance and biomass of terricolous Collembola, Homoptera, Coleoptera

Table 2. Mean values (M) and ± 1 SE (SE) of abundance (A) and biomass (B) of terricolous invertebrate groups caught in this study with pitfall traps. The light gradient consisted of one stand of (from the most shaded to the most sunny habitat): Spruce mire, Mesic spruce, Pine bog and Pine heath. Mean values and SE are based on mean values for five randomly-selected sampling locations in each stand, and the mean values in each sampling location are based on six pitfall traps.

		Spruce mire		Mesic spruce		Pine bog		Pine heath	
		A	B	A	B	A	B	A	B
Collembola	M	10.0	4.7	11.8	15.0	12.6	6.0	15.3	13.0
	SE	1.7	0.8	1.6	7.3	1.7	0.4	1.4	1.4
Diptera	M	7.2	62.2	5.0	29.8	3.5	31.3	4.0	12.5
	SE	1.2	12.7	0.4	6.1	0.5	3.9	0.8	2.5
Homoptera	M	0.3	0.5	0.0	0.0	0.5	0.6	0.7	1.0
	SE	0.1	0.3	0.0	0.0	0.2	0.2	0.1	0.2
Hymenoptera	M	6.7	4.7	6.0	2.8	2.6	1.1	2.1	1.2
	SE	1.7	2.0	1.0	0.2	0.8	0.2	0.5	0.3
Formicidae	M	3.1	88.8	9.6	213.0	7.9	68.0	18.5	368.5
	SE	1.4	37.5	5.6	163.0	2.2	18.3	5.4	175.2
Coleoptera	M	3.4	42.6	2.9	39.6	1.2	104.1	1.6	45.2
	SE	0.6	9.8	0.3	10.2	0.3	61.1	0.3	17.4
Coleoptera, larvae	M	0.2	0.6	0.2	0.3	1.8	4.2	0.6	0.6
	SE	0.1	0.5	0.1	0.1	0.4	1.5	0.3	0.2
Acari	M	0.9	0.7	0.3	0.3	1.4	1.4	3.5	10.3
	SE	0.1	0.1	0.1	0.1	0.4	0.4	1.2	3.5
Araneae	M	3.6	25.7	2.5	15.0	2.7	18.0	3.4	44.9
	SE	0.7	7.1	0.3	3.8	0.5	2.5	0.4	18.3
Total (excl. ants)	M	34.5	412.7	30.8	339.9	27.7	272.9	34.1	408.6
	SE	3.2	46.2	2.9	36.2	2.7	74.6	2.7	76.0
Total (incl. ants)	M	37.6	501.5	40.4	552.9	36.6	340.9	52.5	777.1
	SE	3.7	75.7	4.7	139.1	4.0	84.4	6.5	167.4

larvae and Acari increased from the shaded to the sunny forest habitat, while the opposite pattern was found for Diptera and Hymenoptera (excluding ants) (Table 4, terricolous invertebrates). In addition, the abundance of Formicidae increased while the abundance of Coleoptera decreased from shade to sunny forest habitats (Table 4, terricolous invertebrates). In the field layer both the abundance and biomass of Diptera, Collembola and Lepidoptera larvae decreased from shaded to sunny forest habitats (Table 4, field layer). Further, the abundance of Hymenoptera decreased while the biomass of Hymenoptera larvae (Hymenoptera: Symphyta) increased from shaded to sunny forests (Table 4, field layer). Also, the total biomass of invertebrates decreased from shaded to sunny forests (Table 4, field layer).

5. Discussion

We found that the abundance of terricolous Formicidae increased from the shaded to sunny forests, in agreement with Biström and Väisänen (1988). Ants constitute an important group from several ecological aspects (Petal 1978, Wilson 1990, Hölldobler & Wilson 1990, Cole *et al.* 1992, Way & Khoo 1992, Woodman & Price 1992, Punttila *et al.* 1994) and patterns of ants in forests seems to be dependent on the species composition of the ant fauna, especially the extent to which red wood ants (*Formica* spp.) dominate. Such species are known to found large, multi-nest colonies with high densities of workers (Douwes 1976, Collingwood 1979, Douwes 1981, Nilsson & Douwes 1987, Douwes 1995), and especially

Table 3. Mean values (M) and ± 1 SE (SE) of abundance (A) and biomass (B) of field-layer invertebrate groups caught with sweep-net sampling in this study. The light gradient consisted of one stand of (from the most shaded to the most sunny habitat): Spruce mire, Mesic spruce, Pine bog and Pine heath. Mean values and SE based on mean values for five randomly selected sampling location in each forest stand, and the mean values in each sampling location is based on three sweep-net samples.

		Spruce mire		Mesic spruce		Pine bog		Pine heath	
		A	B	A	B	A	B	A	B
Collembola	M	2.6	0.9	2.1	1.0	0.5	0.5	0.2	0.3
	SE	0.9	0.2	0.6	0.3	0.2	0.1	0.1	0.2
Homoptera	M	0.3	0.9	0.5	0.7	1.0	2.1	0.2	0.1
	SE	0.1	0.4	0.2	0.4	0.2	0.5	0.2	0.1
Lepidoptera, larvae	M	4.6	431.1	2.7	224.5	1.2	13.0	1.8	10.1
	SE	0.3	18.3	0.2	32.2	0.3	5.2	0.4	2.7
Nematocera	M	3.3	2.9	6.2	4.4	1.6	1.2	3.7	6.1
	SE	0.5	0.5	1.5	1.1	0.4	0.4	1.3	2.7
Diptera	M	3.0	13.8	2.1	6.8	1.7	7.6	0.5	0.5
	SE	1.0	5.8	0.8	2.8	0.3	3.3	0.3	0.2
Hymenoptera	M	2.9	1.4	3.8	2.9	2.3	4.7	1.8	2.1
	SE	0.2	0.2	0.7	1.3	0.6	1.7	0.1	0.6
Hymenoptera, larvae	M	0.8	19.9	1.7	35.7	1.3	32.6	2.4	68.5
	SE	0.2	5.4	0.2	5.5	0.3	8.3	1.2	31.4
Formicidae	M	0.2	0.8	0.5	2.3	2.0	8.5	0.9	3.1
	SE	0.2	0.6	0.4	2.2	1.1	4.9	0.4	1.8
Coleoptera	M	0.6	4.1	1.2	11.1	1.8	15.9	0.9	3.7
	SE	0.2	2.5	0.4	4.9	0.4	5.3	0.1	1.6
Coleoptera, larvae	M	0.1	0.3	0.1	0.1	0.9	2.0	0.1	0.1
	SE	0.1	0.2	0.1	0.1	0.3	0.9	0.1	0.1
Acari	M	0.1	0.1	0.3	0.3	0.7	0.3	1.7	0.3
	SE	0.1	0.1	0.1	0.1	0.2	0.1	1.2	0.2
Araneae	M	4.6	6.4	9.8	11.3	6.7	22.3	3.5	8.5
	SE	0.7	1.8	2.3	2.7	1.0	2.3	0.9	3.4
Total	M	24.1	484.7	33.8	306.0	23.3	115.6	18.4	109.8
	SE	2.4	20.8	5.7	39.0	3.6	20.2	4.4	37.6

Formica aquilonia Yarrow, which dominated in the current study, is known to have high worker densities in open and moderately shaded forest habitats (Punttila *et al.* 1991, 1994).

Data from Huhta *et al.* (1967) indicates that abundance of both Acari and Coleoptera larvae decrease from shaded to sunny forests. Our data showed an opposite pattern. However, the results of Huhta *et al.* (1967) were based on litter and humus samples showing a snapshot picture, whereas our pitfall trap data cover longer sampling period. Additionally, a certain proportion of the fauna living in the soil will not be caught by our pitfall traps. We found a significant decrease in the abundance of terricolous Coleoptera from shaded to sunny forests, in agreement with Biström and Väisänen (1988). Earlier studies on terricolous beetles, especially terricolous carabid beetles (Coleoptera: Carabidae), have shown variation in occurrences among habitats; population dynamics and presence/absence of certain microhabitat sites seem to be the mechanisms for much of this variation (Biström & Väisänen 1988, Niemelä 1990, Niemelä *et al.* 1990, 1992). Coleoptera may also be negatively affected by the presence of ants (Niemelä 1990, Niemelä *et al.* 1992) and we also found such a negative relationship since the abundance of Formicidae increased while Coleoptera decreased from shaded to sunny forests.

Table 4. The abundance and biomass of terricolous and field-layer invertebrate groups along a light gradient from shaded to sunny boreal forests. The gradient consisted of one stand of (from the most shaded to the most sunny forest habitat): Spruce mire, Mesic spruce, Pine bog and Pine heath. The data were analysed with Spearman rank correlation (r_s is the correlation coefficient and p the significance level; $n = 20$), based on mean values of five randomly-selected sampling locations in each stand. The mean values for each sampling location for terricolous groups were based on six pitfall traps and for field layer groups based on three sweep-net samples. NS = not statistically significant.

		Abundance		Biomass	
Group	Taxa	r_s	p	r_s	p
Terricolous					
	Collembola	0.478	<0.05	0.557	<0.01
	Diptera	–0.596	<0.01	–0.780	<0.01
	Homoptera	0.536	<0.01	0.469	<0.05
	Hymenoptera	–0.655	<0.01	–0.664	<0.01
	Formicidae	0.723	<0.01	0.357	NS
	Coleoptera	–0.668	<0.01	–0.155	NS
	Coleoptera larvae	0.454	<0.05	0.383	NS
	Acari	0.490	<0.05	0.716	<0.01
	Araneae	0.055	NS	0.101	NS
	Total excl. ants	0.089	NS	–0.155	NS
	Total	0.322	NS	0.217	NS
Field layer					
	Collembola	–0.778	<0.01	–0.524	<0.05
	Homoptera	–0.040	NS	0.267	NS
	Lepidoptera larvae	–0.764	<0.01	–0.876	<0.01
	Nematocera	–0.242	NS	–0.105	NS
	Diptera	–0.496	<0.05	–0.518	<0.05
	Hymenoptera	–0.513	<0.05	0.230	NS
	Hymenoptera larvae	0.284	NS	0.489	<0.05
	Formicidae	0.347	NS	0.309	NS
	Coleoptera	0.308	NS	0.109	NS
	Coleoptera larvae	0.053	NS	0.035	NS
	Acari	0.316	NS	–0.250	NS
	Araneae	–0.272	NS	0.202	NS
	Total	–0.318	NS	–0.884	<0.01

In agreement with earlier studies (Stuen 1983, Spidsö & Stuen 1988, Stuen & Spidsö 1988), we found that the abundance and biomass of Diptera decreased from shaded to sunny forests. The pattern found in our study was mainly caused by high abundance and biomass of Dolichopodidae in the shaded forests. The abundance and biomass of terricolous Hymenoptera as well as the abundance of Hymenoptera in the field layer decreased from shaded to sunny forests, in agreement with Stuen and Spidsö (1988). A high proportion of the Hymenoptera in our study are parasitoids and might be related to the pattern of herbivorous Lepidoptera larvae (see below).

The abundance and biomass of terricolous Homoptera increased from shaded to sunny forests. White (1970 and references therein) found that high concentrations of soluble nitrogenous compounds in their food plant was favourable for psyllids (Homoptera: Psyllidae). High concentrations of soluble nitrogen may be produced in plants receiving high solar radiation and/or being under water stress (White 1984), corresponding to the conditions for field layer plants in sunny forests and may offer one explanation for the observed pattern in the present study. Another possible (or contributing) reason for the observed pattern may be that ants tend many species of Homoptera (Larsson 1943), and both groups had high abundance in sunny forests. In accordance with earlier studies (Atlegrim 1989, Atlegrim & Sjöberg 1996) the biomass of Hymenoptera larvae increased from shaded to sunny forests. We have no explanation for the increase of terricolous Collembola from shaded to sunny forests and the opposite pattern shown by field layer Collembola, or why terricolous and field-layer Collembola showed opposite patterns.

We found a significant decrease in both the abundance and biomass of Lepidoptera larvae from shaded to sunny forests, in accordance with other studies (Stuen 1983, Kastdalen & Wegge 1985, Kastdalen 1986, Atlegrim 1991, Atlegrim & Sjöberg 1996). We suggest that this pattern can be explained by a change in the composition of Lepidoptera larvae, availability and quality of the food plant bilberry and ant predation along the gradient. We observed that geometrid larvae (Geometridae) decreased from shaded to sunny forests while tortricids and pyralids (Tortricidae and Pyralidae) showed the opposite pattern. Geometrid larvae are relatively large and heavy which partly may explain the decrease in biomass from shaded to sunny forests. Holliday (1985) concluded that high temperatures may be injurious for winter moth larvae (*Operophtera brumata* L.), a geometrid larvae which dominated in our study. Atlegrim (1991) showed that, compared to sunny habitats, bilberry (the main food plant in the field layer) in shaded habitats has a lower concentration of phenols, and a higher concentration of nitrogen and water. For leaf-eating larvae, such as the geometrid larvae feeding on bilberry (Atlegrim 1991), low water concentration usually indicates high leaf toughness which negatively influence the feeding of leaf eating larvae (e.g. Stamp & Bowers 1990), and Feeny (1968, 1970) found, besides that increased leaf toughness prevented larval feeding, that the growth rate and pupal weight of *O. brumata* were reduced by increasing levels of tannin (a phenolic acid). In contrast, pyralids and tortricids mainly feed on the reproductive parts of bilberry, and bilberry growing in sunny forests has higher reproduction compared to shaded habitats (Atlegrim 1991). Predation from ants has been found to considerably reduce the abundance of Lepidoptera larvae, especially leaf-eaters (Laine & Niemelä 1980, Niemelä & Laine 1986). Geometrid larvae, which crawl on the leaves while feeding are more exposed to bird predation (Atlegrim 1989, 1991, 1992, Atlegrim & Sjöberg 1995a), and may also be more exposed to ant predation, compared to tortricids and pyralids which conceal themselves more by feeding inside bilberry leaves they have spun together. Thus, a change in the composition of the Lepidoptera larvae group together with changes in the food plant bilberry with respect to availability (leaf and reproductive parts) and quality (leaf chemistry and leaf toughness), and ant predation may explain our observed decrease in Lepidoptera larvae from shaded to sunny forests, both in abundance and biomass. We also found, as did earlier studies (Stuen 1983, Kastdalen 1986, Spidsö & Stuen 1988, Stuen & Spidsö 1988) that the total biomass of invertebrates in the field layer decreased from shaded to sunny forests, which in our study was caused by a high abundance of Lepidoptera larvae, especially geometrids, in the shaded forests.

Our study was conducted in June, the breeding season for many species of insectivorous birds in the boreal forest. Atlegrim and Sjöberg (1995b) compiled literature data on the prey of bird species breeding in the boreal forest and showed that Lepidoptera larvae were utilised as prey by 81% of the bird species included in the study, followed in decreasing order by Araneae, Coleoptera, Formicidae, Hymenoptera larvae, Diptera and Homoptera. For several of these invertebrate groups we found significant patterns in the studied gradient (see above). Field layer Lepidoptera larvae and terricolous Coleoptera (abundance), two invertebrate groups used by many bird species (Atlegrim & Sjöberg 1995b), showed a significant decrease from shaded to sunny forests and also both field layer and terricolous Diptera showed the same pattern. In contrast, Formicidae, Hymenoptera larvae and Homoptera showed the opposite pattern, while Araneae showed no significant pattern in the gradient. Taken together, these results indicate that shaded forests have a higher food availability of invertebrate groups used by several birds, especially with respect to Lepidoptera larvae (which are an important prey during the breeding season; see Atlegrim & Sjöberg [1995b], and references therein), Coleoptera and Diptera. Even though we found higher abundance of Formicidae, Hymenoptera larvae and Homoptera in sunny forests these are utilized by far fewer bird species (Atlegrim & Sjöberg 1995b). In Scandinavia, much emphasis is currently placed on preserving buffer zones and fragments of wet, shaded forests in forest management during final felling. In this perspective our data indicates that this may well be a good strategy because food availability for birds, especially during the breeding season, seems to be high in these habitats.

Fluctuations in abundance and biomass of invertebrates may occur between years (e.g. Stuen & Spidsö 1988). Our pitfall data show relative abundance and biomass, and sweep-net data give a momentary picture of the invertebrate community during one season. Our results should, therefore, be interpreted with some caution, and we suggest additional studies. As it now stands, however, our data are consistent with current management practices to retain fragments of wet, shaded forests.

6. Conclusions

Our results showed that there are patterns in abundance and biomass of invertebrate groups along a gradient from shaded to sunny forests. Within the terricolous group, we found contrasting results, since Collembola, Homoptera, Acari, Formicidae and Coleoptera larvae increased from shaded to sunny forests while Diptera, Hymenoptera and Coleoptera showed the opposite pattern. Within the field layer, most groups were found to decrease from shaded to sunny forest including Collembola, Lepidoptera larvae, Diptera, Hymenoptera and the total biomass of invertebrates, while Hymenoptera larvae increased. We suggest that the pattern may be explained by changes in the composition of the group, food plant availability and quality, and ant predation along the gradient.

Our study was conducted during the bird breeding season (June), so it has implications with respect to food availability for birds. Today, forestry aims at protecting buffer zones and wet, shaded forest fragments at final felling. Our data are consistent with the idea that this is a good strategy, since we found, in addition to a higher total biomass of invertebrates in the field layer, a high abundance and/or biomass of invertebrate groups, such as Lepidoptera larvae and Coleoptera (both important prey for birds during the breeding season), in shaded forests.

Acknowledgements. We would like to express out gratitude to John P. Ball for comments on the manuscript. The study was supported by the Swedish Environmental Protection Agency (SNV).

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5: 169–211.

Atlegrim, O. 1989: Exclusion of birds from bilberry stands: impact on insect larvae density and damage to the bilberry. — Oecologia 79: 136–139.

Atlegrim, O. 1991: Interactions between the bilberry (*Vaccinium myrtillus*) and a guild of insect larvae in boreal coniferous forest. — Ph.D. Thesis, Report 19, Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Umeå, Sweden.

Atlegrim, O. 1992: Mechanisms regulating bird predation on a herbivorous larva guild in boreal coniferous forests. — Ecography 15: 19–24.

Atlegrim, O. & Sjöberg, K. 1995a: Lepidoptera larvae as food for capercallie chicks (*Tetrao urugallus*): a field experiment. — Scand. J. For. Res. 10: 278–283.

Atlegrim, O. & Sjöberg, K. 1995b: Effects of clear-cutting and selective felling in Swedish boreal coniferous forest: response of invertebrate taxa eaten by birds. — Entomol. Fennica 6: 79–90.

Atlegrim, O. & Sjöberg, K. 1996: Comparison of invertebrate abundance and biomass between a clear-cut stand and four stands under tree cover in Swedish boreal coniferous forests. — Entomol. Fennica 7: 17–27.

Biström, O. & Väisänen, R. 1988: Ancient-forest invertebrates of the Pyhän-Häkki national park in central Finland. — Acta Zool. Fennica 185: 1–69.

Cole, F. R., Medeiros, A. C., Loope, L. L. & Zuehlke, W. W. 1992: Effect of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrublands. — Ecology 73: 1313–1322.

Collingwood, C. A. 1979: The Formicidae (Hymenoptera) of Fennoscandia and Denmark. — Fauna Entomologica Scandinavica, Vol. 8, Scandinavian Science Press Ltd, Klampenborg, Denmark. 174 pp.

Douwes, P. 1976: Sveriges myror — illustrerade bestämningstabeller över arbetarna. — Entomologen 5: 37–54. [In Swedish].

Douwes, P. 1981: Identification key for the workers of the Formica rufa group in Sweden. — Ent. Tidskr. 102: 80–82. [In Swedish with English abstract].

Douwes, P. 1995: The Swedish ants. — Ent. Tidskr. 116: 83–99. [In Swedish with English abstract].

Eurola, S., Hicks, S. & Kaakinen, E. 1984: Key to Finnish mire types. — In: Moore, P. D. (ed.), European mires: 11–117. Academic Press, London, England.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997: Boreal forests. — Ecol. Bull. 46: 16–47.

Feeny, P. P. 1968: Effects of oak leaf tannins on larval growth of the winter moth *Operophtera brumata*. — J. Insect Physiol. 14: 805–814.

Feeny, P. P. 1970: Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. — Ecology 51: 567–581.

Forslund, H. 1945. Studier över det lägre djurlivet i nordsvensk skogsmark. — Meddel. Statens Försöksanst. 34: 1–283. [In Swedish].

Geiger, R. 1961: Das klime der bodennahen Luftschicht. 4th ed. — Braunschweig, Germany. 646 pp.

Haila, Y. 1994: Preserving biological diversity in boreal forests: ecological background, research and management. — Ann. Zool. Fennici 31: 203–217.

Halme, E. & Niemelä, J. 1993: Carabid beetles in fragments of coniferous forests. — Ann. Zool. Fennici 30: 17–30.

Heliövaara, K. & Väisänen, R. 1984: Effects of modern forestry on northwestern European forest invertebrates — a synthesis. — Acta For. Fenn. 189: 1–32.

Holliday, N. J. 1985: Maintenance of the phenology of winter moth (Lepidoptera: Geometridae). — Biol. J. Linn. Soc. 25: 221–234.

Huhta, V. 1965: Ecology of spiders in the soil and litter of Finnish forests. — Ann. Zool. Fennici 2: 260–308.

Huhta, V., Karppinen, E., Nurminen, M. & Valpas, A. 1967: Effects of silvicultural practices upon arthropod, annelid and nematode populations in coniferous forest soil. — Ann. Zool. Fennici 4: 87–145.

Huhta, V., Hyvönen, R., Kaasalainen, P., Koskenniemi, A., Muona, J., Mäkelä, I., Sulander, M. & Vilkamaa, P. 1986: Soil fauna of Finnish coniferous forests. — Ann. Zool. Fennici 23: 345–360.

Hämet-Ahti, L. 1983: Human impact on closed boreal forest (Taiga). — In: Holzner, W., Werger, M. J. A. & Ikusima, I. (eds.), Man's impact on vegetation: 201–211. Junk, Hague, Netherlands.

Hölldobler, B. & Wilson, E. 1990: The ants. — Harvard Univ. Press, Cambridge, MA, USA. 733 pp.

Kalela, A. 1961: Waldsvegetationszonen Finlands und ihre Klimatische Parallelltypen. — Arch. Soc. Bot. Fenn. 'Vanamo' 16: 65–83.

Kastdalen, L. 1986: Food selection in capercallie and black grouse chicks in South-East Norway. — M.Sc. thesis, University of Oslo, Oslo, Norway. [In Norwegian with English summary].

Kastdalen, L. & Wegge, P. 1985: Animal food in capercallie and black grouse chicks in South East Norway — a preliminary report. — In: Hudson, P. J. & Lovel, T. W. I. (eds.), Proceedings of the 3rd International Grouse Symposium: 499–509. World Pheasant Association, Reading, and International Council for Game and Wildlife Conservation, York, England, 1984.

Laine, K. J. & Niemelä, P. 1980: The influence of ants on the survival of Mountain Birches during an *Oporinia autumnata* (Lep., Geometridae) outbreak. — Oecologia 47: 39–42.

Larsson, S. G. 1943: Myrer. — Danmarks Fauna, Bd. 49, G.E.C. Gads forlag, Köbenhavn, Denmark. 149 pp.

Muona, J. & Rutanen, I. 1994: The short-term impact of fire on the beetle fauna in boreal coniferous forest. — Ann. Zool. Fennici 31: 109–122.

Niemelä, J. 1990: Spatial distribution of Carabid beetles in the southern Finnish taiga: the question of scale. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 191–200. Intercept Ltd, Andover, Hampshire, England.

Niemelä, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. & Punttila, P. 1988: The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forests. — Ann. Zool. Fennici 25: 107–119.

Niemelä, J., Haila, Y., Halme, E., Pajunen, T. & Punttila, P. 1990: Diversity variation in carabid assemblages in the southern Finnish taiga. — Pedobiologia 34: 1–10.

Niemelä, J., Haila, Y., Halme, E., Pajunen, T. & Punttila, P. 1992: Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. — J. Biogeography 19: 173–181.

Niemelä, J., Spence, J. R., Langor, D., Haila, Y. & Tukia, H. 1993: Logging and boreal ground-beetle assemblages on two continents: implications for conservation. — In: Gaston, K. J., New, T. R. & Samways, M. J. (eds.), Perspectives in insect conservation: 29–50. Intercept Ltd, Andover, Hampshire, England.

Niemelä, J. Tukia, H. & Halme, E. 1994: Pattern of carabid diversity in Finnish mature taiga. — Ann. Zool. Fennici 31: 123–130.

Niemelä, P. & Laine, K. 1986: Green islands — predation not nutrition. — Oecologia 68: 476–478.

Nilsson, O. & Douwes, P. 1987: Key to the ants of northern Sweden. — Natur i Norr 6: 49–90. [In Swedish with English summary].

Paine, R. T. 1969: A note on trophic complexity and community stability. — Am. Nat. 103: 91–93.

Pajunen, T., Haila, Y., Halme, E., Niemelä, J. & Punttila, P. 1995: Ground-dwelling spiders (Arachnida, Aranae) in fragmented old forests and surrounding managed forests in southern Finland. — Ecography 18: 62–72.

Petal, J. 1978: The role of ants in ecosystems. — In: Brian, M. V. (ed.), Production ecology of ants and termites: 293–325. Cambridge Univ. Press, Cambridge, England.

Punttila, P., Haila, Y., Pajunen, T. & Tukia, H. 1991. Colonisation of clearcuts by ants in the southern Finnish taiga: a quantitative survey. — Oikos 61: 250–262.

Punttila, P., Haila, Y., Niemelä, J. & Pajunen, T. 1994: Ant communities in fragments of old-growth taiga and managed surroundings. — Ann. Zool. Fennici 31: 131–144.

Spidsö, T. K. & Stuen, O. H. 1988. Food selection by capercallie chicks in southern Norway. — Can. J. Zool. 66: 279–283.

Stamp, N. E. & Bowers, M. D. 1990: Phenology of nutritional differences between new and mature leaves and its effect on caterpillar growth. — Ecol. Entomol. 15: 447–454.

Stuen, O. H. 1983: Storfugelkyllingenes (*Tetrao urogallus*) naeringvalg i Vegårshei om sommaren. — Institutt for naturforvaltning, ÅS-NHL.

Stuen, O. H. & Spidsö, T. K. 1988: Invertebrate abundance in different forest habitats as animal food available to capercallie *Tetrao urogallus* chicks. — Scan. J. For Res. 3: 527–532.

Topping, C. J. & Sunderland, K. D. 1992: Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. — J. Appl. Ecol. 29: 485–491.

Törmälä, T. 1982: Evaluation of five methods of sampling field layer arthropods, particularly the leafhopper community, in grassland. — Ann. Entomol. Fenn. 48: 1–16.

Way, M. J. & Khoo, K. C. 1992: Role of ants in pest management. — Ann. Rev. Entomol. 37: 479–503.

White, T. C. R. 1970: Some aspects of life history, host selection, dispersal, and oviposition of adult *Cardiaspina densitexa* (Homoptera: Psyllidae). — Aust. J. Zool. 18: 105–117.

White, T. C. R. 1984: The abundance of invertebrate herbivores in relation to the availability of nitrogen. — Oecologia 63: 90–105.

Wilson, E. O. 1990: Success and dominance in ecosystems: the case of the social insects. — In: Kinne, O. (ed.), Excellence in ecology: 1–104. Konrad Triltsch, Graphischer Betreib, Wurzburg, F.R. Germany.

Woodman, R. L. & Price, P. W. 1992: Differential larval predation by ants can influence willow sawfly community structure. — Ecology 73: 1028–1037.

Zar, J. H. 1984: Biostatistical analysis. — Prentice-Hall International Inc., Engelwood Cliffs, New Jersey, USA. 718 pp.