Altitudinal zonation of the invertebrate fauna on branches of birch (*Betula pubescens* Ehrh.)

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The invertebrate fauna on branches of birch (*Betula pubescens* Ehrh.) was investigated during 1967 at Sogndal, western Norway, by sweep-netting at the following altitudes: 10–40 m, 250–300 m, 450–500 m, 650–700 m, and 850–900 m. From the lowest to the highest station, the following numbers of Heteroptera species were recorded: 12, 5, 4, 3, 0; of Cicadidae: 11, 10, 7, 3, 2; of Coleoptera: 21, 16, 18, 13, 8; and of Araneida: 9, 5, 8, 2, 1. The generally low number of species above 500 m accompanies a change from mixed forest to an almost purely birch forest. The density of Araneida, Heteroptera, and *Anthocoris nemorum* (L.) (Het.) decreased greatly with increasing altitude. Cicadidae showed similar densities up to 500 m, but markedly lower densities above. Psocoptera was most numerous in the middle of the gradient. Predators and parasites collectively decreased greatly in density with increasing altitude. Total invertebrate densities were lowest above 500 m. The material that year was dominated by larvae of Geometridae (Lep.), which had a mass occurrence during 1966–67. Trophic relationships at different altitudes are discussed.

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Some invertebrate groups have been investigated with respect to the altitudinal zonation of their species composition. Among these investigations are Lindberg's (1945) study of the Heteroptera-fauna in the mountains of Bulgaria, Lindroth's (1949) study of Carabidae (Col.) in Scandinavia, a study of the same group by Ponomarchuk (1963) in the Carpates, a study of the zonation of Lamellicornia (Col.) species by Pek (1961) in the Kirgisia Mountains north of the Himalayas, and Kopaneva's (1962) work on Orthoptera in the Caucasian Mountains. The general trend seems to be that, within a given taxonomic group, the number of species decreases with increasing altitude. This is, however, not always the case. In a study of Araneida in Chile, Zapfe (1961) found the highest number of species in the middle ranges of the gradient.

Most species seem to have a vertical occurrence which includes the lowlands and is limited upwards. A few species may be endemic for high altitudes. Species endemic to certain sections of the altitudinal gradient have been identified in Orthoptera by Pravdin (1965) and in Lepidoptera by Kuznetsov (1958). The vertical occurrence of a given species is usually continuous, but the density may vary much over the range of occurrence.

In most such studies, the intention has been to record the total number of species at different altitudes. The altitudinal zonation of the total number of species depends on many factors, among which the altitudinal zonation of vegetation communities is of high importance. However, if the habitat could be kept relatively constant, the changes in species composition would mainly be a response to changing climate. Of course, biotic factors such as predators, parasites, or competing species may still be relevant. However, maintaining constant habitat greatly standardizes the situation.

In this study, branches of birch (*Betula pubescens* Ehrh.) were chosen as the habitat. The field work was performed during 1967 on a rather steep mountain slope near Sogndal, Sogn og Fjordane County, in the western port of South Norway. That year, the density

Fig. 1. Part of the forest at the lowest station, 10–40 m a.s.l. The most common tree species besides birch are *Prunus padus* L., *Sorbus aucuparia* L., and *Tilia cordata* Mill.

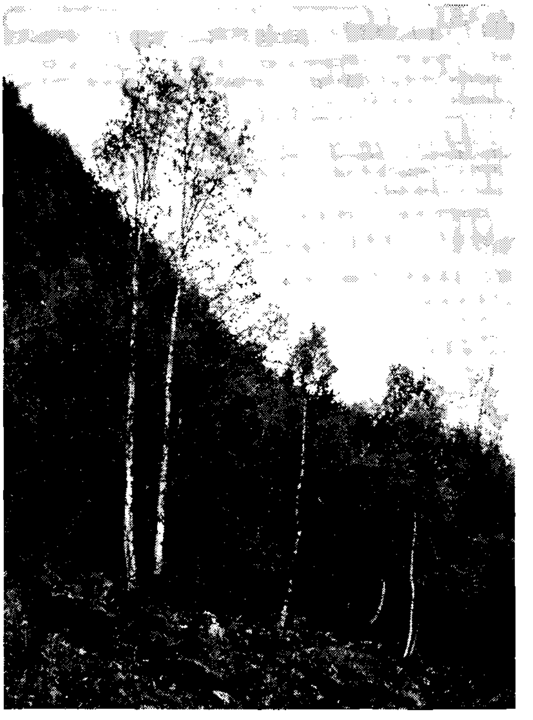

Fig. 2. Part of the forest at the second station, 250–300 m a.s.l. Epiphytic lichens on birch are more common than at sea level. Other tree species are *Sorbus aucuparia*, *Populus tremula* L., *Alnus incana* (L.), *Pinus silvestris* L., and *Juniperus communis* L.

of geometrid larvae (Lep.) on birch was especially high. The data achieved on the altitudinal zonation of geometrid larvae has been published earlier (Hågvar 1972). The present paper deals with the altitudinal zonation of the species composition within Araneida, Heteroptera, Cicadidae, and Coleoptera. An analysis of the altitudinal zonation of the density is also presented, which covers all invertebrate groups recorded. Some information is given on the trophic structure of the invertebrate fauna at the respective altitudes.

MATERIAL AND METHODS

Five stations were chosen, one at each of the following altitudes: 10–40 m, 250–300 m, 450–500 m, 650–700 m and 850–900 m. The timber line is at 900 m. The photos in Figs. 1–5 show representative views of each station. The actual 'habitat' is not quite constant throughout the gradient. At the upper part of the slope, the trees grow more slowly, are smaller, are more covered with epiphytic lichens, and often have crooked stems because of larger seasonal accumulation of snow.

Invertebrates were collected from branches on the lowest three metres of the trees by a sweep-net, as described by Zubareva (1930). For each sampling at a given station, a new group of trees was chosen. The net was used on all sides of each tree. The effectiveness of the sweep-net may be somewhat different for different taxonomic groups, but the method gives a picture of the composition of the total invertebrate fauna. Within a given species or group, the method is less selective. At each collection, from 100 to 400 sweeps were made. The density of animals is given as number per 100 sweeps. Acarina and Collembola were not collected.

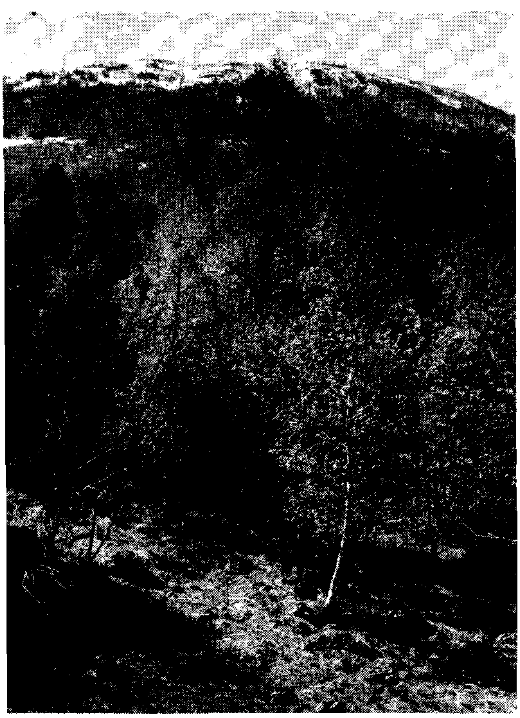

Fig. 3. Part of the forest at the third station, 450–500 m a.s.l. Among the birches are some *Sorbus aucuparia, Prunus padus, Alnus incana, Pinus silvestris,* and *Juniperus communis.*

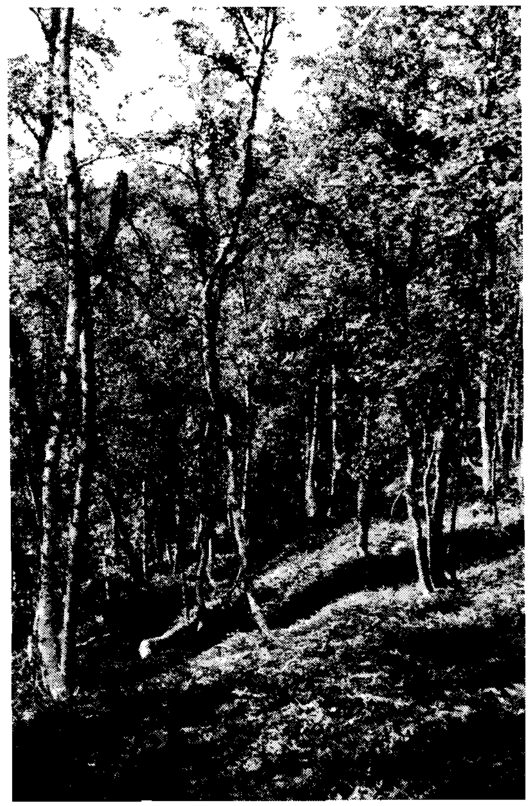

Fig. 4. Part of the forest at the fourth station, which at this altitude, 650–700 m a.s.l., is an almost pure birch forest. A few specimens of *Sorbus aucuparia, Populus tremula, Pinus silvestris* and *Juniperus communis* occur. The birch stems are often more or less crooked due to rather large amounts of snow.

The weather conditions were favourable (without wind or rain) during all collections. Collection dates were: 10–40 m a.s.l.: 14 May, 15 June, 13 July, 27 July and 1 September; 250–300 m a.s.l.: 15 May, 16 June, 14 July, 28 July and 2 September; 450–500 m a.s.l.: 19 May, 17 June, 15 July, 29 July and 4 September; 650–700 m a.s.l.: 24 June, 16 July, I August and 5 September; 850–900 m a.s.l.: 17 July, 5 August and 6 September.

A total of 9384 invertebrates were collected.

RESULTS

Altitudinal zonation in number of species

Tables I–III show at which altitudes the different species from the four groups mentioned were recorded. A few species not naturally occurring on birch are excluded in the tables. The data is based on the 68 adult Heteroptera collected, and some of the larvae, on the 377 adult Cicadidae, the 497 adult Coleoptera, and 183 of the Araneida, including all adults and some of the juveniles.

No species of Heteroptera and only a few species of the other groups were recorded at the timber line. In all groups, the greatest number of species was found at the lowest station, and the lowest number at the highest station.

The number of Heteroptera species recorded dropped rapidly with increasing altitude. Among Cicadidae, the number of species decreased more gradually, but most slowly in the beginning. As for Coleoptera and Araneida, the number of species recorded at the second lowest station was somewhat lower than at the two neighbouring stations. In Coleoptera, the number dropped evenly from the middle to the uppermost station. In Araneida, the two uppermost stations showed

Fig. 5. Part of the forest at the fifth and upper station, 850–900 m a.s.l., just below the timber line. The branches and stems may be rather densely covered by lichens. Large amounts of snow at this altitude have resulted in markedly crooked stems. Scattered *Juniperus communis* and *Betula nana* L. occur.

Table I. The occurrence of different species of Hemiptera (Heteroptera and Homoptera Cicadidae) on branches of birch (Betula pubescens) at different altitudes (m a.s.l.). "sp." denotes that the genus has been recorded.

	10–40	250–300	450–500	650–700	850–900
Heteroptera					
Anthocoris nemorum (L.)	x	x	x	x	
Psallus betuleti (Fall.)			x		
Psallus falleni Reuter	x	x	x		
Temnostethus gracilis Horvath	x	x	x		
Stenodema holsatum (Fabr.)	x	x			
Loricula pselaphiformis Curtis	x				
Lygocoris contaminatus (Fall.)	x				
Blepharidopterus angulatus (Fall.)	x				
Psallus ambiguus (Fall.)	x				
Acalypta carinata (Panzer)	x				
Elasmucha grisea (L.)	x				
Elasmostethus interstinctus (L.)	x				
Additional species (larvae)	1	1		2	
Total number of species	12	5	4	3	0
Homoptera, Cicadidae					
Oncopsis flavicollis (L.)	x	x	x	x	x
Oncopsis tristis (Zett.)	x	x	x	x	x
Speudotettix subfusculus (Fall.)	x	x	x	x	
Oncopsis subangulatus J. Sahlb.	x	x	x		
Linnavuoriana decempunctata (Fall.)	x	x	x		
Kybos betulicola W. Wagner	sp.	x	x		
Typhlocyba bergmani Tullgren	x	sp.	x		
Alnetoidia alneti (Dahlbom)	x	x			
Oncopsis planiscuta (Thomson)		x			
Empoasca flavescens (F.)	x	sp.			
Cixius cunicularius (L.)	x				
Cixius distinguendus (Kbm.)	x				
Total number of species	11	10	7	3	2

low numbers of species compared with the three lowest stations.

Probably the picture of zonation becomes more correct if we assume that the vertical distribution of each species is continuous. By filling such empty holes in Tables I–III, the number of Coleoptera species from the lowest to the highest station becomes: 21, 21, 20, 14, 8 and of Araneida species: 9, 8, 8, 2, 1. If we furthermore assume that all species listed may occur down to sea level, the number of species is as follows: Heteroptera: 13, 6, 4, 3, 0; Cicadidae: 12, 10, 7, 3, 2; Coleoptera: 31, 27, 24, 14, 8 and Araneida: 15, 11, 9, 3, 1.

These corrections do not change the zonation pattern in Heteroptera and Cicadidae. They do, however, indicate that the number of Coleoptera and Araneida species is not markedly changed in the lower half of the gradient, but clearly lower in the two uppermost stations.

According to Ossiannilsson (pers. comm.), *Kybos betulicola* and *Oncopsis subangulatus* (Cicadidae) are new to Norway.

In addition to the four groups mentioned, small numbers of Psyllidae were also identified. *Psylla nigrita* (Zett.) and *P. sorbi* (L.) were recorded at the three lowest stations. *P. corcontum* Sulc was found at the medium station and *P. alni* (L.) at the uppermost station. The material indicates that the Psyllidae species are limited mainly to the three lowest stations.

Altitudinal zonation of density

Figs. 6–10 show how the density of some major groups changes from May to September at different altitudes (Araneida, Heteroptera, *Anthocoris nemorum* (L.) (Heteroptera), Cicadidae and Psocoptera). The figures

Table II. The occurrence of different species of Coleoptera on branches of birch (*Betula pubescens*) at different altitudes (m a.s.l.).

	10 - 40	250 - 300	450 - 500	650 - 700	850 - 900
Polydrosus undatus Fabr.	x	x	x	x	x
Podistra pilosa Payk.	x	x	x	x	x
Anthophagus omalinus Zett.	x	x	x	x	x
Anoplus plantaris Naezen		x	x	x	x
Otiorrhynchus salicis Strøm	x	x	x		x
Anthophagus alpinus Fabr.			x	x	x
Malthodes fuscus Waltl.				x	x
Rabocerus foveolatus Ljungh				x	x
Acrotrichis rugulosa Rossk.	x	x	x	x	
Athous subfuscus Müll.		x	x	x	
Malthodes guttifer Kies.	x			x	
Malthodes brevicollis Payk.	x			x	
Malthinus frontalis Mrsh.				x	
Anaspis rufilabris Gyll.				x	
Coccinella 14-guttata L.	x	x	x		
Malthodes marginatus Latr.	x	x	x		
Anthophagus caraboides L.	x	x	x		
Apion simile Kirby	x	x	x		
Polydrosus pilosus Gredl.	x	x	x		
Rhagonycha limbata Th.		x	x		
Corymbites affinis Payk.	x		x		
Malthodes mysticus Kies.	x		x		
Podistra rufotestacea Letzn.	x		x		
Malthodes spathifer Kies.			x		
Deporaus betulae L.	x	x			
Dolopius marginatus L.	x	x			
Coeliodes rubicundus Hbst.		x			
Schizotus pectinicornis L.	x				
Rhinosimus planirostris Fabr.	x				
Cis alni Gyll.	x				
Phytodecta intermedius Hellies.	x				
Total number of species	21	16	18	13	8

include larval or juvenile stages. For simplicity, the altitudes are denoted as 0, 300, 500, 700 and 900 m a.s.l.

Characteristic for Figs. 6–8 is a decreasing density with increasing altitude. In no case was the maximum density found to be higher at a given altitude than at any lower station. There is a great difference in maximum density between the lowest and the uppermost station at which a group was recorded. The maximum density of imagines in Heteroptera (Fig. 7, vertical lines) and in *A. nemorum* (Fig. 8, vertical lines) also decreases with increasing altitude.

In Cicadidae, both the total density and the density of imagines were similar for all three of the lowest stations, but clearly lower at the two uppermost stations (Fig. 9). Psocoptera (Fig. 10) showed a very high maximum density at the second and third station relative to the density at sea level and in the highest part of the gradient.

Table III. The occurrence of different species of Araneida on branches of birch (*Betula pubescens*) at different altitudes (m a.s.l.).

	10 - 40	250 - 300	450 - 500	650 - 700	850 - 900
Araneus patagiatus Cl.					x
Lepthyphantes expunctus (Cambr.)		x	x	x	
Araneus cucurbitinus Cl.	x	x	x	x	
Linyphia peltata Wider.			x		
Pityohyphantes phrygianus (Koch)			x		
Lepthyphantes obscurus (Blw.)	x		x		
Helophora insignis (Blw.)	x		x		
Dictyna pusilla Thorell	x		x		
Theridion pallens Blw.	x	x	x		
Philodromus aureolus (Cl.)		x			
Meta segmentata (Cl.)		x			
Anyphaena accentuata (Walck.)	x				
Theridion varians Hahn	x				
Bathyphantes nigrinus (Westr.)	x				
Lepthyphantes alacris (Blw.)	x				
Total number of species	9	5	8	2	1

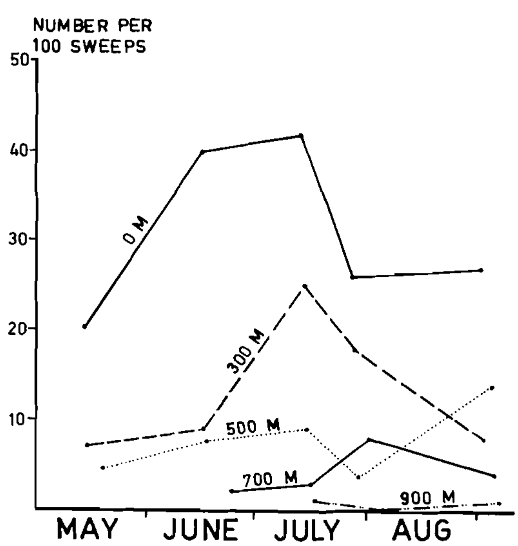

Fig. 6. Density of Araneida, given as number per 100 sweeps, during summer at different altitudes.

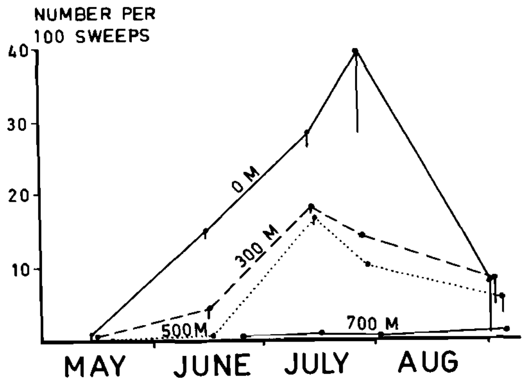

Fig. 7. Density of Heteroptera, given as number per 100 sweeps, during summer at different altitudes. Heteroptera were not recorded at 900 m a.s.l. Length of vertical lines denotes the density of imagines.

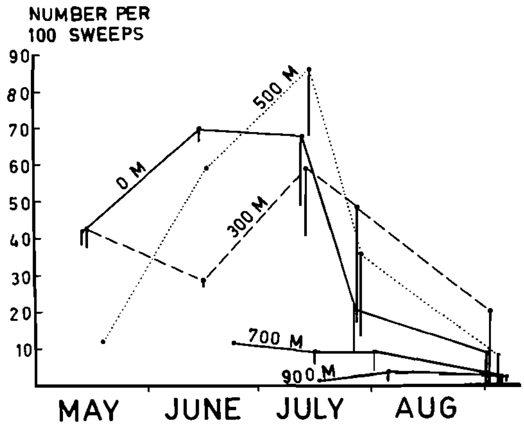

Fig. 9. Density of Cicadidae (Homoptera), given as number per 100 sweeps, during summer at different altitudes. Length of vertical lines denote the density of imagines.

The seasonal variations in density at different altitudes of the other groups recorded are shown in Table IV, together with the total catches of invertebrates. Some groups are so sparsely represented in the actual habitat that the material gives no good picture of their altitudinal zonation, but merely their presence at certain altitudes (viz. Opiliones, Ephemeroptera, Plecoptera, Thysanoptera, Neuroptera, Trichoptera, Hymenoptera symphyta, insect larvae and pupae).

The maximum density of Aphidae recorded at the four lowest stations is very similar (11–16 animals per 100 sweeps), but a much higher density (112) was recorded at the uppermost station in July. This may have been a local phenomenon. Some three weeks later the density was again low, but the density of Formicidae was then high (48), probably as a response to the peak in aphid density.

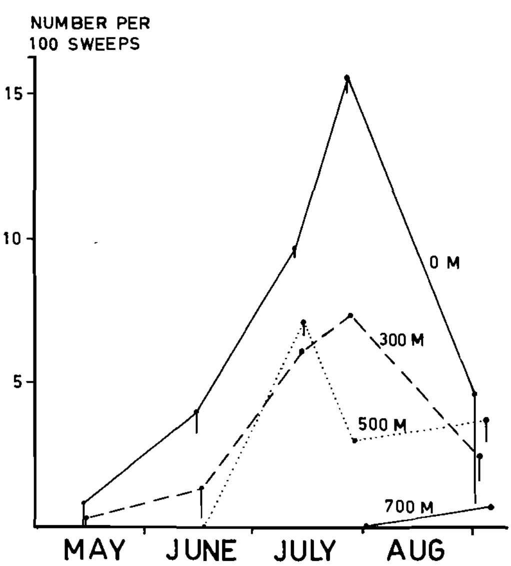

Fig. 8. Density of *Anthocoris nemorum* (Heteroptera), given as number per 100 sweeps, during summer at different altitudes. The species was not recorded at 900 m. Length of vertical lines denote the density of imagines.

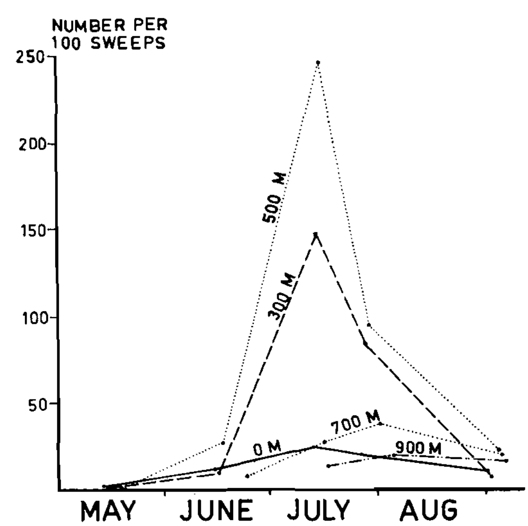

Fig. 10. Density of Psocoptera, given as number per 100 sweeps, during summer at different altitudes.

Table IV. Number of invertebrates collected per 100 sweeps with a sweep-net on birch (Betula pubescens) during different months (from May to September) and at different altitudes. The actual collecting dates are given in "Material and methods" The following groups have been excluded in the table, as their densities are presented elsewhere: Araneida (Fig. 6), Heteroptera (Fig. 7), Cicadidae (Fig. 9) and Psocoptera (Fig. 10). These groups are, however, included in "TOTAL CATCHES". All figures are calculated to the nearest whole number.

Altitude	10 - 40 m					250 - 300 m					450 - 500 m					650 - 700m				850 - 900 m		
Month	M	J	J	J/A	S	M	J	J	J/A	S	M	J	J	J/A	S	J	J	J/A	S	J	J/A	S
Opiliones				1	4			4	1	2			4	2	3		1	2	2			1
Ephemeroptera			1	1																	1	
Plecoptera							1	1		1	<1	2	2	1	1	2	3			20	5	2
Thysanoptera								1			1	2	7			<1						
Homoptera:																						
Aphididae	2	16	8	12	15	<1	4	5	14	6		3	8		14	<1	4	11	2	112	8	1
Psyllidae			118	7				1	2		1		1	1	1						1	
Hemiptera, total	45	102	222	81	32	43	37	83	80	34	13	62	112	48	28	12	13	20	5	113	12	3
Neuroptera			1		2			1		3		1		1							1	
Trichoptera			3																			
Microlepidoptera	1	1	6	19	1		1	2	15	4		1		1				1	1			
Coleoptera:																						
Cantharidae			19	4	4		1	4				1	6	2			2	4			1	
Staphylinidae			19	4	13			17	12	3			49	30	2		4	14		7	14	
Curculionidae	1	12	6	10	2	1	5	12	8			2	7	6	2	1	3	2	4	5	3	
Other Coleoptera		4		1	3	<1	5	1	1	1		1	2		1	<1	1	1	1		1	
Coleoptera, total	1	16	44	19	23	2	10	34	21	3		3	64	38	4	1	10	21	5	12	18	
Diptera:																						
Brachycera		7	26	8	5		8	24	14	6		13	28	15	5	6	7	14	3	14	10	
Cyclorrhapha	1	30	14	15	10	1	9	14	22	9		10	12	14	19	10	6	7	2	3	7	1
Nematocera	53	109	78	32	9	11	33	60	55	12	2	185	47	10	21	46	8	14	7	8	3	5
Diptera, total	54	146	118	55	24	12	49	98	91	27	2	207	86	38	45	62	21	35	12	25	19	6
Hymenoptera:																						
Formicidae							2									<1	2				48	3
Hym. parasitica	9	18	19	9	21	2	11	6	10	21	<1	6	1	10	8	6	3	2	4	5	5	1
Hym. symphyta		1					1									<1				1		
Hymenoptera, total	9	19	19	9	21	2	13	6	10	21	<1	6	1	10	8	7	5	2	4	6	53	4
Larvae, Geometridae (Lep.)	30	636	3		5	49	1792	45	2		10	1188	217	11		123	32	6		384	11	
Insect larvae (not Lep.)	<1	7	5	1	6		1	11	1			1	1	2	1		1				1	2
Insect pupae		1	5	3	3		1	5	5	5	1		3	3	2		2	5	3	1	3	2
TOTAL CATCHES	161	979	493	235	158	115	1921	463	329	115	32	1505	752	251	128	216	118	138	46	575	140	36
Total catches except larvae of Geometridae	131	343	490	235	153	66	129	418	327	115	22	317	535	240	128	93	86	132	46	191	129	36

Psyllidae, generally sparsely represented throughout the gradient, showed a high density at sea level in July. This was due to a mass occurrence of *P. sorbi*, probably representing a local and temporary aggregation. The data on Microlepidoptera may indicate that this group occurs mainly in the lower part of the gradient. Hymenoptera parasitica were recorded in all collections, with the densities being highest at the lower stations.

Brachycera and Cyclorrhapha, from among the Diptera, showed very similar maximum densities at each given altitude. The maximum density within each group varied between 19 and 30 animals per 100 sweeps at the three lowest stations and was somewhat lower (7–14) at the two uppermost stations. Nematocera appears to be well represented in the defined habitat. The density of this group varied greatly at the first, third and fourth station throughout the season, probably depending upon varying swarming activity. Only very low densities were, however, recorded at the upper station. Total Diptera density was greatest at the three lowest stations.

Cantharidae, Staphylinidae, and Curculionidae were the dominant coleopterous groups. While the catches of Cantharidae and Curculionidae indicate a slightly higher density in the lower part than in the upper part of the gradient, Staphylinidae were most numerous at the middle station. The material of this last group consisted of three *Anthophagus* species, which are typical inhabitants of birch (Strand, pers. comm.). *A. omalinus* preferred the medium range of the gradient, with the following maximum densities per 100 sweeps from the lowest to the highest station: 7, 16, 48, 13, 14. Corresponding numbers for *A. caraboides* were 16, 3, 2, 0, 0, indicating a preference for the lower part, and for *A. alpinus:* 0, 0, 1, 1, 6, indicating a preference for the upper part of the gradient. As shown in Table IV, the total density of Coleoptera did not change greatly throughout the gradient. The two upper stations had the lowest maximum densities, and the highest density was recorded at the middle station.

Hemiptera collectively showed rather high maximum densities at all altitudes except 650–700 m.

The maximum total density of invertebrates recorded at each altitude depended wholly upon the occurrence of geometrid larvae. At their maximum density, the latter group made up the major part of the invertebrate material throughout the gradient. For both geometrid larvae and invertebrates as a whole, the sequence of stations with decreasing maximum total density was: 250–300 m, 450–500 m, 10–40 m, 850–900 m and 650–700 m.

If we exclude the geometrid larvae, the plot of total invertebrate densities across the season at the three lower stations is much the same (Table IV). The values at the two uppermost stations are clearly lower, however, and rather similar. At the time of maximum invertebrate density at each level, different groups dominated when geometrid larvae were disregarded, as follows: Psyllidae, 24% at 10–40 m; Psocoptera, 35% at 250–300 m; Psocoptera, 46% at 450–500 m; Psocoptera, 29% at 650–700 m; and Aphidae, 59% at 850–900 m.

The main conclusion that can be made concerning altitudinal zonation in total density is that the two uppermost stations showed clearly lower densities than any of the three lowest stations, both when geometrid larvae are included and when they are not.

A short description of the invertebrate fauna characteristic to each altitude

The fauna collected at each altitude can be characterized as follows:

10–40 m: Highest recorded number of species among Heteroptera, Cicadidae, Coleoptera, and Araneida. Highest maximum density of Heteroptera in general, of the species *Anthocoris nemorum,* and of Araneida. Probably preferred altitude of *Anthophagus caraboides* (Col., Staphylinidae).

250–300 m: Highest maximum density of invertebrates and highest degree of defoliation in the gradient, mainly caused by larvae of *Operophthera* sp. (Lep., Geometridae), which prefer this altitude. Relatively high maximum density of Psocoptera.

450–500 m: Highest maximum density of Psocoptera and of *Anthophagus omalinus* (Col., Staphylinidae). Lowest station at which populations of *Oporinia autumnata* Bkh. (Lep., Geometridae) were recorded.

650–700 m: Overlapping zone between geometrid larvae of *O. autumnata* and *Operophthera* sp. Lowest maximum density of invertebrates and of geometrid larvae. Lowest degree of defoliation. Few species of Araneida, Heteroptera, and Cicadidae.

850–900 m: Absence of Heteroptera. Lowest number of species from among Cicadidae, Coleoptera, and Araneida. Low maximum density of invertebrates. Preferred altitude for larvae of *O. autumnata,* and probably of *Anthophagus alpinus* (Col., Staphylinidae).

Trophic relationships at different altitudes

Although the effectiveness of the method may be somewhat different for different groups, it is of interest to analyze roughly the catches in view of the trophic position of the invertebrates. The recorded fauna can be divided into three trophic groups:

1. *Birch leaf or sap feeders:* Thysanoptera, Homoptera, Heteroptera except the predatory species mentioned below, the coleopterous families Curculionidae, Elateridae and Chrysomelidae, Lepidoptera larvae, larvae of Hymenoptera symphyta and probably a few other insect larvae recorded. 2. *Feeders on fungi, lichen, excrements or detritus and non-feeders on birch:* Diptera adults; Psocoptera; Trichoptera; Ephemeroptera; Plecoptera; the coleopterous families Cisidae, Ptiliidae, probably the actual Staphylinidae, Cantharidae and Heteromera; imagines of Lepidoptera and of Hymenoptera symphyta; Formicidae (probably eating excrements of aphids); larvae of Dermaptera and insect pupae. 3. *Predators and parasites:* Araneida, Opiliones, Hymenoptera parasitica, probably the few Neuroptera imagines and larvae collected, and the following Heteroptera species: *Anthocoris nemorum, Temnostethus gracilis, Loricula pselaphiformis* and *Blepharidopterus angulatus.*

The highest density of birch leaf or sap feeders, 1836 animals per 100 sweeps, was recorded in June at the second lowest station, where the density of geometrid larvae was highest. In the actual sample, geometrid larvae made up 97.6% of this trophic category.

Psocoptera and Nematocera dominated the second trophic group (Table IV). The highest density of this category, 393 animals per 100 sweeps, was found at the middle station in July. In this sample, Psocoptera represented 63% of the group.

The density of predators and parasites was always highest at the lowest level and decreased with increasing altitude (Fig. 11). At all stations, the density changes from July to September were rather small. Araneida dominated this trophic group.

Fig. 12 shows the relative dominance of each trophic group in the different catches. Because of the dominance of geometrid larvae in early summer over the whole gradient, there is a distinction made between this group

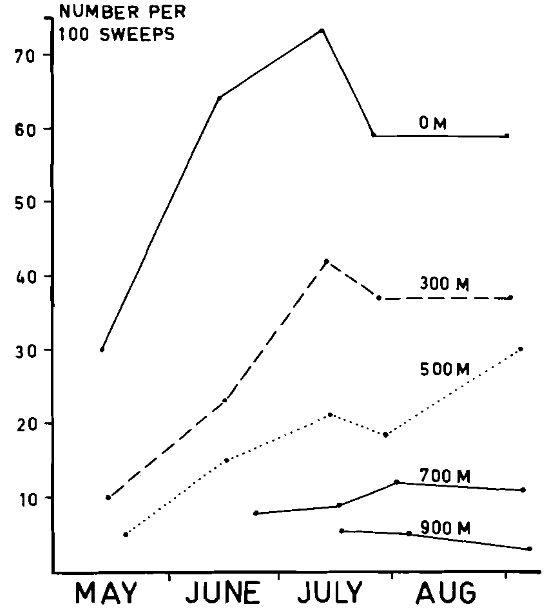

Fig. 11. Density of invertebrate predators and parasites, given as number per 100 sweeps, during summer at different altitudes.

and the rest of the first trophic category. This remainder always constituted less than 50% of the total catches. When the geometrid larvae had disappeared or was only found incidentally, this percentage remained fairly constant throughout the gradient, varying between 17 and 29.

It is a general feature of all altitudes that the second trophic group becomes dominant when the density of geometrid larvae has dropped.

Due to a rather stable density of predators and parasites at each altitude from July to September (Fig. 11) and to a general decline in total invertebrate density at all stations during the last half of the summer (Table IV), the relative dominance of predators and parasites increased at all stations during the latter period (Fig. 12). The highest percentage achieved by this trophic group, 37%, was recorded at the lowest station in September.

Of the total season's catches at each altitude, the first trophic group was represented by the following percentages, listed from the lowest to the highest station: 56, 74, 64, 43, and 72%. Corresponding values for geometrid larvae alone were 33, 64, 53, 31, and 53%, and for the rest of this trophic group 23, 10,

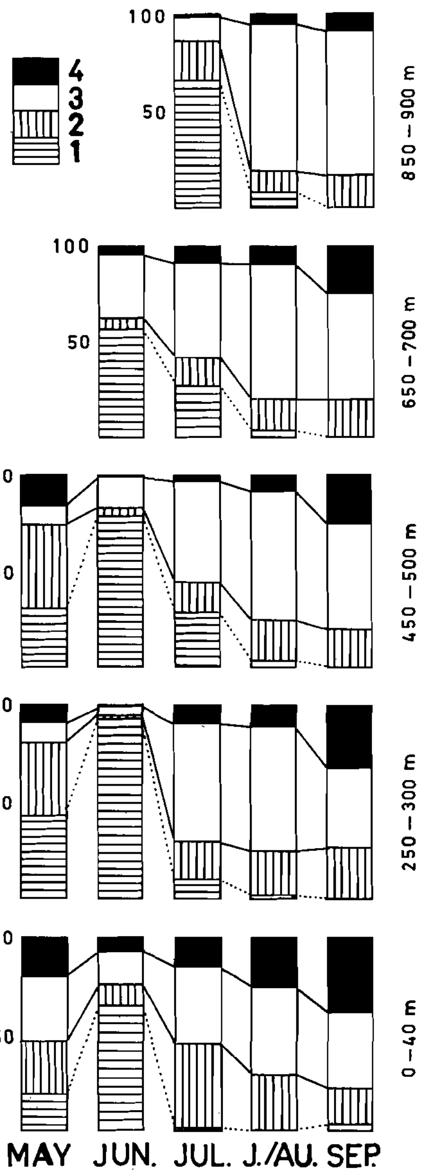

Fig. 12. Relative composition (in % of total number) of the invertebrate fauna on branches of birch during summer at different altitudes. 1: Larvae of Geometridae. 2: Other leaf or sap feeders. 3: Feeders on fungi, lichen, excrements or detritus and non-feeders on birch. 4: Predators and parasites. Further explanation in text.

11, 12, and 19%. For the second trophic group, these mean values were 29, 21, 33, 49, and 27%. For the third trophic group, they were 14, 5, 3, 8, and 2%.

If we pool all catches over the whole gradient during the season, the mean value for the first trophic group was 65% (geometrid larvae 51% and other 14%), for the second group 29%, and for the third group 6%.

Altitudinal zonation of development

In spring, the birch leaves developed about four days later for every 100 m increase in altitude. It is reasonable to infer that this delay also retards the start of development of the invertebrate species at different altitudes. In addition, the lower mean temperatures occurring at higher altitudes will slow down the developmental rate.

Anthocoris nemorum (Heteroptera) may serve to illustrate the altitudinal zonation of development. The species overwinters as imago and lays eggs in young leaves. As shown in Fig. 13, the development of the species is delayed one larval stage between

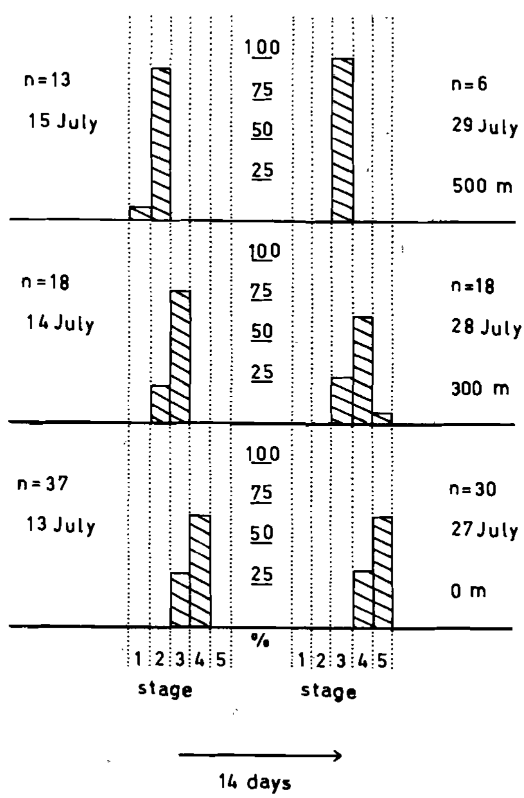

Fig. 13. Percentage distribution of larval stages in *Anthocoris nemorum* (Heteroptera) at different altitudes. Data from two samplings in July, 14 days apart, at each station. n = number of larvae.

the first and second station and between the second and third station. This is evident both when stage four dominates at sea level, and when stage five dominates fourteen days later.

DISCUSSION

The results clearly demonstrate that the invertebrate fauna on branches of birch changes with altitude. The change can be characterized by the species number and species composition; the presence, density or absence of certain groups; the preferred altitude of groups or single species; the relative dominance of groups at different altitudes; and by the total density of invertebrates.

No invertebrate orders clearly preferred the upper part of the gradient, neither by their level of highest density nor by their level of highest number of species when these were identified. Among single species, *O. autumnata* occurred mainly in the upper half of the gradient and had its highest density at the uppermost station. The preference for the timber line level is typical for the species (Tenow 1972). No other species identified, with the possible exception of *A. alpinus,* showed any clear preference for the upper two stations.

Psocoptera are characterized by mainly inhabiting the middle part of the gradient. Being to a high degree dependent on lichens as food (Landin 1967), the group would favour the higher altitudes where there is greater lichen growth on the trees. As climate, however, probably becomes less favourable with increasing altitude, it seems reasonable that a central range of the gradient may offer Psocoptera the most optimal environmental conditions.

A. omalinus, occurring at all altitudes, also prefers the centre of the range. This may, at least partly, be a result of competition with *A. alpinus* on the upper half, and with *A. caraboides* on the lower half of the mountain slope.

That the maximum observed density level of *Operophthera* sp. was in the lower half of the birch wood gradient confirms earlier observations (Tenow 1972).

All groups in which the species were identified, except the geometrid larvae (Hågvar 1972), showed a higher number of species in the lower part of the gradient than in the upper part. The groups respond differently, however, to the gradient, the number of species being reduced most rapidly among Heteroptera. Lindberg (1945) also found a strong decline in the total number of Heteroptera species over the altitudinal gradient from the deciduous forests (*silva frondosa*) in the Bulgarian mountains, through the coniferous forest belt (*silva acerosa*) to the areas above the timber line (*regio alpina*). Among 180 species recorded by him, only one species was endemic for *regio alpina.*

The number of Cicadidae species decreased rather evenly over the gradient, whereas with Coleoptera and Araneida the most marked difference occurred between the three lowest and the two uppermost stations. A general decline in the number of Carabidae species (Col.) with increasing altitude has been previously demonstrated in Scandinavia by Lindroth (1949). The relative low number of Coleoptera species in alpine habitats has also been demonstrated by Brundin (1934), Fridén (1968 and 1971), Østbye (1969), and Fjellberg (1972).

The drop in the number of species occurring from the three lowest to the two highest stations is correlated with a change in the composition of the forest. While the forest in the lower part of the gradient contains a mixture of many tree species, it becomes an almost purely birch forest above 500–600 m. This change may exclude species that prefer a more varied habitat than found in the purely birch forests.

Just as the number of species within a given animal group generally decreases with increasing altitude, the species number also usually decreases with increasing latitude, i.e., increasing distance from equator (Fisher 1960). Usually, there is a correlation between altitudinal and latitudinal distribution of single invertebrate species. Examples of such studies are those of Lindberg (1945) and Lindroth (1949). The altitudinal distribution of the present material has been compared with the known latitudinal distribution of the relevant species of Heteroptera, Cicadidae, Curculionidae, and Staphylinidae. The correlation is, however, not good. This may be explained by the fact that the direction of the isotherms in western Scandinavia is NE to SW, probably due to the Gulf Stream.

Brinck & Wingstrand (1949) found that the subarctic Scandinavian birch forests just below the timber line have few endemic invertebrate species and should be regarded as a transition zone between the lower forests and the treeless mountain areas. The present material confirms this view.

At the three uppermost stations, no collections were made just after the birch leaves were developed in 1967. However, samplings during that same phase the next spring at 450-500 m and 650–700 m did not reveal additional species, indicating that the species composition recorded in the upper part of the gradient is representative.

It is difficult to estimate the effect of the high densities of geometrid larvae on the other part of the invertebrate fauna. It is, however, reasonable to assume that the species composition has been little if at all affected. The population density of certain leaf-eating species or groups may have been seriously affected in the zones of most heavy defoliation (Hågvar 1972). Predators and parasites of geometrid larvae may have been positively affected.

Koponen (1973) studied the density and composition of the invertebrate fauna of the mountain birch *B. tortuosa* Led. (synonymous with *B. pubescens* in the present study) at Kevo, Finnish Lapland. Birch leaf or sap feeders represented 78.7% of the total material; fungi, lichen, detritus or non-feeders 16.0%, and predators and parasites 5.4%. In the present material, there was generally a somewhat lower percentage of the first trophic group and a higher percentage of the second group. The differences are partly due to a relatively low occurrence of Psocoptera in Koponen's (1973) material (averaging 1.8% during 1971–1972). In the present material, Psocoptera were well represented even on the 'mountain birch' at the two upper stations, viz. 16% of the total catches at 650–700 m and 6% at 850–900 m. The mean percentage of parasites and predators is roughly the same in the two investigations, both over the gradient as a whole, and when the two upper 'mountain' stations are concerned.

The unusual high density of geometrid larvae in the present material makes it difficult to compare directly the composition of the herbivorous trophic group with Koponen's (1973) data. However, a pronounced difference exists because of the fact that Psyllidae and larvae of Hymenoptera symphyta totally dominated this trophic group on birch at Kevo, while the groups were almost absent over the altitudinal gradient at Sogndal. The rather high catch of Psyllidae at sea level in July probably reflects swarming activity. In this investigation, Cicadidae was generally the dominant herbivore group next to geometrid larvae. If geometrid larvae were disregarded, Cicadidae would represent 63–98% of the herbivores recorded at the four lowest stations in May and June. At the uppermost station, however, the density of Cicadidae was always very low. In this last respect, the present results correspond with the conditions at Kevo, where the occurrence of Cicadidae was also quite insignificant.

It is interesting to note that the changes in relative dominance of the three trophic groups followed a very similar pattern throughout the summer at all altitudes, although the absolute densities were different. It is also a remarkable feature of the fauna of this habitat that a major part of it belonged to the second trophic group, i.e. either non-feeders on birch, or species which obtained their food from other sources than from birch leaves or by predation/parasitizing. This trophic group became dominant at all stations when the geometrid larvae left the habitat. The main reason for this dominance is the consistently rather high densities of lichen-feeding Psocoptera and non-feeding Diptera.

The very clear decrease in density of predators/parasites with increasing altitude, shown in Fig. 11, may partly be a response to lower density of prey or host specimens, although this cannot be ascertained from this material.

As the vertical range covered by each species is anticipated to be quite constant from year to year, even during heavy outbreaks of geometrid larvae, the picture achieved regarding the altitudinal zonation in species number is most probably representative.

However, the altitudinal zonation in total invertebrate density, and in the relative dominance of different taxonomic groups, should be regarded as quite flexible from year to year. This is due to the occurrence of several 'unstable' groups in the habitat, which during special years, or during shorter periods (and sometimes rather locally) may occur in great numbers. Typical examples of this are geometrid larvae, Psyllidae, Aphidae and probably Psocoptera, or species which may migrate from other habitats, such as swarming Diptera. Koponen (1973) found marked differences in the relative composition of the invertebrate fauna on birch in two successive years. Due to the mass occurrence of geometrid larvae during the present study, the total invertebrate densities were most certainly higher than in 'normal' years.

It may, however, be suggested that the total invertebrate density in most years will be lower at altitudes above 500–600 m than in the lower part of the mountain slope. This highest part of the gradient, being an almost purely birch forest, does not seem to be preferred by any of the typical 'eruptive' taxonomic groups.

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