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The impact of wood ants (Hymenoptera: Formicidae) on the structure of invertebrate community on mountain birch (*Betula pubescens* ssp. *czerepanovii*)

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We studied the effect of wood ants on the mountain birch canopy-invertebrate community by sampling a total of 840 trees at different altitudes on the mountain slopes in northeastern Lapland, Finland. We also estimated the degree of herbivory on birch leaves, and monitored the prey of the wood ants. We addressed three questions: (1) How invertebrates are distributed along the altitudinal gradient and on a larger regional scale, (2) how wood ants (*Formica aquilonia*) affect the distribution of herbivores and predators in the mountain birch canopy, and (3) how the potential prey of wood ants vary in relation to altitude, season and year. Our results demonstrate that the number of sawfly larvae and the degree of herbivory on birch leaves increases with elevation, with the largest impact on mid elevation areas previously damaged during autumnal-moth (*Epirrita autumnata*) outbreaks. Wood ants and ant-tended aphids (*Symydobius oblongus*) were most abundant at lower elevations. Wood ants affected most invertebrate groups negatively at all elevations where the wood ants existed, and the effect was quite stable in time. Further, herbivores were found to comprise a large proportion of prey of wood ants. Because birches are often killed during the outbreak years of moths, trees gain long-term protection by wood ants at reasonably low yearly costs — growth reduction owing to sap sucking by ant-tended aphids. Through this protection, wood ants may prevent the recession of the timberline during outbreak years. Further, defoliated forests may recover substantially faster when birch propagules spread from the green islands of birches surviving around the ant mounds.

Introduction

The populations of many herbivores in the northern hemisphere display typically large fluctuations that often result in mass outbreaks (Koponen 1980a, Koponen 1983). In northern Fennoscandia, the populations of *Epirrita autumnata* (Lepidoptera, Geometridae) and two allied species exhibit mass outbreaks at approximately ten-year intervals (Tenow 1972). This results in large-scale defoliation of mountain birch (*Betula pubescens* subsp. *czerepanovii*), and large areas of birch forests may turn into treeless tundra, especially in the upper parts of the mountain slopes (Tenow 1975). This happened most recently in Finnish Lapland during a severe outbreak of *E. autumnata* in 1964–1965 (Kallio & Lehtonen 1973). In this region, large-scale defoliation is usually limited to the upper zones of the mountain slopes, whereas wood-ant colonies (mainly *Formica aquilonia*; Hymenoptera, Formicidae) are restricted to lower elevations. In the overlap area of these two zones, green islands of undamaged birches are commonly found around wood-ant mounds (Laine & Niemelä 1980, Niemelä & Laine 1986).

Although the role of spiders and parasitic wasps as important predators of the insect herbivores of mountain birch in Finnish Lapland has been emphasized (Jussila & Nuorteva 1968, Nuorteva & Jussila 1969, Nuorteva 1971, Koponen 1975, Koponen & Ojala 1975, Ruohomäki 1994), wood ants may also have major effects on herbivores (Laine & Niemelä 1980, Niemelä & Laine 1986, Karhu 1998, Karhu & Neuvonen 1998). Because wood-ant populations sometimes reach very high densities (Laine & Niemelä 1980, 1989, Vepsäläinen *et al*. 1984), their impact on mountain-birch herbivore populations may be high.

Wood ants impact the community structure of other ground-living arthropods (Kaczmarek 1963, Kolbe 1968, 1969, Cherix & Bourne 1980, Niemelä *et al*. 1992, Koivula 2002) and their importance extends to the tree canopy, where they tend aphid colonies (Buckley 1982). The role of wood ants in affecting herbivores and in structuring herbivore communities has been debated for a long time (Gösswald 1951, Adlung 1966, Way & Khoo 1992). As experimental data have accumulated (e.g., Laine & Niemelä 1980, Skinner & Whittaker 1981, Fowler & MacGarvin 1985, Warrington & Whittaker 1985a, 1985b, Whittaker & Warrington 1985, Karhu 1998, Karhu & Neuvonen 1998, Sipura 2002), the importance of wood ants has been recognized and their potential usefulness in biological control of forest pests has been noted (Way & Khoo 1992). However, there remains only limited knowledge of ant effects on the structure of invertebrate communities on tree canopies. One reason for this lack of information is that reliable sampling of the canopies of tall trees is difficult or impossible to perform. Mountain birch is a relatively small tree and, consequently, the canopy fauna is easy to sample. Therefore mountain birch offers good opportunity to study relationships between ants and canopy invertebrate community.

In this study we try to answer the following questions: (1) What is the distribution of invertebrates and the structure of invertebrate communities of the mountain birch in relation to altitude, season and year, and how spatially stable is the community (on regional scale)? (2) How do wood ants affect the invertebrate community, and the degree of herbivory experienced by birches? (3) What is the abundance of prey collected by wood ants in relation to altitude, season and year? We approached these questions by sampling invertebrates from trees, estimating the degree of herbivory on birch leaves, and monitoring prey captured by wood ants.

Material and methods

Study area

Most of the field work was carried out in the surroundings of the Kevo Subarctic Research Station (69°45´N, 27°01´E). The vegetation of the area varies widely according to altitude, with the river valleys being predominantly mixed pine-birch forests changing to birch forests at higher elevations (*see* Laine & Niemelä 1989). For detailed vegetational and climatological descriptions of the area, *see* Hämet-Ahti (1963) and Kärenlampi (1972). For a larger regional sample, we extended the survey to a number of mountains in a larger area in northeastern Lapland (16–56 km from Kevo).

In order to study local and temporal variation, we sampled from six mountains in the vicinity of the Kevo Station in July and August 1977–1979 (Table 1). Three altitudinal zones were covered: *mountain foot* (hereafter termed F), midslope zone, which was subdivided according to the occurrence of *E. autumnata* damage into *midslope-healthy* (MH) and *midslope-damaged* (MD), and *mountain top* (T). The regional data

Table 1. The altitudes (Alt,), habitat types (Hab; *see* Hämet-Ahti 1963), mean height of birches (*h*), density of birches (*d*), and the numbers of mountain birches sampled at different altitudinal zones on the mountains (Zone; F = mountain foot, MH = midslope-healthy, MD = midslope-damaged, and T = top) in July and August 1977–1979, and Ju

Mountain	Zone	Alt (m a.s.l.)	Hab	*h* (m)	*d* (trees ha^{-1})	No. of trees sampled							Total
						1977		1978		1979		1983	
						July	Aug	July	Aug	July	Aug	July	
Puksalskaidi	F	100	UEMT	4.2	1210	–	20	20	20	–	–	–	60
	MH	190	sELiT	1.8	1220	–	20	20	20	–	–	10	70
Jesnalvaara	F	80	UEMT	4.7	970	20	20	–	20	–	–	–	60
	MH	220	sELiPIT	3.1	550	20	20	–	20	20	20	5	105
	MD	240	sELiT	1.3	980	20	20	–	20	–	–	5	65
	T	320	sELiT	1.0	660	20	20	–	20	–	–	10	70
Skallovaara	F2	80	sELiT	3.8	520	–	–	–	20	–	–	–	20
	F1	100	UVET	4.1	370	–	–	20	20	–	–	–	40
	MH	240	sELiPIT	3.9	440	–	–	20	20	–	–	–	40
	MD	250	sELiT	1.5	170	–	–	20	20	–	–	–	40
	T	300	sELiT	2.5	870	–	–	20	20	–	–	10	50
Petsikko	T	300	?	?	?	–	20	20	–	–	–	10	50
Fierbmeluoyddeskaidi	MD	290	?	?	?	–	20	20	–	–	–	–	40
	T	310	?	?	?	–	20	20	–	–	–	–	40
Kamahpelvarri	MH	285	?	?	?	–	20	20	–	–	–	–	40
Tsieskadasoaivi	MH	260	?	?	?	–	–	–	–	–	–	10	10
Karigasniemi–Ailigas	T	360	?	?	?	–	–	–	–	–	–	10	10
Kistuskaidi	T	340	?	?	?	–	–	–	–	–	–	10	10
Utsjoki-Ailigas	T	300	?	?	?	–	–	–	–	–	–	10	10
Mierasrova	MH	180	?	?	?	–	–	–	–	–	–	10	10
Total						80	200	200	220	20	20	100	840

were collected at altitudes susceptible to *Epirrita* outbreaks on the mountain slopes (i.e., 240–300 m a.s.l.) from the same sites and a number of additional mountains in July 1983.

The habitat characteristics of the local-scale sampling sites and an overview of the sampling scheme for both local and regional-scale sampling are given in Table 1. The habitat classification follows Hämet-Ahti (1963).

Invertebrate samples

We sampled invertebrates from trees using the beating method (Southwood 1978). Trees were beaten strongly with a wooden club covered with leather. The efficiency of the method was tested on 20 trees. The test trees were beaten five times and the number of captured animals was counted after each stroke. Finally, the trees were wrapped in plastic bags and brought into the laboratory, and all remaining invertebrates were counted. The mean percentages of captured animals from trees after 1 to 5 strokes were 56%, 79%, 88%, 94% and 98%, respectively. We limited our sampling to ca. 1.5–3.0-m tall trees to reduce stochastic variation caused by the size of the trees. Thus, neither large trees (common at lower elevations) nor bush-like trees (typical at mountain tops) were included in our data.

In our sampling, we used five strokes per tree. At each sampling site, 20 trees were sampled during each period in 1977–1979 for the local-scale data set (740 trees in total; Table 1). For the regional comparison, we sampled 10 trees at each site in 1983 (100 trees in total; Table 1; at Jesnalvaara, the sample included both damaged and healthy birch forest). For each sample, we collected from a new set of trees so that previous sampling could not affect the results. The animals were identified and counted *in situ* on a 1.5×2.5-m^2 plastic sheet spread under the trees sampled. To make identification less laborious, we used as broad taxonomical categories as possible without compromising ecological information. Aphids were identified to the species since their specific relationships with ants (tended *vs.* untended), and thus indirectly with birch trees, differ drastically among the species. Adults and juveniles (nymphs or larvae) were pooled for groups in which the developmental stages do not differ much as prey for wood ants (Araneae, Heteroptera, Coleoptera; in Coleoptera, a very small proportion of individuals were larvae, and the larvae identified had a rather tough body surface which is not comparable to the soft body in sawfly and moth larvae). For Symphyta and Lepidoptera, the data consist exclusively of larvae.

Additionally, we sampled invertebrates from a total of 83 trees at different altitudes on the mountain slopes in July 1978. We measured the height of these birches to examine the effect of tree height on the abundance of invertebrates. The heights of the trees in the regional-scale sample (n = 100) were also measured in July 1983, and we also used this larger data set to test the effect of tree height on the abundance of the canopy invertebrates.

We estimated the degree of herbivory by counting the proportion of leaves that had been chewed or mined by herbivores from 11 pooled samples of 160 birch branches at different altitudinal zones (F, MH, MD and T) along three mountains (Jesnalvaara, Skallovaara and Puksalskaidi) in areas both with and without wood-ant colonies in September 1978. Each pooled leaf sample consisted of leaves of 11–20 (mean 14.5) mountain-birch branches.

Samples of prey collected by wood ants

To study the amount and variety of prey captured by wood ants, we gathered all prey items carried by the workers in their foraging routes into two mounds situated at different altitudinal zones (F and MH) of the mountain Jesnalvaara. Sampling was conducted in one-hour periods with a minimum interval of six hours between sampling periods during nine occasions in June and July 1979–1981.

Statistical analyses

We used non-parametric statistics because our data were not normally distributed and could not be normalised by transformations (BMDP2D statistical software; Dixon 1990). In order to locate the significant differences among the samples after Kruskal-Wallis one-way analysis of variance, we used a Tukey-type measure of differences in medians (BMDP3S statistical software; Dixon 1990). We used Kruskal-Wallis test only when the proportion of positive observations exceeded 2/3 of the total. We calculated log-likelihood ratio tests for the evenness of occurrences in low *vs*. high numbers (classified according to the medians).

In order to test the effect of altitude, season and year on the interactions between wood ants and other invertebrates, we used log-linear models in three-way contingency tables (BMDP4F statistical software; Dixon 1990). In the models, interaction between variables is indicated by "×" between the variables (e.g., A × B), whereas independence of variables is indicated by a comma (e.g., A,B). In interpreting the models, we examined the standardized deviations and their sign (positive or negative) between the observed and expected cell frequencies of models lacking the interaction term of our interest (*see* Toft 1984, Savolainen & Vepsäläinen 1988, Vepsäläinen *et al.* 1988).

Results

The 840 trees sampled yielded a total catch of 119 888 animals (Appendices 1 and 2). The most abundant species was *Euceraphis punctipennis* (Homoptera, Drepanosiphidae). In the regional data, the total numbers of this aphid alone exceeded 95 000. In addition to aphids, other abundant groups were sawfly larvae (Symphyta) and beetles (Coleoptera), whereas moth larvae (Lepidoptera) and hemipterans (Hemiptera) were less abundant. The general faunal structure of the local-scale sampling sites according to altitude and season is illustrated in Fig. 1, where the samples are pooled over the years 1977–1978. For more detailed analyses, *see* below.

Birch mesofauna

Regional scale

The invertebrate samples from ten mountain tops and upper slopes in 1983 revealed that the most abundant invertebrate was the aphid *E. punctipennis*, which apparently had a mass outbreak that year (Appendix 2). In the surroundings of the Kevo Subarctic Research Station, its abundance was the highest ever recorded. Other abundant invertebrates were sawfly larvae, weevils and leaf beetles (Coleoptera: Curculionidae and Chrysomelidae). *Epirrita autumnata* larvae were the most abundant moth species (Appendix 2). The most abundant predators were hover-fly larvae (Diptera: Syrphidae), spiders (Araneae), and soldierbeetles (Coleoptera: Cantharidae), whereas wood ants were absent from these upper slopes. Generally, the faunal differences among the mountains were quite small.

Local scale

The local-scale samples in 1977–1979 were dominated by the same groups as mentioned above, except for drastically lower numbers of the aphid *E. punctipennis* (Appendix 1).

The Puksalskaidi mountain was characterized by high numbers of *Polydrosus ruficornis* (Coleoptera: Curculionidae) and hemipterans (mountain-specific data are not shown here). The Jesnalvaara mountain was dominated by wood ants and its symbiotic aphid *Symydobius oblongus* at lower elevations. *P. ruficornis* and *Coeliodes* spp. (Coleoptera: Curculionidae) were also abundant in these samples. The Skallovaara mountain was characterized by huge numbers of *Dineura virididorsata* (Hymenoptera: Tenthredinidae) and other sawfly larvae. Sawfly larvae were also abundant in the samples from the Petsikko, Fierbmeluoyddeskaidi and Kamahpelvarri mountains, where *P. ruficornis*, and *Archiearis* sp. and *Lycia pomonaria* (Lepidoptera: Geometridae) larvae were also abundant. Regardless of these differences among mountains, the general features of the fauna were quite similar. The most important difference was the absence of the wood ants from most of the sites: wood ants occurred only in samples of Jesnalvaara and Skallovaara (in 33% and 8% of sampled trees in these mountains, respectively).

As the height of the sampled trees diminished along the mountain slope, we calculated Spearman rank correlations between the tree height and

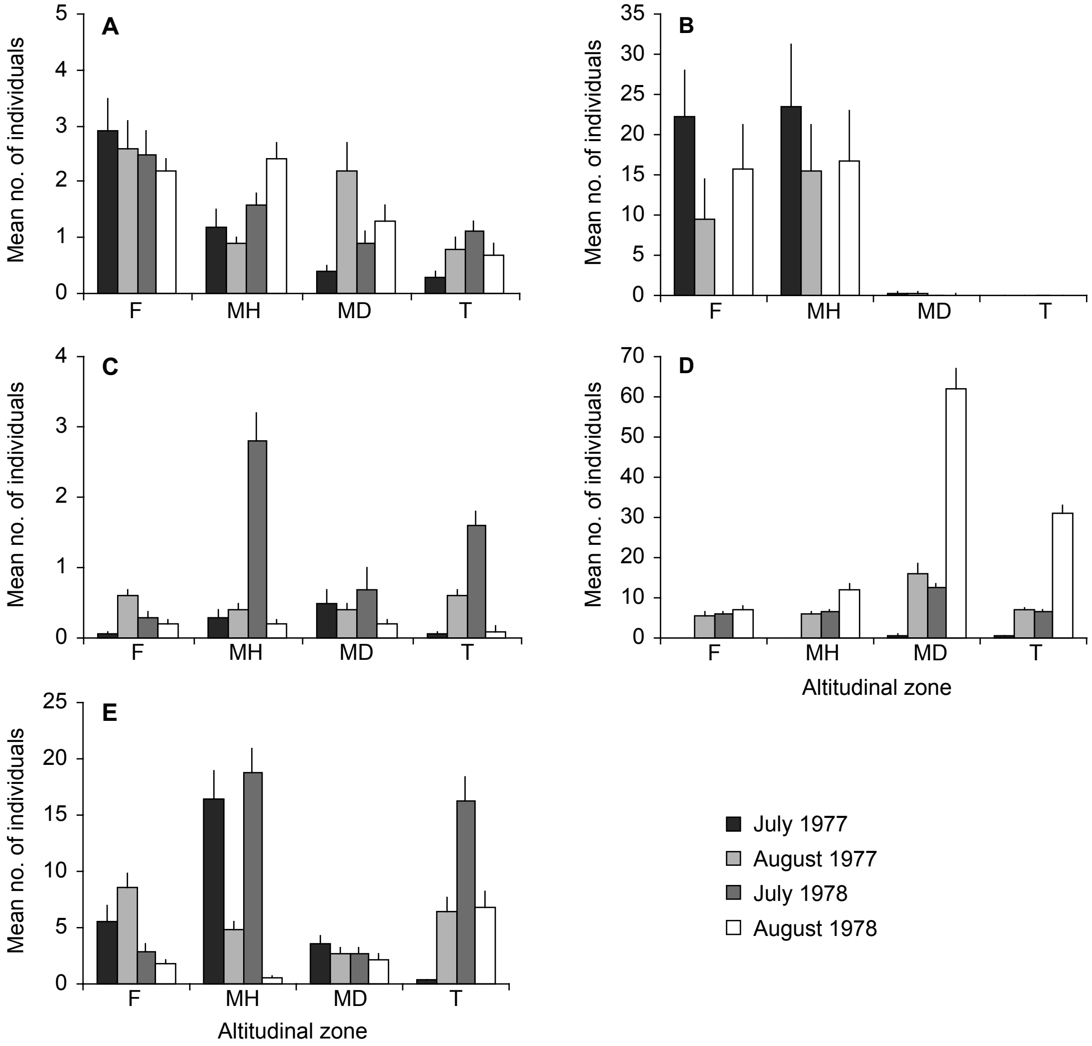

Fig. 1. The average sample sizes (mean + SE) of most abundant invertebrate groups on birches in relation to season (July, August) and altitude (F = mountain foot, MH = midslope-healthy, MD = midslope-damaged, T = mountain top). — **A**: Araneae; — **B**: *Formica aquilonia*; — **C**: Lepidoptera larvae; — **D**: Symphyta; — **E**: Coleoptera. All local-scale sampling sites in 1977–1978 combined (*n* = 700 trees). Note that the scales of the vertical axes differ among the panels.

the abundance of invertebrates for each altitudinal zone (Table 2). The numbers of aphids tended to be positively correlated with the height of the trees at the damaged part of the midslope, whereas cicadellids (Homoptera) showed a negative correlation at higher elevations. Psyllids (Homoptera) occurred in the same numbers regardless of the tree height. The numbers of *F. aquilonia* correlated positively with tree height at mid elevations. Sawfly larvae correlated negatively with the tree height at the midslope and positively at the top (in areas where wood ants were absent). However, if we take the number of tests performed into account (Bonferroni correction of the risk level), only three of the correlations remain statistically significant (ants, and aphids at the damaged part of the midslope). No statistically significant correlations were found between the height of the trees and the abundance of canopy invertebrates in the larger data set (the regional-scale data, *n* = 100, collected at midslope altitudes susceptible to *Epirrita* outbreaks; Table 2).

Altitudinal variation

For altitudinal comparisons, we used four different subsets of trees in July and August 1977–1978 (Table 3). In these analyses we used only sampling sites from which we had data for all altitudes (for the sample sizes *see* Table 1). The altitudinal gradient was fairly clear for most of the invertebrate groups. Spiders, wood ants and the aphid *S. oblongus* tended to be most abundant at the mountain foot, whereas the abundance of sawfly larvae increased with elevation, this effect being highest at the damaged part of the mid elevations in all analyses (Table 3). For beetles and hemipterans, the pattern varied according to the sampling season and year (Table 3).

The proportion of chewed or mined leaves may have increased with increasing altitude (ca. 26%, 39% and 39% at mountain foot, midslope and top, respectively; Fig. 2; tested using a robust χ^2-test using samples pooled for the four altitudinal zones, F, MH, MD and T: $\chi^2_3 = 678.7$, $p < 0.001$), as expected on the basis of our results on herbivore distribution along the altitudinal gradient. The density of wood ants at the sampling sites showed an opposite trend (Table 3), thus it was impossible to separate the effects of altitude and wood-ant predation. At lower elevations, however, the proportion of damaged leaves seemed to be smaller in areas with wood-ant colonies than in areas without wood ants (22% *vs.* 34% and 34% *vs.* 45% in pooled samples at mountain foot and midslope, respectively; Fig. 2; tested using a robust χ^2-test using samples pooled for the absence *vs.* presence of ants in the two lowest altitudinal zones: $\chi^2_1 = 396.9$, $p < 0.001$).

Seasonal variation

For seasonal comparisons, we analysed the three years 1977–1979 separately (Table 4). In these analyses we used only sampling sites from which we had data for both early and late seasons (for the sample sizes *see* Table 1). For most of the invertebrate groups, the seasonal occurrence pattern was quite clear in all the years. Hemipterans, beetles, and moth larvae tended to

Table 2. Spearman rank correlation coefficients (r_s) between the numbers of invertebrates and tree height at different altitudinal zones (F = mountain foot, MH = midslope-healthy, MD = midslope-damaged, and T = top) in: (**A**) local-scale (July 1978) and (**B**) regional-scale (July 1983) data.

A	Altitudinal zone			
Group/data	F	MH	MD	T
F. aquilonia	–0.348	0.816**	0.781***	–
Psyllidae	0.346	0.025	0.309	0.152
Cicadellidae	0.129	–	–0.561**	–0.564*
Aphididae	–0.302	0.588	0.641***	–
Symphyta larvae	0.023	0.223	–0.489**	0.539*
No. of trees	26	10	31	16

B	Midslope	
Group/data	r_s	p
Araneae	0.032	0.749
Euceraphis punctipennis	–0.055	0.588
Lepidoptera larvae	0.035	0.732
Syrphidae larvae	–0.087	0.387
Symphyta larvae	0.073	0.469
Coleoptera	–0.171	0.090
No. of trees	100	

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

be more numerous in the early season, whereas sawfly larvae were more abundant in the late season (Table 4).

Year-to-year variation

For year-to-year comparisons, we used a smaller data set for August in three years (1977–1979), a larger data set for August in two years (1977–1978), and a data set for July in two years (1977 and 1979) (Table 5). In the comparisons, we used only sampling sites with data for all the years (for the sample sizes *see* Table 1). In the three-year comparisons, the numbers of wood ants were lower in 1979, whereas sawfly larvae were more abundant in 1978 than in other years (Table 5). In the two-year comparisons of the

Table 3. Mean number of invertebrates in the samples from birches at different altitudinal zones (F = mountain foot, MH = midslope-healthy, MD = midslope-damaged, and T = top) in July and August 1977–1978, tested with Kruskal-Wallis (H_3; note that Kruskal-Wallis tests differences among the medians, not the means) and log-likelihood ratio tests (G^2_3; G^2 tests whether the occurrence in low *vs.* high numbers is dependent on altitude). The letter code (a–d) indicates the locations of differences among the altitudinal zones: zones sharing a letter do not differ from each other (according to *a posteriori* tests after Kruskal-Wallis at $\alpha < 0.05$). Note that the sample subsets refer to different sampling sites.

Data subset	Group	Altitudinal zone				*H*	*p*	G^2	*p*
		F	MH	MD	T				
July 1977									
	Araneae	2.90	1.20	0.40	0.30			27.28	0.000
	F. aquilonia	22.20	23.55	0.30	0.00				
	Hemiptera	1.00	0.00	1.75	0.00				
	Coleoptera	5.55a	16.40b	3.55a	0.25c	45.96	0.000	43.40	0.000
	Lepidoptera larvae	0.05	0.25	0.45	0.05				
	Symphyta larvae	0.00	0.05	0.60	0.30				
	S. oblongus	4.40	6.25	0.00	0.00				
	No. of trees	20	20	20	20				
August 1977									
	Araneae	2.58	0.87	2.15	0.75			19.33	0.000
	F. aquilonia	9.35	15.62	0.33	0.02				
	Hemiptera	1.40	0.60	1.50	1.28				
	Coleoptera	8.55a	4.75bc	2.63b	6.50ac	21.77	0.000	10.16	0.017
	Lepidoptera larvae	0.58	0.40	0.35	0.60				
	Symphyta larvae	5.43a	5.93a	16.23b	7.02a	31.74	0.000	23.20	0.000
	S. oblongus	9.95	2.70	0.00	0.00				
	No. of trees	40	60	40	60				
July 1978									
	Araneae	2.45	1.58	0.93	1.07			14.00	0.003
	F. aquilonia	0.03	0.02	0.00	0.00				
	Hemiptera	17.23a	3.73a	1.00b	2.03b	45.26	0.000	37.17	0.000
	Coleoptera	2.88a	18.73b	2.55a	16.27b	81.80	0.000	92.00	0.000
	Lepidoptera larvae	0.25	2.78	0.68	1.55			46.58	0.000
	Symphyta larvae	5.93a	6.45a	12.33b	6.50a	29.76	0.000	18.25	0.000
	No. of trees	40	60	40	60				
August 1978									
	Araneae	2.18	2.37	1.25	0.68			17.48	0.001
	F. aquilonia	15.84	16.83	0.08	0.00				
	Hemiptera	3.29	1.92	1.93	7.15			11.30	0.010
	Coleoptera	1.68	0.57	2.08	6.75				
	Lepidoptera larvae	0.20	0.18	0.20	0.13				
	Symphyta larvae	7.15a	12.17b	62.18c	30.78c	138.53	0.000	131.94	0.000
	S. oblongus	3.15	3.67	0.00	0.00				
	No. of trees	80	60	40	40				

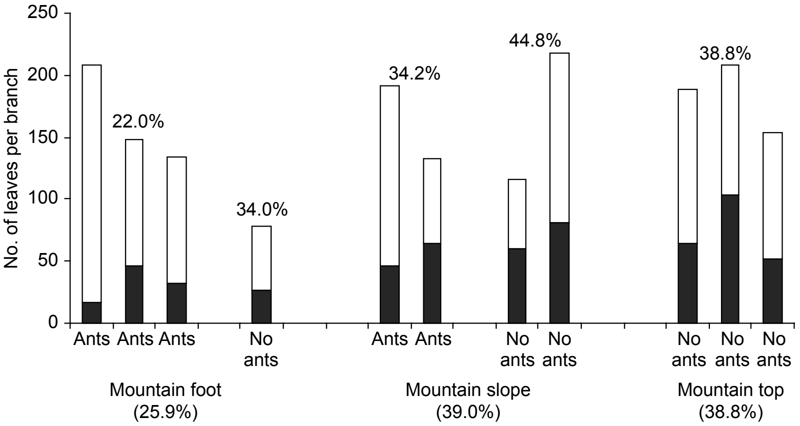

Fig. 2. The degree of herbivory in different altitudinal zones in areas with and without wood-ant colonies, calculated as weighted mean number of leaves per mountain-birch branch (weighting factor was the no. of branches included in each pooled sample). The mean percentages are given both for different altitudinal zones (in parentheses below the graph) and for areas with and without wood ants (above the bars) within the altitudinal zones. White part of the bar = untouched leaves, black part of the bar = chewed or mined leaves.

Table 4. Mean number of invertebrates in the samples from birches in different months (July and August 1977–1979), and Mann-Whitney (*U*; note that Mann-Whitney tests differences among the medians, not the means) and log-likelihood ratio test statistics (G^2_1; G^2 tests whether the occurrence in low *vs.* high numbers is dependent on month). Note that the sample subsets refer to different sampling sites.

Data subset	Group	Month		*U*	*p*	G^2	*p*
		July	Aug.				
1977							
	Araneae	1.20	1.55			0.27	0.607
	F. aquilonia	11.51	16.56				
	Hemiptera	0.69	0.65				
	Coleoptera	6.44	6.41	2944.50	0.380	0.00	1.000
	Lepidoptera larvae	0.20	0.23				
	Symphyta larvae	0.24	4.84				
	S. oblongus	2.66	7.00				
	No. of trees	80	80				
1978							
	Araneae	1.74	2.32			2.04	0.153
	F. aquilonia	0.02	1.19				
	Hemiptera	8.31	4.47	8667.00	0.006	4.96	0.026
	Coleoptera	6.58	2.57			27.34	0.000
	Lepidoptera larvae	0.85	0.17				
	Symphyta larvae	38.10	27.30	3271.50	0.000	43.02	0.000
	S. oblongus	0.00	0.00				
	No. of trees	120	120				
1979							
	Araneae	0.75	0.45				
	F. aquilonia	10.75	33.05	196.50	0.924	0.40	0.527
	Hemiptera	16.50	0.25			34.41	0.000
	Coleoptera	0.90	0.55				
	Lepidoptera larvae	0.25	0.00				
	Symphyta larvae	2.65	1.80	223.00	0.523	0.10	0.749
	S. oblongus	37.70	3.35			1.63	0.202
	No. of trees	20	20				

larger data sets for August 1977–1978, beetles were more abundant in 1977, whereas sawfly larvae were more numerous in 1978 (Table 5). In the two-year comparison for July 1977 and 1979, beetles were more numerous in 1977, whereas *S. oblongus* was more abundant in 1979 (Table 5).

Ant-invertebrate relations and external factors

For the analyses on the relations between wood ants and invertebrates as a function of altitude, season and year, we used only such data from lower elevations where wood ants were present (F, MH, MD) (Table 6). In addition, we used only such sampling sites for seasonal and year-to-year comparisons from which we had data for both early and late season or for both 1977 and 1978, respectively (for the sample sizes *see* Table 1).

Altitude

In the 1977 data, a saturated model (df = 0) for spiders fitted the data best (Table 6). When we compared the observed cell frequencies with those expected for a model from which the three-variable interaction term (Altitude × Araneae × *Formica*) was removed (i.e. for the model Altitude × Araneae, Altitude × *Formica*, *Formica* ×

Table 5. Mean number of invertebrates in the samples from birches in different years (1977–1979) and Kruskal-Wallis (H_2) or Mann-Whitney (U; for comparisons of two groups; note that Mann-Whitney and Kruskal-Wallis test differences among the medians, not the means) and log-likelihood ratio test statistics ($G^2_{1 \text{ or } 2}$; G^2 tests whether the occurrence in low *vs.* high numbers is dependent on year). The letter code (a–c) indicates the locations of differences among the years: years sharing a letter do not differ from each other (according to *a posteriori* tests after Kruskal-Wallis at $\alpha < 0.05$). Note that the sample subsets refer to different sampling sites.

Data subset	Group	Year			H or U	p	G^2	p
		1977	1978	1979				
August 1977–1979	Araneae	1.05	0.40	0.45				
	F. aquilonia	46.85ab	50.50b	33.05ac	6.25	0.044	7.19	0.027
	Hemiptera	0.10	0.05	0.25				
	Coleoptera	2.10	0.40	0.55				
	Lepidoptera larvae	0.15	0.05	0.00				
	Symphyta larvae	1.80ac	6.60b	1.80c	24.71	0.000	17.33	0.000
	S. oblongus	8.10	11.00	3.35			1.76	0.415
	No. of trees	20	20	20				
August 1977–1978	Araneae	1.38	1.42				0.68	0.408
	F. aquilonia	11.04	17.81					
	Hemiptera	0.98	1.53					
	Coleoptera	6.47	2.55		10656.50	0.000	31.00	0.000
	Lepidoptera larvae	0.37	0.13					
	Symphyta larvae	5.68	17.01		3723.50	0.000	23.49	0.000
	S. oblongus	4.67	3.93					
	No. of trees	120	120					
July 1977 and 1979	Araneae	1.20		0.75			3.23	0.073
	F. aquilonia	23.55		10.75	218.00	0.625	0.40	0.527
	Hemiptera	0.00		16.50				
	Coleoptera	16.40		0.90	389.00	0.000	39.57	0.000
	Lepidoptera larvae	0.25		0.25				
	Symphyta larvae	0.05		2.65				
	S. oblongus	6.25		37.70	162.00	0.299	5.38	0.020
	No. of trees	20		20				

Araneae, $G^2_2 = 4.57$, $p = 0.102$), we found out that the relation between spiders and wood ants was negative only at the damaged midslope sites, and positive at lower elevations. The best model for hemipterans and sawfly larvae indicated that in addition to these herbivores being dependent on altitude, wood ants affected them negatively regardless of the altitude (Table 6). For beetles, again a saturated model fitted the data best (Table 6): the effect of wood ants was negative at lower elevations, but positive at the damaged part of the midslopes (this interpretation is based on studying the model Altitude × Coleoptera, Altitude × *Formica*, *Formica* × Coleoptera, $G^2_2 = 7.59$, $p = 0.023$, similarly as above).

For the 1978 data, in addition to both being dependent on the altitude, spiders and wood ants interacted negatively with each other (Table 6). For hemipterans, we found that the saturated model (after studying the model without the interaction term, i.e. the model Altitude × Hemiptera, Altitude × *Formica*, *Formica* × Hemiptera, $G^2_2 = 6.84$, $p = 0.033$; Table 6) indicated a negative effect of wood ants at lower elevations, especially at the healthy parts of midslopes, but the interaction was positive at the damaged parts of the midslopes. The abundance of beetles depended on the altitude but not on the abundance of wood ants, whereas the numbers of sawfly larvae were negatively affected by the wood ants regardless of the altitude (Table 6).

Season and year

The numbers of spiders did not depend on either the season or the abundance of wood ants (Table 6). Wood ants affected hemipterans negatively regardless of the season, whereas the abundance of beetles depended on the season but not on wood ants (Table 6). In addition to the season, sawfly larvae were affected negatively by wood ants (Table 6). The abundance of the aphid *S. oblongus* was positively affected by

Table 6. Models on the abundance of invertebrates in birches derived from three-dimensional contingency tables with sampling altitude, month, or year, and the occurrences in low *vs.* high numbers of invertebrates and *Formica aquilonia*. Best models and their likelihood ratio (G^2) statistics for different subsets of trees are given. The data sets are August 1977 (N = 140 trees) and 1978 (N = 180 trees) separately (only mountain foot, midslope-healthy, and midslope-damaged included) (for Altitude), July and August 1977 (for Month; N = 120 trees), and August 1977–1978 (for Year; N = 200 trees). Symphyta includes only larvae. Hemiptera does not include the ant-tended aphid *Symydobius oblongus*.

Data subset	Model	G^2	df	p
Altitude 1977				
	Altitude × Araneae × *Formica*			
	Altitude × Hemiptera, *Formica* × Hemiptera	8.54	4	0.074
	Altitude × Coleoptera × *Formica*			
	Altitude × Symphyta, *Formica* × Symphyta	5.15	4	0.273
Altitude 1978				
	Altitude × Araneae, Altitude × *Formica*, *Formica* × Araneae	3.01	2	0.222
	Altitude × Hemiptera × *Formica*			
	Altitude × Coleoptera, Altitude × *Formica*	4.32	3	0.229
	Altitude × Symphyta, *Formica* × Symphyta	7.42	4	0.116
Month				
	Month, Araneae, *Formica*	4.67	4	0.323
	Month, *Formica* × Hemiptera	0.31	3	0.959
	Month × Coleoptera, *Formica*	2.05	3	0.562
	Month × Symphyta, *Formica* × Symphyta	2.20	2	0.333
	Month, *Formica* × *Symydobius*	3.29	3	0.350
Year				
	Year × *Formica* × Araneae			
	Year, *Formica* × Hemiptera	3.34	3	0.342
	Year × Coleoptera, *Formica* × Coleoptera	3.02	2	0.221
	Year × Symphyta, Year × *Formica*, Formica × Symphyta	0.19	1	0.663

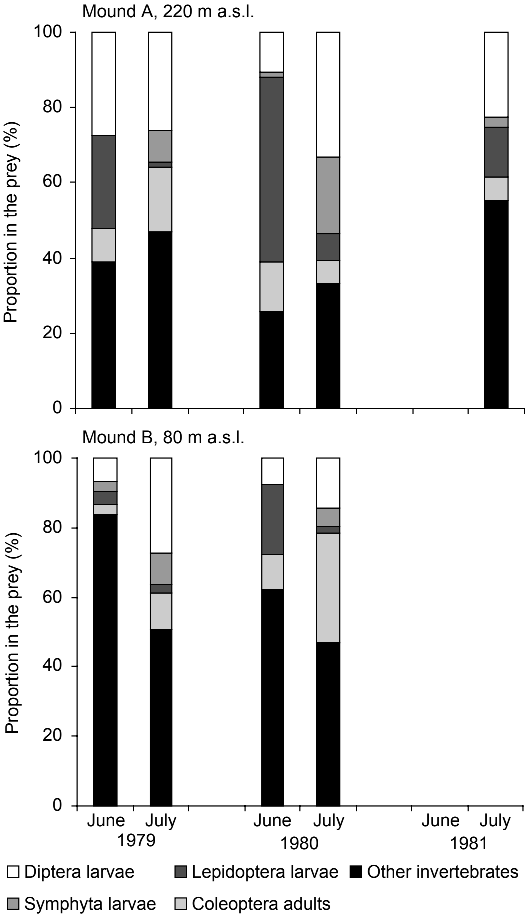

Fig. 3. The proportion of different prey groups in the catches of wood-ant workers in two mounds at different elevations in the nine samples taken in June and July 1979–1981. Mound A situated at the midslope, and Mound B at the mountain foot.

wood-ant abundance regardless of the season (Table 6).

In regard to the sampling year, a saturated model for spiders (Table 6) indicated that they were negatively associated with wood ants in 1978, but positively in 1977 (interpretation based on the reduced model Araneae × Year, *Formica* × Year, *Formica* × Araneae, $G^2_1 = 5.83$, $p = 0.020$, similarly as above). The abundance of hemipterans was negatively affected by wood ants regardless of the year, whereas the abundance of beetles depended on the year in addition to a negative effect of wood ants in both years (Table 6). Both sawfly larvae and wood-ant abundance depended on the year, and the effect of wood ants on sawfly larvae was negative in both years (Table 6).

Prey collected by the wood ants

Dipterans were the most abundant invertebrate prey group for wood ants, sawfly and moth larvae being the next most numerous (Fig. 3 and Appendix 3). Generally, dipterans and moth larvae were caught proportionally more often by the workers at the midslope than at the mountain foot (distribution of prey among the five prey categories in Fig. 3 tested with a robust χ^2-test using samples of years 1979–1980 pooled for the two altitudinal zones: $\chi^2_4 = 64.7$, $p < 0.001$). It seemed that the taxonomical composition of the prey was different according to the month (tested using samples of years 1979–1980 pooled for the two months: $\chi^2_4 = 117.2$, $p < 0.001$), and to the year (tested using samples pooled for the two years, 1979 and 1980: $\chi^2_4 = 24.6$, $p < 0.001$).

Discussion

Spatial and temporal variation in the abundance of the invertebrates

Our data contributes to the knowledge on the general features of the invertebrate fauna of subarctic birch forests. These features are fairly well known owing to extensive work at the Kevo Subarctic Research Station (summarized in, e.g., Haukioja & Koponen 1975a, 1975b, Koponen 1983) and elsewhere (Tenow 1963, Hågvar 1972, 1976, Koponen 1978, 1980a, 1980b, 1983, Koponen & Iso-Iivari 1978). Our results on the altitudinal distribution of invertebrates support earlier results by Hågvar (1972), Haukioja *et al.* (1973), Haukioja and Koponen (1975a), Koponen and Iso-Iivari (1978), Koponen (1981) and Oksanen *et al.* (1981). The relationship between the abundance of invertebrates and altitude was visible also on the level of herbivory along the altitudinal gradient (*see* also Tenow 1990). Hågvar (1976), however, found that the number of species and the densities of most invertebrate groups decreased with increasing altitude. This may be attributable to the mountain-height range covered by his study: some of the sampling sites were much higher on the mountain slopes than the sites in the present study.

An important factor affecting the numbers of invertebrates per tree presumably is the density of birches. The abundance of invertebrates per tree increased with increasing altitude, whereas the density and above-ground biomass of birches show an opposite trend (Haukioja *et al*. 1978). The herbivores seemed to be packed on the sparse birches at higher elevations, which was reflected in the higher degree of herbivory at the mountain tops and upper slopes.

Most of the identified invertebrate groups were more abundant early in the season than in the late summer, with the notable exception of sawfly larvae (mainly Tenthredinidae), which were the only abundant herbivores in the late-summer. Most tenthredinidaean sawfly females need leaf tissue for egglaying (Smith 1993), whereas moth females feeding on boreal deciduous trees commonly lay eggs before the leaves have developed or in the previous autumn, and the eggs or young larvae overwinter (Niemelä *et al*. 1982). Thus, *Epirrita* outbreaks early in the season presumably affect sawfly populations in autumn and this effect may be seen for some years after the outbreak (Nuorteva 1966, Hågvar 1976). It is possible that predation by the wood ants affects more seriously the early-season herbivores, e.g., the moth larvae, because wood ants have their highest protein demand in the beginning of the summer while they rear sexual brood.

Our data indicate that the aphid *E. punctipennis* had a mass outbreak in 1983. This was clearly observable in almost all sampling sites in the regional approach of our study, which reflected the regional character of such phenomena (*see* Tenow 1972).

The role of the wood ants in structuring the invertebrate community

Wood-ant colonies in subarctic birch forests are restricted to the lower elevations of the mountains, e.g. to river valleys (Laine & Niemelä 1989), whereas the *Epirrita* damage typically occurs at higher elevations. Several explanations for the latter phenomenon have been proposed: (1) the winter climate (“cold-air lakes”) at lower elevations kills the eggs of *E. autumnata* (Tenow 1972, 1975, 1983, Niemelä 1979), (2) the nitrogen content of the leaves may be higher at the harsh conditions on upper slopes, presumably providing better-quality leaves for herbivores (for birch, *see* Haukioja *et al*. 1985; for Scots pine, *see* Niemelä *et al*. 1987), and (3) predation by wood ants reduces the numbers of leaf-chewing herbivores at lower elevations in wood-ant territories (Laine & Niemelä 1980, Niemelä & Laine 1986). Our data indicate that (1) the effects of wood ants are remarkable on most invertebrate groups, (2) these effects were observable at all elevations where the wood ants existed, and (3) the negative effect was quite stable in time (over the season and years). Further, herbivores were found to comprise a large proportion of prey of wood ants. In addition to the indirect protection of birches against herbivores, the wood ants may reduce the growth of the trees by tending the sap-sucking aphids on the trees (Whittaker & Warrington 1985, Rosengren & Sundström 1991, Whittaker 1991, Mahdi & Whittaker 1993, Sipura 2002). In England, however, the net effect of the wood ants on birches was small (Mahdi & Whittaker 1993). In our study area the birches are often killed during the outbreak years of *E. autumnata*. Thus, the ant-aphid-birch-herbivore system differs significantly from more southern ones, perhaps due to the long-term consequences of the outbreaks to the survival of birches: wood ants protect birches against the moth larvae within territories and presumably prevent permanent recession of the timber line at the time of the moth outbreaks. Thus, birches gain long-term advantage at reasonably low yearly costs. The area protected by a single wood-ant mound seems to be ca. 700–1250 m^2 (radius of the green islands is 15–20 m according to Laine & Niemelä 1980), and as the density of wood-ant mounds in continuous polydomous ant colonies in pine forests in river valleys is ca. 3 ha^{-1} (Laine & Niemelä 1989), ca. 21%–38% (or, in the areas of maximum mound density of 6 ha^{-1}, 42%–75%) of the forest in these areas may be safe from total defoliation. At higher elevations, however, the population densities are lower although sparse polydomous colonies sometimes occur in the birch zone (Laine & Niemelä 1989). Nuorteva (1966) approximated that a defoliated and destroyed area would need ca. 100–150 years for recovery. A defoliated forest, however, may recover substantially faster if birch propagules from the "green islands" of birches (Laine & Niemelä 1980) survive around the wood-ant colonies.

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Appendix 1. The total samples of invertebrates from the six mountains in the surroundings of the Kevo station in 1977–1979 in different altitudinal zones (F = mountain foot, MH = midslope-healthy, MD = midslope-damaged, and T = mountain top) in early (July) and late (August) season.

Group	Altitudinal zone								Total
	F		MH		MD		T		
	July	Aug	July	Aug	July	Aug	July	Aug	
Araneae	156	277	134	203	45	136	70	72	1093
Heteroptera									
Psallus betuleti	84	15	123	11	13	9	23	5	283
Homoptera									
Cicadellidae	548	36	40	13	9	18	1	–	665
Psyllidae	32	–	324	2	12	–	2	–	372
Aphidae	23	186	46	109	41	110	96	358	969
Euceraphis punctipennis	22	82	21	21	–	–	–	–	146
Symydobius oblongus	88	650	879	449	–	–	–	–	2066
Neuroptera									
Hemerobiidae larvae	–	12	1	7	–	1	–	–	21
Lepidoptera									
Poecilocampa populi larvae	–	15	1	2	–	–	8	3	29
Trichiura crataegi larvae	–	–	1	–	–	–	–	–	1
Achlya flavicornis larvae	–	4	5	1	2	2	2	–	16
Archiearis sp. larvae	1	4	33	4	9	–	30	4	85
Epirrita autumnata larvae	–	–	4	–	4	–	4	2	14
Lycia pomonaria larvae	7	1	123	16	12	13	46	28	246
Other Geometridae larvae	3	2	10	5	9	6	4	4	43
Notodontidae larvae	–	1	–	–	–	–	–	–	1
Diptera									
Syrphidae larvae	1	–	–	1	–	1	–	–	3
Hymenoptera									
Trichiosoma sp. larvae	8	18	2	25	22	103	7	35	220
Dineura virididorsata larvae	25	264	34	474	5	1910	5	276	2993
Other Symphyta larvae	204	507	405	623	478	1123	384	1341	5065
Formica gagatoides	45	17	29	3	–	15	15	3	127
Formica aquilonia	445	1641	687	2608	6	16	–	1	5404
Coleoptera									
Staphylinidae	67	75	361	43	46	6	101	13	712
Cantharis sp.	15	13	51	1	8	2	31	6	127
Malthodes sp.	15	15	22	2	–	–	–	5	59
Nitidulidae	–	–	2	–	–	–	–	–	2
Coccinellidae larvae	1	1	7	–	–	–	–	–	9
Phyllodecta polaris	1	5	–	7	–	–	–	1	14
Other Chrysomelidae larvae	–	37	–	13	–	–	34	–	84
Polydrusus ruficornis	2	314	672	239	45	176	805	484	2737
Coeliodes sp.	109	1	327	3	58	–	3	–	501
Other Coleoptera	16	16	28	22	16	4	7	151	260
Other insecta	–	–	18	9	–	–	–	–	27
Total	1918	4209	4390	4916	840	3651	1678	2792	24394
No. of trees sampled	60	120	100	140	60	80	80	100	740

Appendix 2. The total samples of invertebrates from the ten mountains at altitudes susceptible to *Epirrita autumnata* mass outbreak in July 1983. Ten mountain birches per site were sampled. Mountain abbreviations are: JS = Jesnalvaara slope, JT = Jesnalvaara top, PU = Puksalskaidi, SK = Skallovaara, PE = Petsikko, TS = Tsieskadasoaivi, KA = Karigasniemi Ailigas, KI = Kistuskaidi, UT = Utsjoki Ailigas, and MI = Mierasrova.

Group		Mountain										Total
		JS	JT	PU	SK	PE	TS	KA	KI	UT	MI	
Araneae		4	5	23	3	4	11	5	2	0	11	68
Hymenoptera												
	F. aquilonia	217	0	0	0	0	0	0	0	0	0	217
	F. gagatoides	0	39	0	0	0	0	1	51	0	11	102
	Symphyta larvae	8	27	46	4	28	11	60	25	15	23	247
Heteroptera		18	0	2	0	0	0	1	1	0	6	28
Diptera												
	Syrphidae larvae	4	17	5	12	31	9	27	94	12	5	216
Coleoptera												
	Curculionidae	0	15	0	0	84	15	4	2	0	5	125
	Cantharis spp.	3	78	0	0	0	0	0	0	0	0	81
	Chrysomelidae larvae	0	0	0	0	0	0	0	34	0	1	35
	Coccinellidae	0	0	1	0	0	2	9	3	1	0	16
Homoptera												
	Cicadellidae	0	0	5	0	0	0	0	0	0	0	5
	S. oblongus	34	0	0	0	0	0	0	0	0	0	34
	E. punctiventris	149	225	326	22000	11500	1190	900	35010	22000	960	94260
Lepidoptera												
	E. autumnata larvae	1	1	0	0	7	18	15	0	2	3	47
	P. pomonaria larvae	0	0	1	0	8	1	0	1	0	1	12
	T. crataegi larvae	0	0	0	0	0	0	0	0	0	1	1
Total		438	407	409	22019	11662	1257	1022	35223	22030	1027	95494
Total excl. *E. pun*		289	182	83	19	162	67	122	213	30	67	1234

Appendix 3. The prey of *Formica aquilonia* mounds A and B on different altitudinal zones (F = mountain foot, and MH = midslope-healthy) in June and July 1979–1981.

Group		Wood-ant mound: altitude (zone)									Total
		A: 220 m a.s.l. (MH)					B: 80 m a.s.l. (F)				
		June		July			June		July		
		1979	1980	1979	1980	1981	1979	1980	1979	1980	
Lumbricidae		–	–	–	–	–	–	–	–	1	1
Pulmonata		–	–	–	–	–	1	2	–	4	7
Acarina		–	–	–	–	1	–	–	2	2	5
Araneae		5	4	3	5	23	3	5	4	–	52
Collembola		–	–	–	1	–	–	–	–	–	1
Blattodea		1	1	–	4	7	1	2	–	4	20
Psocoptera		–	–	1	2	–	–	–	2	2	7
Heteroptera		1	1	1	–	21	–	4	–	–	28
Homoptera											
	Cicadellidae	–	1	1	4	4	–	5	1	2	18
	Aphididae	–	–	5	1	71	–	7	13	11	108
	Psyllidae	2	1	2	11	5	54	2	1	21	99
Neuroptera											
	Hemerobiidae larvae	–	–	1	–	8	1	7	–	–	17
Lepidoptera											
	Geometridae larvae	18	40	–	4	28	–	18	1	2	111
	Other larvae	8	2	1	2	17	3	–	1	1	35
Diptera											
	Syrphidae larvae	1	2	–	–	1	1	3	–	–	8
	Other larvae	28	7	21	28	75	4	4	21	21	209
Hymenoptera											
	Symphyta ad.	16	9	–	–	3	2	11	–	1	42
	Symphyta larvae	–	1	7	17	9	2	–	7	8	51
	Parasitica	4	2	–	–	8	–	3	2	1	20
	Formicidae	12	3	–	–	34	–	8	12	18	87
Coleoptera											
	Carabidae	2	2	1	3	1	1	3	–	15	28
	Staphylinidae, Cantharidae, Nitidulidae	–	–	–	1	3	1	6	8	6	25
	Coccinellidae larvae	–	–	–	–	–	–	–	1	1	2
	Elateridae, Chrysomelidae, Curculionidae	7	9	13	1	16	–	–	–	25	71
Other Insecta		–	–	24	–	1	–	–	1	1	27
Total		105	85	81	84	336	74	90	77	147	1079
Observation time (h)		4	1	1	4	6	4	1	1	4	26