The canopy arthropods of old and mature pine *Pinus sylvestris* in Norway

Karl H. Thunes, John Skarveit and Ivar Gjerde

Thunes, K. H., Skarveit, J. and Gjerde, I. 2003. The canopy arthropods of old and mature pine *Pinus sylvestris* in Norway. – Ecography 26: 490–502.

We fogged 24 trees in two pine dominated forests in Norway with a synthetic pyrethroid in order to compare the canopy-dwelling fauna of arthropods between costal (Kvam) and boreal (Sigdal) sites and between old (250–330 yr) and mature (60–120 yr) trees at Sigdal. Almost 30 000 specimens were assigned to 510 species; only 93 species were present at both sites. Species diversity, as established by rarefaction, was similar in old and mature trees. However, the number of species new to Norway (including nine species new to science) was significantly higher in the old trees. We suggest that the scarcity of old trees, habitat heterogeneity and structural differences between old and mature trees may explain these patterns. Productivity and topographic position at the site of growth explained the between-tree variation in species occurrence for the more abundant species, which were mainly Collembola and Oribatida. Species diversity was similar at the boreal and coastal sites, but there were clear differences in species composition.

K. H. Thunes (karl.thunes@skogforsk.no) and I. Gjerde, Norwegian Forest Research Inst., Fanaflaten 4, N-5244 Fana, Norway. – J. Skartveit, Museum of Zoology, Univ. of Bergen, Muséplass 3, N-5007 Bergen, Norway, (present address: Dept of Ecology and Conservation, Scottish Agricultural College, Ayr Campus, Auchincruive Estate, Ayr, Scotland KA6 5HW.

The initiation of canopy arthropod studies some 25 yr ago initiated a new era within conservation biology, biodiversity, taxonomy and community ecology. The overwhelming number of undescribed species collected from forest canopies, especially in tropical areas, has demonstrated that forest canopies have been a neglected component of the forest ecosystem. Canopy studies of arthropods provide a wealth of new information for scientists studying species abundance, guild relationship, herbivory, host specificity, and spatial and temporal variation (Lowman and Wittman 1996, Stork et al. 1997, Basset 2001, Su and Woods 2001, Foggo et al. 2001, Tanabe et al. 2001, Progar and Schowalter 2002).

Hitherto, studies of arthropod species composition in canopies have largely been concentrated in tropical areas (e.g. Erwin 1982, 1983, 1991, Basset 1991, Walter 1995, chapters in Stork et al. 1997 and references therein, Krüger and McGavin 1998, Walter et al. 1998, Basset 2001, Foggo et al. 2001). Fewer studies of comparable scope have been conducted in temperate and boreal forests. Some works have been published from North America (Voegtlin 1982, Mason 1992, Winchester 1997a, b, Behan-Pelletier and Winchester 1998, Schowalter and Ganio 1998, Walter and Behan-Pelletier 1999, Progar et al. 1999, Su and Woods 2001, Progar and Schowalter 2002). From Europe, Overgaard Nilsen (1975), Hågvar and Hågvar (1975), Overgaard Nilsen and Ejlertsen (1977), Southwood et al. (1982), Gunnarsson (1990), Laine et al. (1990), Pettersson et al. (1995), Pettersson (1996), Prinzing (1997) and Ammer and Schubert (1999) present canopy studies on species other than pine, while canopy arthropods of pine have been investigated by Engel (1941), Höregott (1960),

Basset (1985), Borkowski (1986), Chobotow (1993), Simandl (1993), Cmoluchowa and Lechowski (1993), Bankowska (1994), Cholewicka-Wisniewska (1994a, b), Czechowska (1994), Kolodziejak (1994), Wasowska (1994), Sterzynska and Slepowronski (1994), Ozanne et al. (1997, 2000), Brändle and Rieger (1999). Of these, only the studies by Southwood et al. (1982), Simandl (1993) and Ozanne et al. (1997, 2000) were carried out using canopy fogging or similar techniques.

The Norwegian Forest Research Institute initiated in 1998 a study on the arboreal arthropod fauna of pine trees as part of the project "Biodiversity in Norwegian forests", and this paper presents some of the major findings from that study. We document the arthropod species composition of Scots pine *Pinus sylvestris* canopies in two areas in Norway, and relate differences in species composition and richness to tree variables such as age, site variables and geography. Three questions were addressed: 1) Are old trees more species-rich than mature trees? 2) Are some species restricted to, or strongly associated with, old or mature trees, and which environmental variables correlate with variation in species assemblages? 3) Are there regional differences in species composition and species diversity?

Methods and materials

Study areas

Two study areas were selected to represent either coastal or boreal sites in Norway (Fig. 1). The western study area was Geitaknottane in Kvam municipality in Hordaland County (5°53′E, 60°05′N, 180–200 m a.s.l.), referred to as Kvam. It is a *Pinus sylvestris* dominated coastal forest with *Betula pubescens* as the most common deciduous tree. Scattered individuals of *Sorbus aucuparia*, *Corylus avellana*, *Alnus incana* and *Ilex aquifolium* occur in the subcanopy, whereas *Juniperus communis* prevails in the brush layer. The area has an annual precipitation of 2600 mm, and a mean annual temperature of 7.2°C. For more detailed information about Kvam, see Ihlen et al. (2001). The eastern area, Sigdal (annual precipitation 800 mm, mean annual temperature 3.5°C), is a *P. sylvestris* dominated boreal forest located at Heimseteråsen in Sigdal municipality, Buskerud County (9°25′E, 60°03′N, 400–450 m a.s.l.). In Sigdal, however, *Pinus sylvestris* occurs in varied mixtures with *Picea abies*, forming a gradient in forest types from pine dominated forest on poorer soils to spruce dominated forest on richer soils. *Betula pubescens* and *Populus tremula* are the most common deciduous tree species.

Both study areas are continuous forest with scattered bogs and small lakes. Mature forest covers most of the area in Kvam, whereas young conifer plantations comprise one third of the area in Sigdal. Both areas were
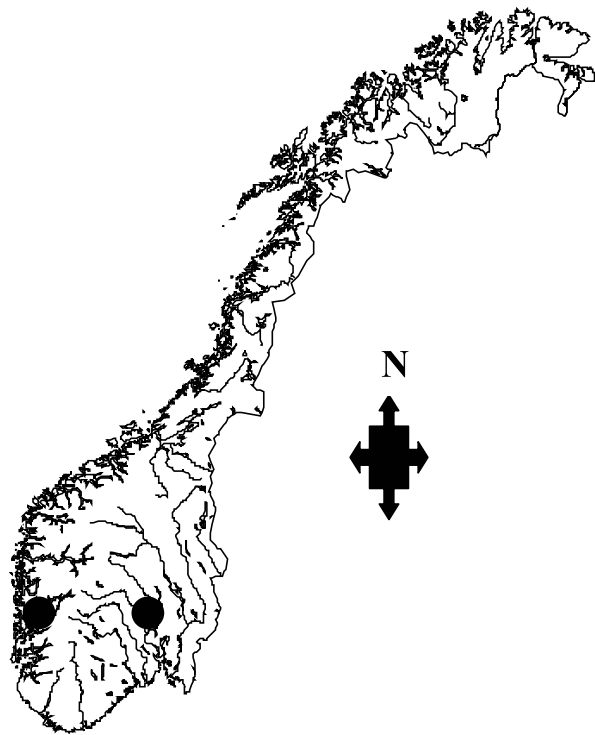

Fig. 1. Study areas in southern Norway: Kvam (west) and Sigdal (east).

selectively cut until ca 1950, resulting in an uneven age structure of trees, with some scattered old pines up to 400 yr in age.

Data collection

From a predefined grid of 100 × 100 m squares, seven easily accessible squares with old trees present, as established from previous investigation of forest history were selected in each study area. In each square one old (250 + yr) and one mature (60–120 yr) tree were chosen and treated as a pair, except in one square at Sigdal where three pairs of trees were selected. These six trees were "paired" post hoc by random selection. The distance between tree pairs was always in the range 15–30 m, and all trees were aged by using increment core samples. The short distance between the old and mature representative ensured similar environmental conditions for the pair. Due to unfavourable weather conditions we only succeeded sampling six trees in Kvam (two old and four mature trees), whereas all 18 trees in Sigdal were sampled.

The arthropods were collected using a 1% solution of a synthetic pyrethroid, "PySekt®" dissolved in non-aromatic white spirit which was applied from the ground using a motorised fogging device. The selected specimens of *P. sylvestris* were treated before sunrise after a

windless and dry night, six trees in Kvam and eighteen trees in Sigdal (Table 2). All trees in Kvam were treated from 26 to 29 May 1998. In Sigdal, three pairs were treated from 5 to 16 June 1998 (tree pairs 1–10, 2–11, 3–12, Table 2), and the remaining six pairs were fogged in the period from 19 June to 17 July 1999. Each tree was treated once. To collect the falling arthropods, 30 cm diameter collecting funnels were placed concentrically on the ground, each circle of funnels spaced by 0.5 m. Within each circle, the funnels were spaced by 1.0 m in Kvam, and by 0.5 in Sigdal. The number of funnels placed on the ground ranged from 27 to 67 (mean = 52.8 ± 18.7) and from 40 to 265 (mean = 115.9 ± 57.2) for any tree in Kvam or Sigdal, respectively. The funnels remained on the ground for approximately one hour after fogging.

Species determination

Forty-one taxonomic experts world-wide, including the authors, were involved in determining the specimens to species (see Acknowledgements). Over 90% of all arthropods collected were identified to species and detailed faunistical results will be presented elsewhere (Thunes et al. unpubl.). Nonetheless, the following taxa could not be identified due to lack of taxonomic expertise or limited time budget: Diptera-Chironomidae and some smaller Diptera families, Hymenoptera other than Formicidae and Symphyta, and Acari other than Oribatida. The material will be deposited in the Norwegian Forest Research Institute's collection at Ås, except for voucher and type specimens retained by the individual taxonomists and their respective collections.

Statistical treatment

To compare richness measures ± SD for old and young trees and among study sites, 500 randomisations of the data were run using the computer program EstimateS ver. 5.0.1 (Colwell 1999) to produce Coleman rarefaction curves. We used individual samples (i.e. number of specimens of a given species in a tree) as input when analysing species richness patterns.

The analysis of differences between old and mature trees was restricted to the Sigdal material, as only two pairs of old and mature trees were sampled in Kvam. However, as no difference in species richness was found for material sampled from old and mature trees in Sigdal, a regional comparison of species richness was carried out using data from all six trees in Kvam (two old and four mature trees) and 18 trees (nine old and nine mature trees) in Sigdal.

We assumed that larger trees would harbor more individuals and consequently more species. In order to "correct" for size or volume in the richness analyses, we

present all results (i.e. species accumulation curves) as species numbers plotted against number of individuals, rather than species numbers on sampling unit (i.e. funnel or tree: Gotelli and Colwell 2001). This was done by averaging the number of individuals over all trees and accumulating the average along the x-axes. Coleman rarefaction curves fit to these data were considered to be significantly different from each other if there was no overlap in the corresponding standard deviations.

Detrended Correspondence Analysis (DCA) and Detrended Canonical Correspondence Analysis (DCCA) were implemented with Canoco ver. 4 (ter Braak and Smilauer 1998) to separate the data into groups of species that were associated with the tree age categories old/mature in an ordination diagram as well as to relate a set of environmental factors to the species data. Detrended CCA was chosen because the gradient length was larger than six standard deviations and an arch was vaguely visible in the ordination of the species. Only species or groups of species that constituted > 0.5% of the total each year were used in the analyses (Table 1). Species abundances were log + 1 transformed and rare species were downweighted. To test for significance of the first ordination axis and the overall DCCA ordination diagram, 999 replications of the Monte Carlo permutation test available with Canoco were performed. Data from 1998 for the Ceratopogonidae from Kvam were not available, and this taxon was thus not included in these analyses.

Environmental data

The following environmental data were recorded for each fogged tree and its associated sampling square: 1) Age: counted growth rings using increment core samples from the tree at breast height. Range: 55–326 yr. Mean: 168.6 ± 102.9 yr. 2) Height: canopy height measured from digital photographs of each tree. Range: 2.2–16.0 m. Mean: 9.5 ± 3.6 m. 3) Cover: density of needles in the tree crown. 0 – dense, 1 – normal, 2 – sparse. Mean: 0.78 ± 0.54; mode = 1. 4) Volume: canopy volume calculated from digital photographs of each tree based on the overall structure of the canopy as a cone, cylinder, sphere, or combinations of these. Range: 20.9–386.9 m^3. Mean: 130.2 ± 114.7 m^3. 5) Width: maximum canopy width measured from digital photographs of each tree. Range: 2.88–6.86 m. Mean: 4.54 ± 1.10 m. 6) Epiphyte: proportion of epiphytic vegetation on the tree. 0 – absent, 1 – sparse, 2 – normal, 3 – dense. Mean: 1.50 ± 0.86; mode = 2. 7) Topopos: topographic position. 1 – flat, 2 – upper part of a south-facing slope. Mean: 1.56 ± 0.51; mode = 2. 8) Productivity: identified using the productivity criteria in Heje and Nygaard (2000). Range: 8–11. Mean: 9.00 ± 1.46. 9) Vegetation: vegetation types, reflecting

Table 1. List of species used in multivariate analyses. Each species constitutes > 0.5% of the total species abundance. Guild definition: Fu – fungivores, Co – cone feeders, To – tourists, Su – suckers, Gr – grazers.

Higher taxa	Species	Guild	N(old)	N(mature)	N(total)
Collembola	*Hypogastrura socialis*	Fu	0	271	271
	Xenylla maritima	Fu	105	14	119
	Entomobrya nivalis	Fu	899	895	1794
	E. marginata	Fu	108	57	165
	Lepidocyrtus lignorum	Fu	1771	469	2240
	Dicyrtomina minuta	Fu	86	37	123
	Deuterosminthurus flavus	Fu	380	100	480
Thysanoptera	*Oxythrips ajugae*	Co	141	67	208
	O. ajugae (juv.)	Co	77	148	225
	O. bicolor	Co	182	158	240
	O. bicolor (juv.)	Co	463	762	1225
Hybotidae	*Euthyneura myrtillii*	To	501	104	605
Muscidae	*Spilogona contractifrons*	To	93	31	124
Sciaridae	*Ctenosciara hyalipennis*	To	109	36	145
Heteroptera	*Loricula pselaphiformis* (juv.)	Su	314	197	511
Auchenorrhyncha	*Aguriahana germari* (juv.)	Su	166	51	217
Psocoptera	*Reuterella helvimaculata*	Gr	88	20	108
	Valenzuela despaxi (juv.)	Gr	164	10	174
Oribatida	*Camisia segnis*	Gr	192	68	260
	Cymberemaeus cymba	Gr	236	192	428
	Phauloppia lucorum	Gr	5504	1654	7158

the richness of the vegetation (Fremstad and Elven 1987). 1 – *Calluna – Vaccinium uliginosum* forest, 2 – *Vaccinium myrtillus* forest. Mean: 1.44 ± 0.51; mode = 1. 10) SumVol: sum of the volume standing live trees. Range: 160–432 m^3 ha^{-1}. Mean: 301.3 ± 111.0 m^3 ha^{-1}. 11) Basarea: basal stem area. Range: 28–64 m^2 ha^{-1}. Mean: 48.0 ± 14.5 m^2 ha^{-1}. 12) Volume *Pinus*: sum of the volume of *Pinus*. Range: 140–320 m^3 ha^{-1}. Mean: 240.0 ± 65.3 m^3 ha^{-1}.

Results

Species richness in old and mature trees

The number of species collected was significantly higher in old trees than in young trees at Sigdal (8 out of 9 cases, Fig. 2, paired sample t-test: $t = -4.00$, $p < 0.005$). Furthermore, there was a positive relationship between number of species collected from old and mature trees in the same sampling square (Fig. 2), suggesting an environmental gradient with impact on species numbers of both old and mature trees at a particular site (linear regression: $R^2 = 0.62$, $F = 11.37$, $p < 0.02$). A higher accumulated number of species was found in old trees than in the same number of mature trees (Fig. 3). However, old trees had larger canopy volumes and consequently a higher number of arthropod specimens were sampled from these trees (Table 2 and 3). When we compared accumulated species numbers in old and mature trees in relation to number of individuals, and thereby removed the bias of canopy volume, there were no differences between old and mature trees (Fig. 4a). The same trend was ob-

tained when only single- and doubletons (locally rare species represented by one or two individuals) were selected and treated in a similar way (Fig. 4b). However, when only species new to Norway were examined (n = 87), the old trees were found to be significantly richer than the mature trees (Fig. 4c), as old trees on average had 25% more species of this group than mature trees.

Twenty-one species were represented with more than 100 specimens in Sigdal. When examining specimen numbers alone (i.e. not "correcting" for canopy vol-
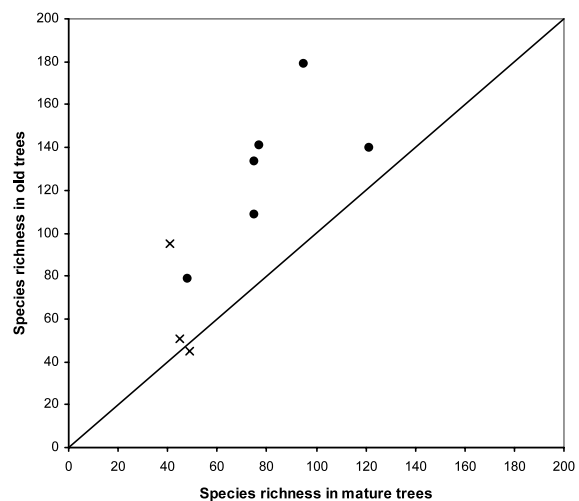

Fig. 2. Number of species from nine pairs of old and mature trees from Sigdal. The diagonal line is a one-to-one line for species numbers in old and mature trees. Crosses indicate species pairs from the one sampling square (see text).
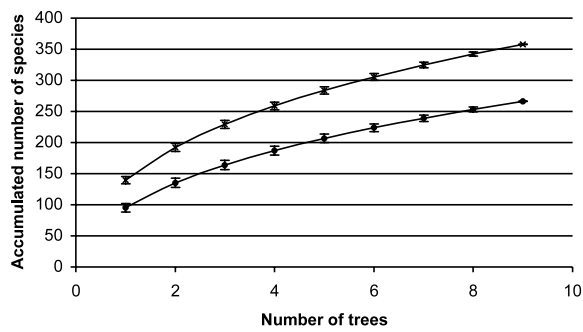
Fig. 3. Coleman rarefaction curves ($\pm$ SD) for mature trees (bottom) and old trees (top) with number of sampled trees.

ume), > 80% of the specimens of four species were in old trees: *Euthyneura myrtillii* Macquart (Diptera – 82.8%), *Reuterella helvimaculata* (Enderlein) (Psocoptera – 83.8%), juvenile *Valenzuela despaxi* (Badonnel) (Psocoptera – 94.3%) and *Xenylla maritima* Tullberg (Collembola – 88.2%). In contrast, all *Hypogastrura socialis* (Uzel) (Collembola) specimens were collected from mature trees in Sigdal. *Euthyneura myrtillii* was probably swarming in one of the old trees as 73.1% of the individuals were sampled from that tree

(tree 7, Table 2). Likewise, 98.1% of all *H. socialis* were sampled from only one tree (tree 12). *Xenylla maritima* was also aggregated (61.3% sampled from tree 2). In contrast, both the psocopterans were rather evenly distributed among the old trees, no single tree accounted for > 35% of the total proportion of specimens collected.

Species composition in relation to tree age and site variables

Overall, 29 732 specimens were identified to 510 species. In 1998, 189 species were found in Kvam and 195 in Sigdal. In 1999, we collected 330 species in Sigdal. In all, 102 species were new to Norway. Of these, nine species were new to science, 3 species new to Europe, and 5 species new to Scandinavia (pers. comm. from taxonomic experts in Acknowledgements, as well as Aakra 2000 and Hagan et al. 2000). In Sigdal, 87 species were new to the Norwegian fauna, and 75 of these were Diptera (Table 3). A higher number of new records were found in the old trees compared with the mature ones, and also more specimens of these species were collected from old trees (Table 3).

Table 2. Tree age measured at breast height, canopy height (m), width (m), volume (m^3) and shape on the fogged trees in Sigdal.

Tree	Number	Age	Height	Width	Volume	Shape
Old	1	270	10.5	6.9	386.9	Cylinder
	2	260	9.5	4.8	175.0	Cylinder
	3	210	10.5	5.4	242.0	Cylinder
	4	300+	2.7	5.9	74.7	Cylinder
	5	326	3.9	3.9	62.5	Two spheres
	6	314	8.4	3.9	100.3	Cylinder
	7	250	16.0	4.9	306.8	Cylinder
	8	250	11.1	4.6	62.7	Cylinder
	9	268	12.8	5.9	349.5	Cylinder
Average $\pm$ SD		256 $\pm$ 32	9.5 $\pm$ 4.1	5.1 $\pm$ 1.0	195.6 $\pm$ 129.6	
Mature	10	72	13.1	3.9	120.2	Cylinder+Cone
	11	72	14.5	3.8	117.7	Cylinder+Cone
	12	70	7.5	4.3	58.7	Cylinder+Cone
	13	80	13.9	4.2	63.9	Cone
	14	75	11.3	5.8	99.9	Cone
	15	67	12.0	3.7	43.1	Cone
	16	117	8.8	3.2	23.2	Cone
	17	55	9.6	2.9	20.9	Cone
	18	110	10.0	3.7	35.2	Cone
Average $\pm$ SD		80 $\pm$ 20	11.2 $\pm$ 2.4	3.9 $\pm$ 0.8	64.8 $\pm$ 39.0	

Table 3. Species and specimen numbers of new species records for Norway (including species new to science) in old and mature trees sampled in Sigdal.

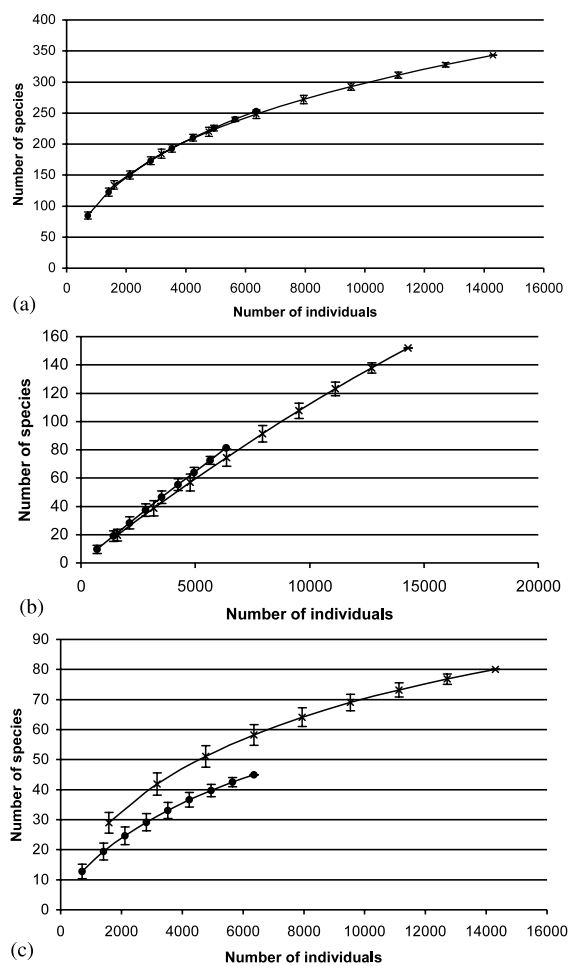| Taxon	Number of new species records			Number of specimens	
	Old trees	Mature trees	Total	Old trees	Mature trees
Thysanoptera	2	1	2	17	13
Diptera	69	36	75	828	270
Araneae	2	1	3	3	1
Oribatida	7	7	7	71	24
Sum	80	45	87	915	312

Fig. 4. Coleman rarefaction curves (± SD) comparing species numbers against numbers of individuals from Sigdal in old (cross) and mature (solid) trees. (a): all species, (b): species with 1 and 2 individuals respectively, representing 50.3% of the total number of species, (c): new species records for Norway (including undescribed species).

Many canopy dwelling species must be assumed to be occasional visitors that use tree crowns as resting or swarming sites. However, the most abundant species may indicate which species are most closely associated with pine canopies. The list of the ten most abundant species (Table 4) is dominated by less motile species (Oribatida and Collembola) as well as herbivores and plant suckers (Thysanoptera and Heteroptera). The hybotid (Diptera) species *Euthyneura myrtilli* Macquart and the ceratopogonid species *Forcipomyia nigrans* Remm, were the only highly vagile species present.

When we included only the most abundant species in a DCA analysis, the first two ordination axes, explaining 25 and 24% of the variation, respectively, did not show a visible age gradient (Fig. 5 and 6). Indeed, none of the environmental factors recorded from trees per se turned out to be important for explaining the faunal differences observed. The important and statistically significant environmental variables, as indicated from forward selection in a CCA analysis previous to the DCCA (Table 5), were productivity (explaining 21% of the variation, Monte Carlo permutation test: F = 8.08, p = 0.001) and topographic position (explaining additionally 7% of the variation, F = 3.20, p = 0.001). The eigenvalues of the first two ordination axes were 0.25 (F = 3.65, p < 0.02) and 0.08 (n.s.), respectively. Overall ordination significance was p < 0.03 (F = 1.78). This indicates that the first ordination axis is predominantly a productivity gradient. Species associated with trees on the more productive soils were all collembolans; *Deuterosminthurus flavus* (Gisin), *Hypogastrura socialis* and *Xenylla maritima*. Species associated with trees on poorer soils were the dipterans *Spilogona contractifrons* (Zetterstedt) and *Ctenosciara hyalipennis* (Meigen), the hemipterans *Loricula pselaphiformis* (juv.) Curtis and *Aguriahana germari* (juv.) (Zetterstedt), the collembolan *Dicyrtomina minuta* (Fabricius), and the oribatids *Camisia segnis* (C. L. Koch), *Cymberemaeus cymba* (Nicolet) and *Phauloppia lucorum* (C. L. Koch). Although poor in explanatory power, the second axis is most likely to represent a climate gradient, as the two local topographic positions recorded here (south-facing slope and flat boggy areas) are related to sun exposure and air humidity. Thus, *D. minuta* and *S. contractifrons* can be inferred to be associated with trees in areas

Table 4. Ranks (in parentheses) for the ten most abundant species.

| Order	Species	Number of specimens			
		Kvam	Sigdal-98	Sigdal-99	Sum
Acari-Oribatida	*Phauloppia lucorum*	24 (21)	1354 (1)	5804 (1)	7182 (1)
Collembola	*Lepidocyrtus lignorum*	204 (2)	285 (5)	1955 (2)	2444 (2)
Collembola	*Entomobrya nivalis*	127 (3)	483 (3)	1311 (3)	1921 (3)
Thysanoptera	*Oxythrips bicolor*	65 (8)	809 (2)	656 (4)	1530 (4)
Diptera-Hybotidae	*Euthyneura myrtillii*	439 (1)	50 (17)	555 (5)	1044 (5)
Hemiptera-Heteroptera	*Loricula pselaphiformis*	0	0	511 (6)	511 (6)
Collembola	*Deuterosminthurus flavus*	0	423 (4)	57 (25)	480 (7)
Thysanoptera	*Oxythrips ajugae*	9 (38)	260 (8)	173 (12)	442 (8)
Acari-Oribatida	*Cymberemaeus cymba*	11 (30)	57 (15)	371 (7)	439 (9)
Diptera-Ceratopogonidae	*Forcipomyia nigrans*	10 (34)	2 (82)	326 (8)	338 (10)
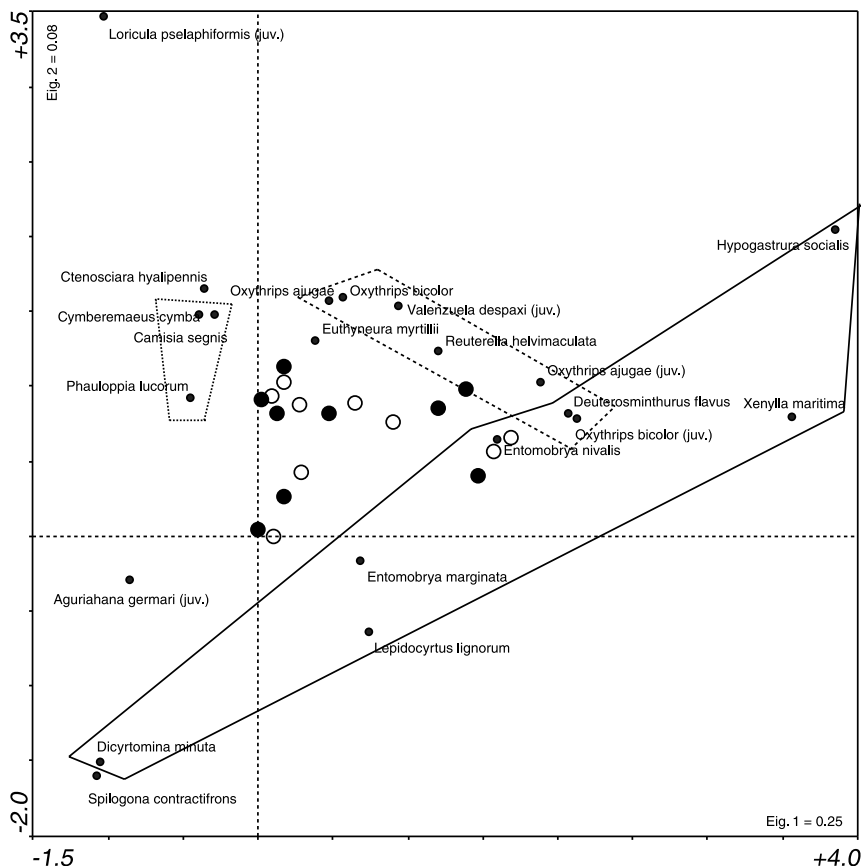
Fig. 5. DCA analysis of abundant species (representing > 0.5% of total specimen numbers) from Sigdal. Closed circles are mature trees while open circles are old trees. Feeding guilds are enclosed by solid lines (fungivores, mostly Collembola), hatched lines (cone feeders, Thysanoptera), or dotted lines (grazers, Oribatida).

exposed to sunlight and heat, and on the other hand, juvenile *L. pselaphiformis*, *C. segnis*, *C. cymba*, *C. hyalipennis*, *P. lucorum* as well as the hybotid *Euthyneura myrtillii* and juveniles of the thysanopterans *Oxythrips ajugae* Uzel and *O. bicolor* (Reuter) were associated with trees on less sun-exposed and more humid areas. Two additional trends are also worth mentioning; the Thysanoptera and Oribatida were grouped nicely together and well separated from the other major groups. Adults of the thysanopterans *Oxythrips ajugae* and *O. bicolor* seem to respond to different environmental factors than do juveniles (Fig. 5) as they were found in greatest numbers in mature trees while their juveniles were mainly found in old trees (Table 1).

Regional and temporal differences

In Kvam, 189 species (3067 specimens) were collected, while similar numbers for Sigdal were 195 species (8643 specimens) in 1998 and 330 species (18 022 specimens) in 1999. Ninety-three species were found in both areas (years combined). In Kvam, 95 species were present that was not found in Sigdal and 321 species were exclusively found in Sigdal (years combined). The shift

in species composition in Sigdal between the two years was large: 71 species were only sampled in 1998, 193 only in 1999.

The Coleman rarefaction curves showed no differences between Sigdal and Kvam (Fig. 7). Although the numbers may be somewhat influenced by the disparity in sampling effort in Sigdal and Kvam, the results indicate that there was no obvious difference in species richness between the two areas. The composition of species differed regionally within the same year (Fig. 8). The first axis explains 47% of the variation, and it is highly likely to represent a gradient related to geography.

Discussion

Many new distribution records resulted from our study. Several previous studies have shown that a specialised conifer canopy fauna exists (e.g. Southwood et al. 1982, Basset 1985, Winchester 1997a, b, Ammer and Schubert 1999, Brändle and Rieger 1999, Winchester et al. 1999) and it is likely that a high proportion of our new records indeed are associated with pine canopies. However, one overall objective of the canopy project was to make as complete a species list as possible of the

Fig. 6. DCCA analysis of abundant species (representing >0.5% of total specimen numbers) from Sigdal. Trees in pairs are enclosed. The group of six trees are samples from 1998, the others were sampled in 1999.
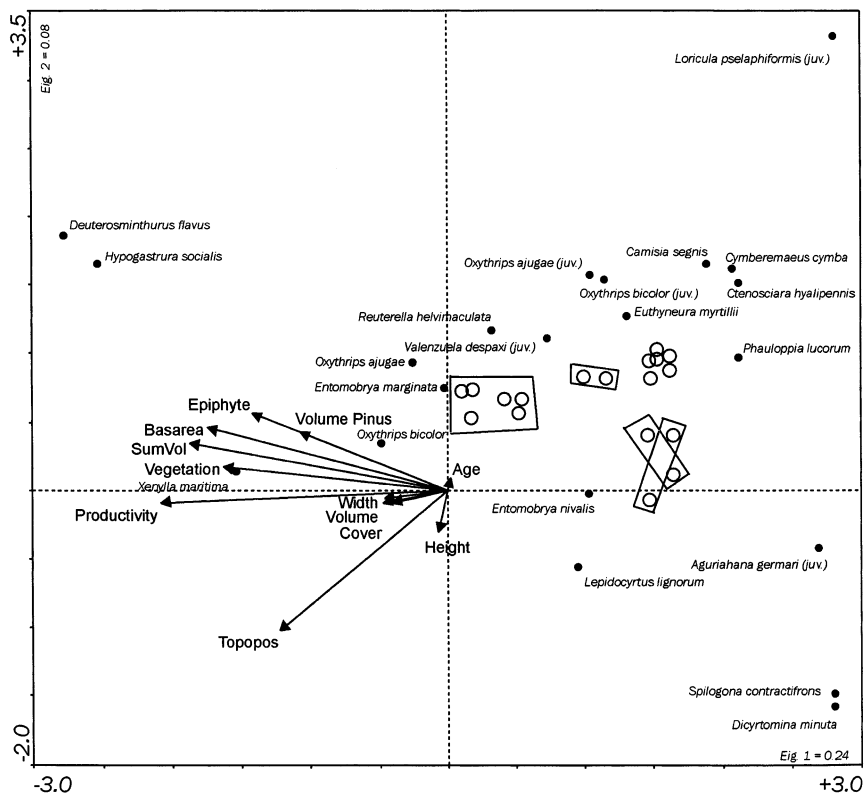
snapshot-fauna that one gathers when sampling with insecticides (Thunes et al. unpubl.). Hence, many taxa that are often neglected when performing quantitative analyses were included here.

Even though few species were found in high numbers, soil dwelling species of Oribatida are known to reside in trees in great numbers (Behan-Pelletier and Winchester 1998, Winchester et al. 1999) and the oribatid *Phauloppia lucorum* was by far the most abundant

species in the pine canopies. All oribatids are considered predominantly wind dispersers (Behan-Pelletier and Winchester 1998) and many oribatids are also known to be residents to the canopies or associated with epiphytes (e.g. Aoki 1973, Walter et al. 1994, Prinzing 1997, Behan-Pelletier and Winchester 1998, Walter and Behan-Pelletier 1999, Winchester and Ring 1999). Some sparsely represented species are certainly arboreal, e.g. carabid species of the genus *Dromius*, the

Table 5. DCCA results for the distribution of species from Sigdal and the significance of environmental variables (see text for explanation). The interset-correlation values show the correlation between the variables and the corresponding DCCA-axes 1 and 2. T-values are the canonical coefficients of the variables. Variance and p-values are the variation explained and the statistical significance (Monte Carlo permutation test) of the individual variable. VIF is the variation inflation factor in which paired values of approximately similar magnitude indicate intercorrelated variables.

| Variable	Inter–set correlation		t-value		Variance	p-value	VIF
	Axis 1	Axis 2	Axis 1	Axis 2			
Productivity	0.91	0.06	2.61	0.51	0.21	0.001	340.65
Topopos	0.55	0.71	−1.95	0.78	0.07	0.001	56.31
Age	−0.10	−0.12	0.17	0.96	0.04	N.S.	7.10
VolumPin	0.46	−0.33	2.24	0.31	0.03	N.S.	99.09
Cover	0.19	0.06	1.55	0.35	0.02	N.S.	4.42
Epiphyte	0.61	−0.38	0.48	−1.23	0.02	N.S.	3.69
Basarea	0.76	−0.34	−2.08	−0.54	0.01	N.S.	360.84
Vegindex	0.71	−0.13	−2.42	−1.11	0.03	N.S.	17.85
Height	0.29	0.23	0.21	0.91	0.01	N.S.	9.63
Volume	0.21	0.04	0.37	0.37	0.02	N.S.	20.15
Width	0.21	−0.01	−0.84	−0.84	0.01	N.S.	6.15
SumVol	0.82	−0.26	0.00	0.00	0.00	N.S.	0.00
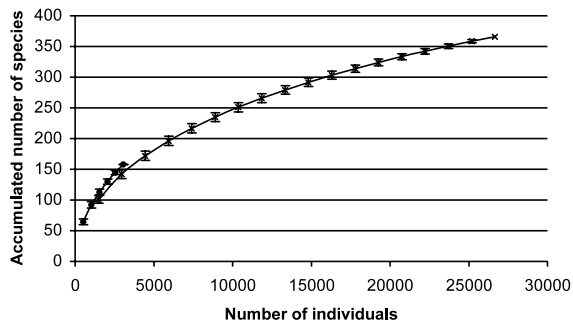
Fig. 7. Coleman rarefaction curves ($\pm$ SD) comparing species numbers against specimen numbers from Sigdal (cross) and Kvam (solid).

thysanopteran genera *Aeolothrips* and *Thrips*, Lepidoptera larvae and the symphytan wasp *Xyela julii*. Many of these species are predators or feed on flowers or cone seeds. In addition, many of the faunistically new records are arboreal in their adult stage (Basset 1985), particularly those species which were abundantly present, such as species of Ceratopogonidae, Empidoidea and Sciaridae.

Other studies in temperate forests (e.g. Hågvar and Hågvar 1975, Tenow and Larsson 1987, Gunnarsson 1990, Laine et al. 1990, Bankowska 1994, Czechowska 1994, Kolodziejak 1994, Pettersson 1996) have shown a relatively higher proportion of arboreal specific species. These studies used methods for qualitative sampling from a small part of the canopy, e.g. branchlet shaking or clipping, arboreal traps or epiphyte sampling (e.g. Hågvar and Hågvar 1975, Tenow and Larsson 1987, Majer and Recher 1988, Bankowska 1994, Majer et al. 1996, Prinzing 1997). Such methods will also collect a number of species that will normally be excluded or underrepresented in fogging samples, simply because the fog knocks out the animals but leaves them suspended in their habitat, as demonstrated by Southwood et al. (1982) and Majer and Recher (1988). Relatively speaking, the main disadvantage with the canopy fog-
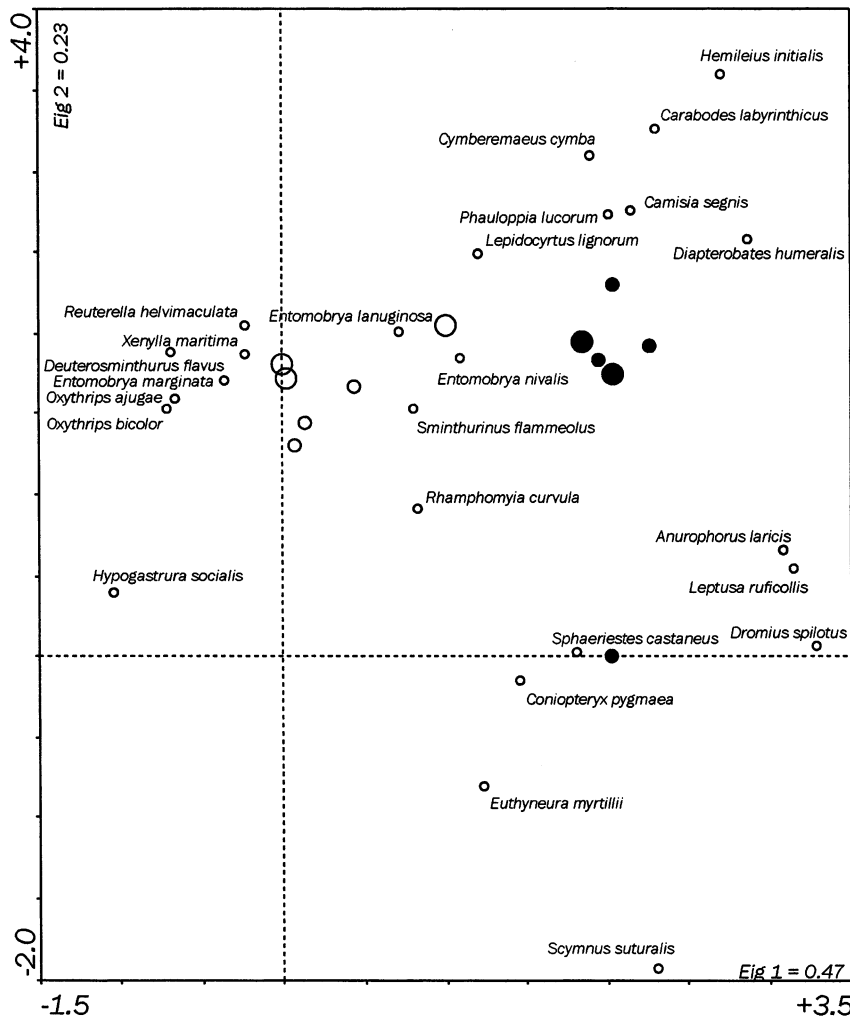

Fig. 8. DCA ordination diagram of abundant species (representing 0.5% of total specimen numbers) sampled from twelve trees in 1998 from Kvam (solid) and Sigdal (open). Old trees are noted with a bigger circle than mature trees.

ging procedure is that a high proportion of non-residents or visitors will be sampled.

Analyses of species richness in old and mature trees showed that old trees were richer than the younger trees due to having broader and more voluminous canopies. As old trees with broad canopies take up more space than younger trees with narrow canopies, a densely stocked forest stand of mature trees may constitute similar or even a larger amount of canopy habitat than a stand of old trees. Therefore, as far as mere species richness is concerned, our results do not indicate a higher diversity of arthropods in old pine stands than in mature pine stands. This was not the case, however, when we considered the new records for Norway, which also included the undescribed species (Fig. 4c). For these species, supposed to be relatively rare on a national scale (not necessarily rare in our material), old trees seem to be of particular importance, and it is not certain that a high number of mature trees can "replace" old trees as habitats for these species. By examining the habitat alone (old/mature trees) without "correcting" for volume, only two species could be assigned old tree associates (> 100 specimens totally and > 80% of the specimens in old trees) while no species was found only in mature trees which did not aggregate on one particular tree.

A few studies have presented results indicating that old trees and old-growth forests are more species rich than younger trees (e.g. Southwood et al. 1982, Wright and Giliomee 1992, Hooper 1996, Martikainen et al. 2000, Sippola et al. 2002). Several studies have presented a unimodal picture at forest stand level, i.e. that middle-aged tree stands are richer in canopy associated species than both the oldest and the youngest stands (e.g. Tenow and Larsson 1987, Simandl 1993, Cholewicka-Wisniewska 1994b, Schowalter 1995). Finally, Sterzynska and Slepowronski (1994) for arboreal spiders in *P. sylvestris* and Bankowska (1994) on pine associated hover flies (Syrphidae) showed that young Polish tree stands (10–20 yr old) had a richer fauna than middle age stands (60 yr old) and mature stands (100 yr old). In contrast to these results, mature pine stands (80–100 yr old) were suggested as refuges for Raphidioptera in a study carried out in Poland (Czechowska 1994).

Comparison of our results with these latter studies is not directly justified as we operated old and mature trees in pairs within a relatively short distance and those termed old trees in most of the other studies are ca 100 yr of age. The oldest trees in our study areas have escaped centuries of selective cutting. These trees are normally not tall trees, but most have relatively large canopy volume. The tallest, most vital trees are most commonly of intermediate age (mature) growing on favourable local sites at the stand level. Thus, one source for biodiversity could be such trees, which are represented by tall, vigorous, nutrient-rich trees available particularly for migrants and occasional visitors (Vaisanen 1992, Brändle and Brandl 2001). However, as pointed out by Southwood et al. (1982), older trees provide a different set of microhabitats than younger trees because of their accumulated associated micro-organisms.

The trees that turned out to be important for new faunistic records and undescribed species, were the old trees – not the tallest trees. Indeed, there was no correlation with tree height and species richness. Vanninen et al. (1996) showed that total tree biomass (from fine root to foliage biomass) increased with age for *P. sylvestris* in Finland. This increase in biomass will certainly represent a higher number of habitats available for associated species, thus higher biodiversity levels of associated species should be expected. Moreover, higher age allows a higher variety of niches, e.g. microflora, lichens, mosses, to develop. With respect to arthropod biomass, however, Hooper (1996) showed a highly variable pattern with age related to dead and live limbs, height along the bole and growth rate for *Pinus palustris*.

The faunistic differences seen in the old trees might also reflect differences in tree chemistry between old and young (mature) trees (Sellin 1996). It is known that some herbivorous vertebrates select old trees for feeding and that the carbon, nitrogen and resin content are important factors (e.g. Bryant et al. 1983, Lindén 1984). For example, Stadler et al. (2001) found that in spruce heavily inhabited by herbivores, the nitrogen contents were lowered compared to trees with fewer herbivores. Furthermore, Wright and Giliomee (1992) showed that gut pH levels of important herbivores of *Protea magnifica* and *P. laurifolia* were adapted to the tannin levels in their hosts. Moreover, Basset (1985) compared the distribution of arthropods between healthy and less vital *Pinus mugo* trees in Switzerland. He found a considerable shift in species and guild composition from healthy trees to trees with reduced vitality. In the less vital trees, tourists, predators and sapsuckers dominated, while tourists, predators and defoliators dominated the healthy ones. A similar pattern was observed in this study, given that productivity can be related to vitality (cf. 1st, axis in Fig. 5). Suckers, grazers and tourists were associated with trees on poor soils, while fungivores dominated trees growing on the more productive soils. No predators or defoliators were included in the multivariate studies due to few specimens.

The DCA and DCCA analyses (Fig. 5, 6 and 8) represent single-species occurrence in individual trees exposed to different environmental regimes. The DCA ordination (Fig. 5) seems to reflect a gradient related to feeding behaviour of the insects. Species from different feeding guilds were separated nicely in the ordination, and by inspecting the raw data underlying the analysed species (Table 1), a higher number of Psocoptera and Oribatida were consistently present in old trees (see also

Winchester et al. 1999), which reflects their habits as alga or lichen feeders. Diverging patterns in arthropod assemblages related to guild structure were also noted by Winchester and Ring (1999). Predominantly flower- and seed-feeding juvenile Thysanoptera were most abundant in mature trees (Table 1), while the adults of the same species were most abundant in the old trees.

Forest productivity and topographic position turned out to be the only significant environmental variables in the direct CCA analysis preceding the DCCA ordination (Fig. 6). This gradient can also be seen in Fig. 2, where species numbers in the three tree-pairs sampled in the same sampling square were plotted similarly. These results relate to tree growth, tree vitality as well as food quality, exposure to wind and excessive sun, which influence arthropod species composition (e.g. Ohmart and Voigt 1981, Basset 1985, Reynolds and Crossley 1997, Richardson et al. 1999).

The Coleman rarefaction species accumulation curve (Fig. 7), suggests no difference in species richness between the canopies treated in the coastal pine forest of Kvam and those in the boreal pine dominated forest of Sigdal. This result contrasts with the established picture of boreal forests being richer in arthropods than coastal conifer forests (e.g. Vik 1991, Brändle and Rieger 1999). The relatively few trees sampled in Kvam may have influenced the result, but there was no big difference in average specimen numbers per sampling unit (i.e. funnel) between the two areas (12.77 specimens funnel^{-1} in Sigdal vs 9.68 specimens funnel^{-1} in Kvam). However, it is noteworthy that the species composition differed and that the most abundant species in Kvam belonged to Oribatida. Many orabatids feed on algae, lichens or fungi – sources that are favoured under humid climatic regimes as in Kvam (Stary pers. comm.).

References

Aakra, K. 2000. New records of spiders (Araneae) from Norway with notes on epigynal characters of *Philodromus fuscomarginatus* (DeGeer) (Philodromidae) and *Araneus sturmi* (Hahn) (Araneidae). – Norw. J. Entomol. 47: 77–88.

Aoki, J.-I. 1973. Soil mites (oribatids) climbing trees. – In: Daniel, R. (ed.), Proceedings of the 3rd international congress of acarology. Junk, pp. 59–64.

Ammer, U. and Schubert, H. 1999. Arten-, Prozeß- und Ressourcenschutz vor dem Hintergrund faunistischer Untersuchungen im Kronenraum des Waldes. – Forstwissenschaftliches Centralblatt 118: 70–87.

Bankowska, R. 1994. Diversification of Syrphidae (Diptera) fauna in the canopy of Polish pine forests in relation to forest stand age and forest health zones. – Fragmenta Faunistica 36: 469–483.

Basset, Y. 1985. Aspects de la répartition des peuplements d'arthropodes dans les couronnes de *Pinus mugo* Turra. – Mitteilungen der Schweizerischen Entomol. Gesellschaft 58: 263–274.

Basset, Y. 1991. The taxonomic composition of the arthropod fauna associated with an Australian rainforest tree. – Aust. J. Zool. 39: 171–190.

Basset, Y. 2001. Invertebrates in the canopy of tropical rain forests – how much do we really know? – Plant Ecol. 153: 87–107.

Behan-Pelletier, V. and Winchester, N. 1998. Arboreal oribatid mite diversity: colonizing the canopy. – Appl. Soil Ecol. 9: 45–51.

Borkowski, K. 1986. Contribution to the knowledge of the insect fauna of Scotch pine tree crowns. – Polskie Pismo Entomol. 56: 667–676.

Brändle, M. and Rieger, C. 1999. Die Wanzenfauna von Kiefernstandorten (*Pinus sylvestris* L.) in Mitteleuropa (Insecta: Hemiptera: Heteroptera). – Faunistische Abhandlungen der Staatliches Museum für Tierkunde Dresden 21: 239–258.

Brändle, M. and Brandl, R. 2001. Species richness of insects and mites on trees: expanding Southwood. – J. Anim. Ecol. 70: 491–504.

Bryant, J. P., Chapin, F. S. and Klein, D. R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. – Oikos 40: 357–368.

Chobotow, J. 1993. Cantharidae (Coleoptera) of pine forests in Poland. – Fragmenta Faunistica 36: 147–156.

Cholewicka-Wisniewska, K. 1994a. The structure of weevil communities (Coleoptera, Curculionidae) of selected Polish pine forests. – Fragmenta Faunistica 36: 397–438.

Cholewicka-Wisniewska, K. 1994b. Communities of weevils (Coleoptera, Curculionidae) in Polish pine forests of different age. – Fragmenta Faunistica 36: 442–457.

Cmoluchowa, A. and Lechowski, L. 1993. Heteroptera communities in pine forests in Poland. – Fragmenta Faunistica 36: 127–145.

Colwell, R. K. 1999. EstimateS: statistical estimation of species richness and shared species from samples, ver. 5.0.1. – User's guide and application published at: < http://viceroy.eeb.uconn.edu/estimates > .

Czechowska, W. 1994. Neuropterans (Neuropteroidea: Raphidioptera, Planipennia) of the canopy layer in pine forests. – Fragmenta Faunistica 36: 459–467.

Engel, H. 1941. Beiträge zur Faunistik der Kiefernkronen in verschiedenen Bestandstypen. – Mitteilungen aus Forstwirtschaft und Forstwissenschaft 4: 334–361.

Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. – Coleopterist's Bull. 36: 74–75.

Erwin, T. L. 1983. Tropical forest canopies, the last biotic frontier. – Bull. Entomol. Soc. Am. 29: 14–19.

Erwin, T. L. 1991. How many species are there? Revisited. – Conserv. Biol. 5: 1–4.

Fremstad, E. and Elven, R. 1987. Enheter for vegetsajonskart-legging i Norge. – Økoforsk Utredning.

Foggo, A. et al. 2001. Edge effects and tropical forest canopy invertebrates. – Plant Ecol. 153: 347–359.

Gotelli, N. J. and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. – Ecol. Lett. 4: 379–391.

Gunnarsson, B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. – J. Anim. Ecol. 59: 743–752.

Hagan, D. V. et al. 2000. Ceratopogonidae from forest habitats in Norway. – Polish J. Entomol. 69: 465–476.

Hågvar, E. B. and Hågvar, S. 1975. Studies on the invertebrate fauna on branches of spruce (*Picea abies*) (L.) during winter. – Norw. J. Entomol. 22: 23–30.

Heje, K. K. and Nygaard, J. 2000. Norsk Skoghåndbok. – Landbruksforlaget, Oslo.

Hooper, R. G. 1996. Arthropod biomass in winter and the age of longleaf pines. – For. Ecol. Manage. 82: 115–131.

Höregott, H. 1960. Untersuchungen über die qualitative und quantitative Zusammensetzung der Arthropodenfauna in der Kiefernkronen. – Beiträge zur Entomol. 10: 891–916.

Ihlen, P. G., Gjerde, I. and Sætersdal, M. 2001. Structural indicators of richness and rarity of epiphytic lichens on *Corylus avellana* in two different forest types within a nature reserve in south-western Norway. – Lichenologist 33: 215–229.

Kolodziejak, E. 1994. Communities of Lachnidae (Aphidoidea) inhabiting pine canopies in Polish pine forests situated in three forest health zones. – Fragmenta Faunistica 36: 378–385.

Krüger, O. and McGavin, G. C. 1998. Insect diversity of *Acacia* canopies in Mkomazi game reserve, north-east Tanzania. – Ecography 21: 261–268.

Laine, A., Orell, M. and Itämies, J. 1990. Invertebrate fauna on Norwegian spruce (*Picea abies*) branches in northern Finland. – Entomol. Fenn. 1: 193–199.

Lindén, H. 1984. The role of energy and resin contents in the selective feeding of pine needles by the Capercaillie. – Ann. Zool. Fenn. 21: 435–439.

Lowman, M. D. and Wittman, P. K. 1996. Forest canopies: methods, hypotheses, and future directions. – Annu. Rev. Ecol. Syst. 27: 55–81.

Majer, J. D. and Recher, H. F. 1988. Invertebrate communities on western Australian eucalypts: a comparison of branch clipping and chemical knockdown procedures. – Aust. J. Ecol. 13: 269–278.

Majer, J. D., Recher, H. F. and Keals, N. 1996. Branchlet shaking: a method for sampling tree canopy arthropods under windy conditions. – Aust. J. Ecol. 21: 229–234.

Martikainen, P. et al. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. – Biol. Conserv. 94: 199–209.

Mason, R. R. 1992. Populations of arboreal spiders (Araneae) on Douglas-firs and true firs in the interior Pacific Northwest. – Environ. Entomol. 21: 75–80.

Ohmart, C. P. and Voigt, W. G. 1981. Arthropod communities in the crowns of the natural and planted stands of *Pinus radiata* (Monterey pine) in California. – Can. Entomol. 113: 673–684.

Overgaard Nilsen, B. 1975. The species composition and community structure of the beech canopy fauna in Denmark. – Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 138: 137–170.

Overgaard Nilsen, B. and Ejlertsen, A. 1977. The distribution pattern of herbivory in a beech canopy. – Ecol. Entomol. 2: 293–299.

Ozanne, C. M. P. et al. 1997. The significance of edge effects in the management of forests for invertebrate biodiversity. – In: Stork, N. E., Adis, J. and Didham, R. K. (eds), Canopy arthropods. Chapman and Hall, pp. 534–550.

Ozanne, C. M. P. et al. 2000. Isolated trees and forest patches: patterns in canopy arthropod abundance and diversity in *Pinus sylvestris* (Scots pine). – For. Ecol. Manage. 137: 53–63.

Pettersson, R. B. 1996. Effect of forestry on the abundance and diversity of arboreal spiders in the boreal spruce forest. – Ecography 19: 221–228.

Pettersson, R. B. et al. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. – Biol. Conserv. 74: 57–63.

Prinzing, A. 1997. Spatial and temporal use of microhabitats as a key strategy for the colonization of tree bark by *Entomobrya nivalis* L. (Collembola: Entomobryidae). – In: Stork, N. E., Adis, J. and Didham, R. K. (eds), Canopy arthropods. Chapman and Hall, pp. 453–476.

Progar, R. A. and Schowalter, T. D. 2002. Canopy arthropod assemblages along a precipitation and latitudinal gradient among Douglas-fir *Pseudotsuga menziesii* forests in the Pacific Northwest of the United States. – Ecography 25: 129–138.

Progar, R. A., Schowalter, T. D. and Work, T. 1999. Arboreal invertebrate responses to varying levels and patterns of green-tree retention in northwestern forests. – Northwest Sci. 73: 77–86.

Reynolds, B. C. and Crossley, D. A. Jr 1997. Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. – Environ. Entomol. 26: 1232–1239.

Richardson, B. J. et al. 1999. Arboreal arthropod biodiversity in woodlands: effect of collection procedures and geographic distance on estimates of diversity found on two species of *Melaleuca*. – Aust. J. Ecol. 24: 544–554.

Schowalter, T. D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. – For. Ecol. Manage. 78: 115–125.

Schowalter, T. D. and Ganio, L. M. 1998. Vertical and seasonal variation in canopy arthropod communities in an old-growth conifer forest in southwestern Washington, USA. – Bull. Entomol. Res. 88: 633–640.

Sellin, A. 1996. Sapwood amount in *Picea abies* (L.) Karst determined by tree age and radial growth rate. – Holzforschung 50: 291–296.

Simandl, J. 1993. Canopy arthropods on Scots pine: influence of season and stand age on community structure and the position of sawflies (Diprionidae) in the community. – For. Ecol. Manage. 62: 85–98.

Sippola, A. L., Siitonen, J. and Punttila, P. 2002. Beetle diversity in timberline forests: a comparison between old-growth and regeneration areas in Finnish Lapland. – Ann. Zool. Fenn. 39: 69–86.

Southwood, T. R. E., Moran, V. C. and Kennedy, C. E. J. 1982. The assessment of arboreal insect fauna: comparisons of knockdown sampling and faunal lists. – Ecol. Entomol. 7: 331–340.

Stadler, B., Solinger, S. and Michalzik, B. 2001. Insect herbivores and the nutrient flow from the canopy to the soil in coniferous and deciduous forests. – Oecologia 126: 104–113.

Sterzynska, M. and Slepowronski, A. 1994. Spiders (Araneí) of tree canopies in Polish pine forests. – Fragmenta Faunistica 36: 485–499.

Stork, N. E., Adis, J. and Didham, R. K. 1997. Canopy arthropods. – Chapman and Hall.

Su, J. C. and Woods, S. A. 2001. Importance of sampling along a vertical gradient to compare the insect fauna in managed forests. – Environ. Entomol. 30: 400–408.

Tanabe, S. I., Toda, M. J. and Vinokurova, A. V. 2001. Tree shape, forest structure and drosophilid community. Comparison between boreal and temperate birch forests. – Ecol. Res. 16: 369–385.

Tenow, O. and Larsson, S. 1987. Consumption by needle-eating insects on Scots pine in relation to season and stand age. – Holarct. Ecol. 10: 249–260.

ter Braak, C. J. F. and Smilauer, P. 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (ver. 4). – Microcomputer Power, Ithaca.

Vaisanen, R. 1992. Distribution and abundance of diurnal Lepidoptera on a raised bog in southern Finland. – Ann. Zool. Fenn. 29: 75–92.

Vanninen, P. et al. 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). – Trees – Structure and Function 10: 231–238.

Vik, A. 1991. Catalogus Coleopterorum Norvegica. – S. O. Hansen, private publication.

Voegtlin, D. J. 1982. Invertebrates of the H. J. Andrews experimental forest, Western Cascade Mountains, Oregon. A survey of arthropods associated with the canopy of old-growth *Pseudotsuga menziesii*. – For. Res. Lab., School of Forestry, Oregon State Univ. Spec. Publ. 4: 1–29.

Walter, D. E. 1995. Dancing on the head of a pin: mites in the rainforest canopy. – Records of the Western Aust. Mus. Suppl. 52: 49–53.

Walter, D. E. and Behan-Pelletier, V. 1999. Mites in the forest canopies: filling the size distribution shortfall? – Annu. Rev. Entomol. 44: 1–19.

Walter, D. E., O'Dowd, D. and Barnes, V. 1994. The forgotten arthropods: foliar mites in the forest canopy. – Mem. of the Queensland Mus. 36: 221–226.

Walter, D. E. et al. 1998. Mites in the mist: how unique is a rainforest canopy knockdown fauna? – Aust. J. Ecol. 23: 501–508.

Wasowska, M. 1994. Leaf beetles (Coleoptera, Chrysomelidae) of selected pine forests in Poland. – Fragmenta Faunistica 36: 388–395.

Winchester, N. N. 1997a. The arboreal superhighway: arthropods and landscape dynamics. – Can. Entomol. 129: 595–599.

Winchester, N. N. 1997b. Canopy arthropods of coastal Sitka spruce trees on Vancouver Island, British Columbia, Canada. – In: Stork, N. E., Adis, J. and Didham, R. K. (eds), Canopy arthropods. Chapman and Hall, pp. 151–168.

Winchester, N. N. and Ring, R. A. 1999. The biodiversity of arthropods from northern temperate ancient coastal rainforests: conservation lessons from the high canopy. – Selbyana 20: 268–275.

Winchester, N. N., Behan-Pelletier, V. and Ring, R. A. 1999. Arboreal specificity, diversity and abundance of canopy-dwelling oribatid mites (Acaro: Oribatida). – Pedobiologia 43: 391–400.

Wright, M. G. and Giliomee, J. H. 1992. Insect herbivory and putative defense-mechanisms of *Protea magnifica* and *P. laurifolia* (Proteaceae). – Afr. J. Ecol. 30: 157–168.