Species composition of Coleoptera families associated with live and dead wood in a large Norway spruce plantation in Denmark

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For decades, the idea of various biotope types hosting unique plant and animal species associations and thus forming well-delimited species communities have continuously been debated. At any rate, it remains a practical empirical working concept in intensively exploited mosaic landscapes like in Denmark where biotope fragments are distinctly separated by man-made borders. In Denmark, conifer plantations dominated by Norway spruce, *Picea abies* L. constitute such a well-delimited biotope type – at the same time widely distributed and with an insect fauna only poorly known.

In two years, 1980-81, in Gludsted Plantation, Central Jutland, the arthropod fauna was studied in six stands of mature well-tended Norway spruce on poor sandy acidic soils. A variety of sampling methods was employed with a minimum of four white bucket traps and two tray traps on the ground in each stand. In both years in some stands, ground emergence traps were set up as well as vertical series of white buckets in canopies at mean levels 6.6, 10.6 and 13.2 m. Additional sampling comprised vertical sticky trap series in canopies, sweep net sampling in low branches and winter bark search. Ground beetles, sawflies and the aphid-aphidophagous fauna were analysed in previous papers. For this paper, all saproxylic and phytophagous beetle families potentially associated with Norway spruce were included and the total material comprised c. 12,000 specimens.

The most frequent species comprised *Athous subfuscus* (16%), *Anaspis rufilabris* (15), *Rhizophagus depressus* (9), *Hylastes cunicularius* (6), *Dasytes cyaneus* (5), *Malthodes fuscus*, *Otiorrhynchus singularis*, *Strophosoma melanogrammum*, *Hylurgops palliatus* (all 3), *Rhizophagus dispar*, *Cryphalus abietis*, *Leptura melanura* (all 2), *Rhagonycha atra* and *Strophosoma capitatum* (both 1%). Species composition was fairly similar among ground trap types – emergence traps, however, missed some species. Most species were caught almost entirely or most often in ground traps, but a few species were caught equally often in canopies (e.g. *H. palliatus*) or almost entirely in canopies (e.g. *D. cyaneus*, *Cimberis attelaboides*, *Cryphalus abietis*). Most species were fairly evenly distributed among stands but a few generally abundant species were totally absent from some stands, particularly the non-flying weevils, *O. singularis* and *Strophosoma capitatum*. Supplementary data on emergence densities, phenologies and sex ratios are given.

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Introduction

The existence of rather stable associations of plant and/or animal species, thus forming more and less well-defined 'species communities' is fundamental to our intuitive perception, characterization and naming of biotope and habitat types. Currently, such 'habitat types' forms the basis of the EU Habitat Directive (Anon. 1996). For decades, community ecologist have debated whether such delimited species community associations exist in natural communities or whether, alternatively, all species are spaced evenly and overlap across niche ranges in a multi-dimensional niche space (Whittaker 1975). In Denmark, however, landscapes are heavily fragmented, exploited and managed resulting in numerous biotope fragments most of which are fairly uniform and sharply delimited with steep man-made interfaces between adjoining fragments (e.g. hedgerow vs. field, forest vs. meadow, beech vs. spruce stands).

For such reasons, in Danish landscapes, we argue that it may be practical and empirically sound to describe the animal species communities associated with various dominant cropped or semi-natural biotope types. However, most biotope types occur in small patches and hence, they are often heavily influenced by species interchange across borders. Thus, preferably, species communities of biotope types should be studied in large patches.

In terrestrial biotopes, almost all descriptive community ecology has been based on plant communities whereas animal communities are far less studied and consequently less well-known. One reason may be that animals move and often exploit several biotopes seasonally (e.g. Nielsen, 1970). Another reason may be the labour, skills and other practical problems associated with proper sampling and identification of arthropods – e.g. arthropod samples are very susceptible to sampling method and great seasonal and annual population changes require extended sampling programmes (Southwood, 1978).

Norway spruce (*Picea abies* L.) have been a dominant plantation tree species from the beginning of Danish afforestation from c. 1800 and particularly so on poor sandy soils (Fritzbøger, 1994). In Denmark, Norway spruce plantations constitute a widely distributed perennial crop monoculture but often, they also constitute large areas relatively free of human disturbances such as soil cultivation, fertilization and pesticide use thus allowing a number of natural processes such as soil formation, nutrient balances, hydrology, decomposition and colonization, extinction and interactions of plant, fungi and insect species.

In 1980-81, our study of Nun-moth (*Lymantria monacha* L.) outbreaks in Norway spruce in Gludsted Plantation (Jensen & Bejer, 1985) was accompanied by a major arthropod sampling programme. This paper reports on the species composition of saproxylic and phytophagous beetles families mainly associated with live and dead wood in a large Danish plantation of mature Norway spruce. Previous reports comprise sawflies (Jensen, 1988), ground beetles (Reddersen & Jensen, 1991) and the aphid-aphidophagous insect community (Reddersen & Jensen, 2002).

Methods

Site and stand description

The study area was located in Central Jutland in central parts of the c. 5000 ha Gludsted Plantation (UTM 32V NH 21) which, together with neighbouring plantations, constituted the largest coherent conifer forest area in Denmark. Annual rainfall is considerable (c. 750 mm), topography is uniformly flat and soils are poor acidic alluvial sands. During the study period, Norway spruce (*Picea abies* L.) was very dominant in these plantations and age structure was very much skewed towards mature stands (80-100 yrs.). Today, most of these stands have disappeared due to fellings and tree fall by strong gales in 1981 and 1999 and have, in many cases, been replaced by other tree species.

In two years, 1980-81, trapping was carried out in six stands located within a 2.5 x 2.5 km^2 central plantation area, and all were pure stands of well-tended and thinned mature Norway spruce. Canopies were dense and forest floor vegetation was mainly scattered patches of Wavy Hair Grass (*Deschampsia flexuosa* L.), mosses and lichens. Stands 77 and 94 were sampled in both years, while stands 29 and 55 and stands 136 and 140, resp., were sampled in 1980 and 1981 only. Forest authorities conducted insecticide treatments in some stands due to an outbreak of the Nun-moth, *Lymantria monacha* L. (Jensen & Bejer, 1985). However, the advantages of maintaining stand replication was prioritized over the disadvantages of insect populations possibly affected by insecticides in some stands, cf. Reddersen & Jensen (2002).

Arthropod trapping

Arthropod activity was sampled using a variety of methods. Primarily, we used white bucket traps, trays and emergence traps accompanied by supplementary sampling using sticky traps, sweep-netting and winter bark search.

On the forest floor ('ground') as well as in the canopies ('canopy'), we used white bucket traps (h: 17 cm; d: 22 cm). In each stand and year, four buckets were placed on the forest floor in the corners of a c. 20 by 20 m square. Vertical bucket trap series were established in both 1980 (4) and 1981 (3) and each series included one of the ground bucket traps at mean heights 0.2 m (ground), 6.6 m (lower needleless canopy), 10.6 m (central green canopy) and 13.2 m (upper green canopy).

Initially, each vertical bucket trap series was accompanied by two sticky trap series, consisting of standing (ground level) or hanging (canopy) 1½ l bottles with exchangeable plastic bags covered with glue ('Brunonia' Raupenleim, Germany). For practical reasons, sticky traps were only employed until late summer 1980 and not all samples were used.

Two yellow trays (HxWxL: 4x25x35 cm) were placed in the middle of all ground bucket trap squares. One of the two trays in each stand were supplied with a vertical 25 x 18 cm window at the middle.

A number (6-13) of emergence traps (tilting roof isolated silver-painted 'box' model – HxWxL: 10x50x50 cm) were placed in three stands in one or two years (29(2); 77(1) and 94 (2)) from summer to late fall (1980) and early spring to late fall (1981). Additionally, in summer, in both years, scattered sweep netting were performed in lower green canopies at stand fringes along dirt roads at heights 1.5-3 m. In winter 1980-81, insects hibernating in crevices and under bark flakes on lower trunks of mature spruce were searched and collected.

Trays, buckets and emergence trap collection unit were half filled with a 1% formaldehyde solution with detergent added. Trapping periods and emptying was rather irregular and varied from 5 to 43 days in 1980 and from 10 to 50 days in 1981 (cf. Reddersen & Jensen (2002) for further details).

Identification and nomenclature

All specimens were identified using »Danmarks Fauna« (Hansen 1938, 1945, 1950, 1951, 1956, 1965, 1966, 1968) – supplemented by volumes of 'Die Käfer Mitteleuropas'. When identification included genitalia characters, sex was also recorded. Taxonomy and nomenclature follow Silvferberg (1979).

For this paper, we selected beetle families compromising between traditional taxonomic criteria and functional criteria. Functionally, we included all beetle species which are associated with mature Norway spruce being either saproxylic[1] or phytophagous (Table

1: Saproxylic species are species that are dependent during some part of their life-cycle on dead or dying wood, wood-inhabiting fungi or on the presence of other saproxylic species (Schiegg, 2000).

	Niche	Total (indv.)	Total (%)
Spp. feeding on live/dead wood:		**1607**	
Hylastes cunicularius Erichs.	S	*729*	*6.2*
Hylurgops palliatus (Gyll.)	C	*306*	*2.6*
Cryphalus abietis (Ratz.)	C	*198*	*1.7*
Leptura melanura L.	DC	*187*	*1.6*
Hylobius abietis (L.)	SP	*34*	*0.3*
Crypturgus subcribrosus Eggers	C	*34*	*0.3*
Pityogenes chalcographus (L.)	S	*27*	*0.2*
Dryophilus pusillus (Gyll.)	C	*18*	*0.2*
Dryocoetes autographus (Ratz.)	S	*11*	
Anoplodera rubra (L.)	SP	*10*	
Hylastes brunneus Erichs.	P	*10*	
Rhagium bifasciatum F.	DC	*8*	
Melanotus erythropus (Gmel.)	DC	*7*	
Trypodendron lineatum (Oliv.)	C	*7*	
Pityogenes bidentatus (Herbst)	P	*4*	
Xylechinus pilosus (Ratz.)	S	*3*	
Ips typhographus (L.)	S	*3*	
Pogonochaerus fasciculatus (DeGeer)	SP	*2*	
Pissodes pini (L.)	SP	*1*	
Poligraphus poligraphus (L.)	S	*1*	
Alosterna tabacicolor (DeGeer)	D	*1*	
Trypodendron domesticum (L.)	D	*1*	
Prosternon tessellatum (L.)	C	*1*	
Molorchus minor (L.)	C	*1*	
Ernobius angusticollis (Ratz.)	C	*1*	
Ernobius abietis (F.)	C	*1*	
Ernobius abietinus (Gyll.)	C	*1*	
Phytophagous spp. / roots+soil:		**2616**	
Athous subfuscus (Müller)	*	*1861*	*15.9*
Otiorrhynchus singularis (L.)	DC	*355*	*3.0*
Strophosoma melanogrammum (Forst.)	DC	*329*	*2.8*
Strophosoma capitatum (DeGeer)	DC	*64*	*0.5*
Dalopius marginatus (L.)	(+XDC)	*4*	
Athous vittatus (F.)	*	*1*	
Phyllobius pyri (L.)	DCH	*1*	
Polydrosus pallidus (Gyll.)	D	*1*	
Predatory spp.		**5442**	
Anaspis rufilabris (Gyl.)	X	*1719*	*14.7*
Epuraea spp.	I	*1293*	*11.1*
Rhizophagus depressus (F.)	I	*1031*	*8.8*
Dasytes cyaneus (F.)	X	*564*	*4.8*
Malthodes fuscus (Waltl.)	X	*381*	*3.3*
Rhizophagus dispar (Payk.)	I	*238*	*2.0*
Rhagonycha atra (L.)	X	*60*	*0.5*
Glischrochilus hortensis (Fourcr.)	I	*39*	*0.3*
Malthodes marginatus (Latr.)	X	*36*	*0.3*
Anthribus nebulosus Forst.	S (DC)	*35*	
Salpingus planirostris (F.)	X	*14*	
Pityophagus ferrugineus (L.)	I	*11*	
Rhizophagus ferrugineus (Payk.)	I	*5*	
Glischrochilus quadripunctatus (F.)	I	*5*	
Rhizophagus grandis (Gyll.)	I	*3*	
Podabrus alpinus (Payk.)	X	*2*	
Malthodes pumilus (Breb.)	X	*2*	
Rhagonycha lutea (Müll.)	X	*1*	
Malthodes brevicollis (Payk.)	X	*1*	
Pocadius ferrugineus (F.)	I	*1*	
Cerylon histeroides (F.)	I	*1*	
Other phytophagous aboveground spp.		**2021**	
Meligethes spp.	H	*1954*	*16.7*
Cimberis attelaboides (F.)	S	*30*	*0.3*
Rhynchaenus fagi (L.)	D	*22*	*0.2*
Ceuthorrhynchus pallidactylus (Marsh.)	H	*4*	

Ceuthorrhynchidius floralis (Payk.)	H	*4*	
Ceuthorrhynchus spp.	H	*3*	
Stereonychus fraxini (DeGeer)	D	*1*	
Sitona lineatus L.	H	*1*	
Micrelus ericae (L.)	H	*1*	
Apion virens Herbst	H	*1*	
Total		**11686**	*100*

Table 1: Total catches (all methods, stands and years) of species in saproxylic and phytophagous beetle families associated with Norway spruce (sorted by main trophic groups and total number). Niche codes - Feeding on live/dead plant material: Coniferous trees (C), Pine (P), Spruce (S), Deciduous trees (D), Herbs (H), Phytophagous but maybe partly predatory (*) – Predators within live/dead wood: Associated with larval Ipidae in galleries (I), Otherwise associated with live/dead wood (X).

Totale fangster (alle metoder, afdelinger og år) af arter i saproxyliske og fytophage billefamilier tilknyttet rødgran (efter trofisk gruppe og antal). Niche koder – Fortærer levende/dødt plantemateriale: Nåletræer (C), Fyr (P), Gran (S), Løvtræer (D), Urter (H), Planteædende men måske delvist prædatoriske (*) – Prædatorer i levende/dødt ved: Tilknyttet barkbillelarver i gangene (I), Tilknyttet levende/dødt ved (X).

1). However, sap-feeding phytophages and their predators have allready been dealt with in a separate publication (Reddersen & Jensen, 2002) and rove beetles (Staphylinidae) were not identified. In order to comply with traditional faunistics as well, we report the species composition of the entire coleopteran families involved.

Data manipulation and statistics

Data were, in many respects, both unbalanced and scarcely replicated concerning variables year, stand, trap type, trapping periods and height. Hence, species composition and species frequencies could not be properly analysed. A few aspects of the dataset were, however, analysed separately (horizontal and vertical distribution) without considering interactions. Numbers are presented as totals or simple means: e.g. 'mean catch per 7 traps per year' in case of vertical canopy trap series. Estimates on insect emergence density are calculated as 'mean number of individuals emerged per m^2' using only 1981 whole season trapping data.

When analysing vertical distribution, ground traps from stands without vertical trapping series were excluded resulting in a total of 20 ground and 21 (7+7+7) canopy traps. χ^2-tests were applied for tentative evaluation on total catches concerning differences in Canopy:Ground and Male:Female ratios.

Results

General species composition

The total material of species within saproxylic and phytophagous Coleoptera totalled 11,686 specimens in at least 66 species including 2 genera (*Epuraea* spp. and *Meligethes* spp.). **Table 1** lists all species by relative frequency along with main trophic group and niche. Twelve species constituted more than 1% of the total material, viz. *Athous subfuscus, Anaspis rufilabris, Rhizophagus depressus, Hylastes cunicularius, Dasytes cyaneus, Malthodes fuscus, Otiorrhynchus singularis, Strophosoma melanogrammum, Hylurgops palliatus, Rhizophagus dispar, Cryphalus abietis* and *Leptura melanura* along with *Epuraea* spp. og *Meligethes* spp. (mainly *M. aeneus* (F.)).

Far most of the species feeding on live or dead wood were conifer specialists, mainly within spruce, fir and pine or even within spruce alone. Among the saproxylic predatory species, a number of species were specialists feeding on bark beetle larvae (Ipidae) in

METHOD **Height**	BUCK 0.15	BUCK >6.6	STICK 0.15	STICK >6.6	TRAY 0.05	EMERG 0.10	NET 1.5-3	SEARCH 0.2-1.5
Elateridae:								
Athous vittatus (F.)	1							
Athous subfuscus (Müller)	433	73	35	12	1135	76	97	
Prosternon tessellatum (L.)							1	
Melanotus erythropus (Gmel.)	2				3	2		
Dalopius marginatus (L.)	1	1			1		1	
Cerambycidae:								
Rhagium bifasciatum F.	7				1			
Alosterna tabacicolor (DeGeer)	1							
Anoplodera rubra (L.)	9				1			
Molorchus minor (L.)	1							
Leptura melanura L.	177				10			
Pogonochaerus fasciculatus (DeGeer)	1					1		
Anthribidae:								
Anthribus nebulosus Forst.	2	17		4	4			8
Nemonychidae:								
Cimberis attelaboides (F.)	2	6		21	1			
Apionidae:								
Apion virens Herbst	1							
Curculionidae:								
Otiorrhynchus singularis (L.)	191	25			70	56	13	
Phyllobius pyri (L.)	1							
Polydrosus pallidus (Gyll.)	1							
Strophosoma melanogrammum (Forst.)	124	32		1	77	59	36	
Strophosoma capitatum (DeGeer)	29	5			16	12	2	
Sitona lineatus L.				1				
Stereonychus fraxini (DeGeer)						1		
Rhynchaenus fagi (L.)	2	5	1	12	2			
Hylobius abietis (L.)	24					10		
Pissodes pini (L.)					1			
Micrelus ericae (L.)					1			
Ceuthorrhynchus pallidactylus (Marsh.)	2	1			1			
Ceuthorrhynchus spp.					3			
Ceuthorrhynchidius floralis (Payk.)	2			1		1		
Scolytidae:								
Hylurgops palliatus (Gyll.)	117	158	1		23	7		
Crypturgus subcribrosus Eggers	11	3	6	3	11			
Trypodendron lineatum (Oliv.)	2	1		1	2	1		
Cryphalus abietis (Ratz.)	12	66	21	90	5	1	3	
Trypodendron domesticum (L.)	1							
Hylastes brunneus Erichs.	8	1			1			
Pityogenes bidentatus (Herbst)	1	2		1				
Xylechinus pilosus (Ratz.)	2				1			
Hylastes cunicularius Erichs.	242	3	5		103	376		
Poligraphus poligraphus (L.)	1							
Dryocoetes autographus (Ratz.)	8				3			
Pityogenes chalcographus (L.)	*3*	*4*	*9*	*5*	*3*	*1*	*2*	
Ips typhographus (L.)		*2*			*1*			
Cantharidae:								
Podabrus alpinus (Payk.)		*1*					*1*	
Rhagonycha lutea (Müll.)					*1*			
Rhagonycha atra (L.)	*11*	*5*	*3*	*1*	*16*	*2*	*22*	
Malthodes marginatus (Latr.)	*14*	*1*	*1*	*2*	*10*	*7*	*1*	
Malthodes brevicollis (Payk.)						*1*		
Malthodes fuscus (Waltl.)	*107*	*1*			*147*	*124*	*2*	
Malthodes pumilus (Breb.)	*2*							

Anobiidae:								
Dryophilus pusillus (Gyll.)		10		7			1	
Ernobius abietinus (Gyll.)					1			
Ernobius abietis (F.)	1							
Ernobius angusticollis (Ratz.)		1						
Melyridae:								
Dasytes cyaneus (F.)	8	400	2	146	6		2	
Nitidulidae:								
Meligethes spp.	1853	28	2		70		1	
Epuraea spp.	538	13	6		736			
Pocadius ferrugineus (F.)					1			
Glischrochilus quadripunctatus (F.)	2				3			
Glischrochilus hortensis (Fourcr.)	17				22			
Pityophagus ferrugineus (L.)	4				4	3		
Rhizophagidae:								
Rhizophagus grandis (Gyll.)	3							
Rhizophagus depressus (F.)	843	52	20	1	110	5		
Rhizophagus ferrugineus (Payk.)	4				1			
Rhizophagus dispar (Payk.)	190	2			43	3		
Cerylonidae:								
Cerylon histeroides (F.)	1							
Salpingidae:								
Salpingus planirostris (F.)	1	9	1	2	1			
Anaspidae:								
Anaspis rufilabris (Gyl.)	471	7	3	3	1226		9	
TOTAL NO. OF SPECIES	52	31	15	19	43	21	16	1
TOTAL NO. OF INDV.	*5492*	*935*	*116*	*314*	*3878*	*749*	*194*	*8*
PERCENTAGE (indv.) IN TRAP TYPE	*47.0*	*8.0*	*1.0*	*2.7*	*33.2*	*6.4*	*1.7*	*0.1*

Table 2: Total catches within all species listed by beetle family (families with species directly feeding on dead or live spruce above) and listed by trap type (BUCK: white buckets – STICK: sticky traps – TRAY: trays – EMERG: emergence traps – NET: sweep net sampling – SEARCH: winter bark search. 0.05-0.15m: ground trap positions and >6.6m: canopy trap positions). Total number of species and specimens below.

Totale fangster af samtlige arter opført efter familie (familier med arter, der direkte æder død eller levende rødgran øverst) og opført efter indsamlingsmetode (BUCK: hvide spande – STICK: klæbefælder – TRAY: fangbakker – EMERG: klækkefælder – NET: vegetationsketcher – SEARCH: eftersøgninger under bark om vinteren. 0,05-0,15m: jord-jordnære fældepositioner og >6,6m: fældepositioner i kronelaget. Totalt antal arter og individer anført nederst.

bark and wood galleries. In contrast, the phytophagous species with soil-living root-feeding larvae were mainly generalists (both coniferous and deciduous trees). Phytophages with larvae feeding on above-ground plant parts were infrequent apart from *Meligethes* spp. (herbal hosts), and, apart from *Cimberis attelaboides* (feeding on spruce male flowers), none were associated with the spruce forest habitat.

The total material is rearranged in **Table 2** to show traditional species composition by taxonomy. It also shows the contribution of the various trap types to the total material. In general, species composition among various ground trap types were rather similar: the dominant species in the total material (cf. above) were similarly dominant in each single ground trap type (buckets 0.15m, sticky traps 0.15m, trays and emergence traps). Ground buckets and trays caught far most individuals (47 and 33% of total, resp.) as well as species (52 and 43 species, resp., out of total 66).

	Ground	Canopy-low	Canopy-mid	Canopy-top	Chi-test
Bucket trap catches, N	7*	7	7	7	
Sticky trap catches, N					
Cimberis attelaboides (F.)	0,7	0	0	6	-
	0	*0*	*0*	*20*	-
Otiorrhynchus singularis (L.)	25,9	16	7	2	+G ***
	0	*0*	*0*	*0*	-
Strophosoma melanogrammum (Forst.)	27,0	16	7	7	+G ***
	0	*0*	*1*	*0*	-
Strophosoma capitatum (DeGeer)	7,7	5	0	0	-
	0	*0*	*0*	*0*	-
Hylurgops palliatus (Gyll.)	25,6	76	76	7	-CT ***
					-
Cryphalus abietis (Ratz.)	1,4	14	3	2	
	21	*70*	*20*	*0*	*-CT ****
Athous subfuscus (Müller)	98,4	32	23	21	+G ***
	35	*4*	*4*	*4*	*+G ****
Dryophilus pusillus (Gyll.)	0	0	0	5	-
	0	*0*	*0*	*7*	-
Dasytes cyaneus (F.)	2,8	14	203	183	+ CT ***
	2	*2*	*60*	*84*	*+ CT ****
				skrives	
Rhizophagus depressus (F.)	295	25	19	8	+ G ***
	20	*1*	*0*	*0*	–

Table 3: Selected species relatively frequent in canopy trap catches showing vertical distribution in white buckets (upper rows) and sticky traps (lower rows). Numbers are total catches – except for Ground level buckets (*normalized to 'catch per 7 traps' comparable to canopy traps). Significantly more frequent at ground stratum shown as (+G), at canopy top as (+CT) or exactly avoiding canopy top as (-CT).

*Udvalgte arter med relativt stor hyppighed i kronefældefangster med angivelse af vertikal fordeling i hvide spande (øvre rækker) og limfælder (nedre rækker). Tallene viser totale fangster (*undtaget ved Jord-niveauet, hvor spandfangsten er normaliseret til 'fangst pr. 7 fælder' svarende til kronefælderne). Signifikant større hyppighed ved jordniveauet er vist som (+G), til kronetoppen vist som (+CT) eller netop undgående kronetoppen vist som (-CT).*

Vertical distribution

Thus, in most species, ground traps caught more individuals (and thus species) compared to canopy traps. When comparing canopy vs. ground trap catches within trap type, however, it is striking that a few species diverged from this pattern: they were caught equally often or almost entirely in canopy traps (**Table 2**: buckets >6.6m, sticky traps >6.6m) including *Anthribus nebulosus, Cimberis attelaboides, Hylurgops palliatus, Cryphalus abietis, Pityogenes chalcographus, Dryophilus pusillus, Dasytes cyaneus* and *Salpingus planirostris.* In general, results on vertical distribution from bucket trap lines and sticky trap lines were very similar (**Table 3**). However, the sticky trap glue were remarkably inefficient in retaining the larger and thus heavier species, particularly larger weevils and bark beetles.

Although occurring occassionally in canopy catches (**Table 3**), *O. singularis, S. melano-*

Year	1980				1981				I alt
Stand no. (no. of vertical trap series)	55	29*	77*	94**	136	140	77*	94**	
Wingless, less mobile spp.:									
Otiorrhynchus singularis (L.)	3	0	119	0	93	20	52	0	*284*
Strophosoma melanogrammum (Forst.)	9	49	13	97	20	3	7	35	*224*
Strophosoma capitatum (DeGeer)	3	0	27	0	0	0	20	0	*47*
Winged, more mobile spp.:									
Athous subfuscus (Müller)	268	318	117	385	216	93	100	158	*1387*
Anaspis rufilabris (Gyl.)	514	274	39	77	401	47	31	71	*940*
Rhizophagus depressus (F.)	38	7	13	107	104	74	48	311	*664*
Dasytes cyaneus (F.) – §	0	129	85	198	0	0	0	1	*413*
Malthodes fuscus (Waltl.)	11	0	8	10	166	16	35	34	*269*
Hylurgops palliatus (Gyll.) – §	2	1	0	4	9	3	33	189	*239*
Rhizophagus dispar (Payk.)	35	3	7	20	44	74	23	41	*212*
Hylastes cunicularius Erichs.	25	2	4	25	15	13	33	96	*188*
Leptura melanura L.	23	121	12	2	4	12	11	6	*168*
Hylobius abietis (L.)	0	8	3	3	3	2	5	0	*24*

Table 4: Total catches (specimens) in tray and bucket traps of the most dominant beetle species distributed by mobility categories and by trapping year and stand. * indicates the number of vertical bucket trapping series in particular stand (0-2) which, in case of high canopy catches, may influence total catches heavily (species marked with §, cf. Table 3).
*Totale fangster (individantal) i bakker og hvide spande af de mest hyppige biller arter fordelt på mobilitetskategori og på fangstår og afdeling. * viser antallet af vertikale spand fældeserier i afdelingen (0-2), der i tilfælde af høje kronefangster, kan påvirke fangsterne betydeligt (arter mærket med §, jf. Tabel 3).*

grammum, *A. subfuscus* and *R. depressus* were still caught in far greater numbers in ground traps. *H. palliatus*, *C. abietis* and possibly *S. capitatum* were caught at the ground and in lower parts of canopies but very infrequently in upper canopies. Finally, *D. cyaneus*, and possibly *C. attelaboides* and *D. pusillus* (small numbers), were almost exclusively caught in upper canopies.

Horizontal and temporal distribution

Total species numbers from bucket and tray catches within each standyear combination (**Table 4**) give some indication of a fairly even horizontal distribution of the abundant species. Some species were very evenly distributed (e.g. *Athous subfuscus*) and most other species at least occurred in each standyear. A few species, however, diverged from this pattern and for two different reasons, the one biological and the other methodological:
(1) Among wingless species, weevils *O. singularis* and *S. capitatum* were frequently caught in some stands and never in others (both species absent from 29/1980 and 94/1981 and *S. capitatum* absent in 136/1981 and 140/1981). This pattern was exactly similar in emergence trap catches (not shown).
(2) Among winged species, two species were primarily caught in canopy bucket traps, viz. *D. cyaneus* and *H. palliatus* (cf. above), and, for obvious reasons, they were not or only rarely caught in stands without canopy traps.

Table 4 also indicate that most frequent species occurred numerously in both years with only one-two remarkable exception(s). *D. cyaneus* were very frequent in 1980 and almost entirely absent in 1981, while the opposite was true for *H. palliatus*.

	Occur in ground traps	Occur in canopy traps	Density X±95%CL (indv./m²)	Phenology (emergence)	Phenology (activity)	Sex-ratio M:F
M. fuscus	++	–	14.8±7.7	pJul	Jul	2 : 1 ***
A. subfuscus	++	(+)	nc	?	mMay-pAug	
D. cyanueus	+	+++	≅0	?	May	
R. depressus	+	(+)	nc	?	uApr-pJun	
R. dispar	+	–	nc	?	uApr-mAug	
A. rufilabris	+	–	≅0	?	pMay-mAug	1 : 1.1 NS
L. melanura	+	–	≅0	?	uJun-Aug	1 : 0.8 NS
O. singularis	++	–	7.9±6.8§	Apr-Oct	Apr-Oct	
S. melanogrammum	++	–	3.6±1.9	Apr-Oct	Apr-Oct	
S. capitatum	++	–	1.6±1.4§	Apr-Oct	Apr-Oct	
H. palliatus	+	++	≅0	Apr ?	mApr-mMay	
H. cunicularius	++	–	50±24	mMay-mJun	mMay-pJun	

§: Density estimates much influenced by data from stands where species did not occur
***: Chi-test; P<0.001; NS (non-significant)

Table 5: Summary of results on twelve most frequent saproxylic or phytophagous beetle species associated with mature Norway spruce (Picea abies L.) in Gludsted Plantation 1980-81 – showing relative frequency in ground and canopy traps, respectively (+ occur / – not occurring), 'density' estimated from emergence trap data from 1981 (N=3 stand x 10 traps x 0.25 m^2), 'phenology' determined by emergence trap data and bucket+tray trap data, respectively (p/primo; m/medio; u/ultimo), and, finally, sex-ratios.

Oversigt over resultaterne for de tolv talrigeste billearter tilknyttet levende eller dødt ved i afdelinger med moden rødgran (Picea abies L.) i Gludsted Plantage 1980-81 med oplysninger - om forekomst (+ høj; - ingen) i hhv. jordfælder (ground) og kronefælder (canopy) - om tætheder (density) skønnet fra klækkefældedata i 1981 (N = 3 afdelinger x 10 fælder x 0,25 m^2) - om fænologi fastlagt vha. hhv. klækkefælder (emergence) og spand- og bakkefælder (activity – p/primo; m/medio; u/ultimo) – samt om kønsfordeling.

In this publication, phenological data are not presented in any detail as incomplete and irregular time-series data conflicted with the extended activity periods of most of these beetle species. In 1980, traps were not set up before early May and time-series plots of 1980-81 species data clearly showed that in most of these species catches were high even in early spring. Some results on phenology, however, are summarized in **Table 5** along with tentative density estimates (emergence traps) and sex ratios in some species. Most species were caught at least fairly frequently across extended periods of the spring-summer-autumn season and, in particular, the large weevils, *O. singularis, S. melanogrammum* and *S. capitatus*, were caught frequently from early fall to late autumn. In most species, catches were low in mid-summer (July) with *A. subfuscus, A. rufilabris* and *M. fuscus* as outstanding exceptions.

It was not always simple to delimit the saproxylic beetle community. Quite a number of species which were mainly associated with micro- or macrofungi were not clearly associated with Norway spruce. Nonetheless, they will, in practice, often be found along with saproxylic species and a species list is provided in **Table 6**. As samples were not searched systematically, frequencies are only given as order of magnitude.

Discussion

Our study included vertical trapping series, which showed that most phytophagous and saproxylic beetle species were caught in far greater numbers in ground traps compared to canopy. Actually, both most specimens and most species were caught in ground traps, viz. trays and buckets placed, conveniently for emptying, on the ground. This means

Species	Abundance index
LEIODIDAE:	
Agathidium spp.	****
Anisotoma humeralis (F.)	****
Anisotoma glabra (Kugel.)	***
LATHRIDIIDAE:	
Aridius nodifer (Westw.)	****
Stephostethus lardarius (DeGeer)	*
Stephostethus rugicollis (Oliv.)	***
Enicmus transversus (Oliv.)	*
Enicmus testaceus (Steph.)	***
Cortinicara gibbosa (Hbst.)	**
Corticaria serrata (Payk.)	***
Corticaria indet. spp.	**
Dienerella filum (Aube)	**
CRYPTOPHAGIDAE:	
Cryptophagus abietis (Payk.)	*****
Cryptophagus setulosus Sturm	**
Cryptophagus indet. spp.	****
Cis hispidulus (Payk.)	*

Table 6: Supplementary list of other beetle species which may also occur in decaying wood and its fungi. As the material was not systematically searched for these taxa, the species list is not complete and frequencies are only indicated roughly as order of magnitude (*:1; **: 2-5; ***: 6-25; ****: 26-125 and *****: 126-525).
Ekstra liste over andre billearter, som også kunne medregnes som saproxyliske og bl. a. forekommer i dødt ved og tilhørende svampe. Da arterne ikke er systematisk udsorteret i materialet, er artslisten næppe komplet og antallene er kun groft anført som størrelsesorden (:1; **: 2-5; ***: 6-25; ****: 26-125 and *****: 126-525).*

that only few species were seriously underestimated or entirely overlooked by omitting canopy sampling, which was also the case in most ground beetles (Reddersen & Jensen, 1991), *Cephalcia* sawflies (Jensen ,1988) and in syrphid flies (Reddersen & Jensen, 2002). However, in both these and the present study, a lesser number of species was most frequently or almost entirely caught in canopy traps. Provided that trap catch patterns mirrors real world activity patterns, almost any insect group comprise at least a few species which are almost exclusively active in the canopy stratum – at least certain developmental stages or sex: e.g. *Dromius* ground beetles (Reddersen & Jensen, 2002), females of some *Cephalcia* sawflies (Jensen, 1988) and most adult and larval Neuroptera and Coccinellidae among the aphidophagous community (Reddersen & Jensen, 2002) and among the phytophagous/saproxylic beetles in this study particularly *Dasytes cyaneus*, *Anthribus nebulosus* (larvae predatory on scale insects) and *Cimberis attelaboides* (larvae feeding on spruce male flowers). Koziol (2000) reported on similar faunasegments closely associated with spruce canopies.

In conclusion, in general, canopy traps prove to be well worth the much greater effort and here, we found white buckets superior to sticky traps. Sticky traps were both more time-consuming, and the glue often complicated species identification and also could not always retain the heavier beetle species.

In the present study, stand replication seemed appropriate as species composition or at least species occurrence was fairly similar across stands and years. Dramatic variation across years was rare (*D. cyaneus*). Extreme variation across stands occurred in a few species which were characterised by being very immobile (lacking wings). In several stands, *O. singularis* and *S. capitatum* were entirely absent in both years even though they were abundant in nearby and seemingly similar stands. Studying conifer forest weevils, Skov (2000) likewise found *S. melanogrammum* to be widely distributed while *O. singularis* and particularly *S. capitatum* were less distributed.

In Denmark and surrounding countries, quantitative data on the species composition of characteristic forest habitats are rarely produced and when they are produced, they are often not or only partly published (e.g. Nielsen, 1974; Nielsen & Toft, 1989; Rost, 1992; Nielsen, 1994). Thus, along with Jensen & Bejer (1985), Jensen (1988), Reddersen & Jensen (1991) and Reddersen & Jensen (2002), the present study forms the largest and most complete account of the above-ground insect community in Danish spruce plantations.

The material presented here is, admittedly, impaired from occasional missing samples, from delayed onset of sampling in one of two years, from irregular emptying of traps and a partly unbalanced trapping design. However, we consider our material to be fairly representative for Danish conditions for the following reasons (1) the stands examined were all uniform and mature Norway spruce plantation, (2) the plantation was large and uniform and situated in an area and region holding the largest concentration of spruce forest in Denmark, (3) the insect material derived from the application of a suite of different methods, including vertical trap series extending into canopies and (4) the insect material derived from a total of six stand replications and two years during most of the season.

Further, our species composition was remarkably similar to that reported by Thiede. (1977) from spruce forest in Northern Germany using various emergence trap types Comparing to insect catches from deciduous forests also in Jutland, Denmark (Nielsen, 1974; Jørum, 1988), there were both similarities and dissimilaries and this applies to other insect groups as well (Reddersen & Jensen, 1991; Reddersen & Jensen, 2002). However, it must be stressed that larger stands of Norway spruce only exist in planted, thinned and otherwise intensively managed stands. Here, trees are all of the same age and very few old trees are allowed to die, fall and decompose. The saproxylic beetle community will be favoured by the maturity of stands but are otherwise limited in such plantations. We found a rather restricted species composition of saproxylic weevils, bark beetles, click beetles and longhorn beetles which may well be a characteristic feature of the mature but well-tended and sound stands of Norway spruce. Thus, for saproxylic species in particular, the species composition reported here are not representative for natural spruce or conifer forest (Nilssen, 1978; Schiegg, 2000) nor for e.g. stands with small clearings caused by wind-felling (Otte 1989a,b; Weslien, 1992). The saproxylic beetle fauna was clearly more sharply delimited from other forest types compared to the phytophagous beetle fauna, i.e. click-beetles and weevils (cf. Bejer-Pedersen & Jørum, 1977; Grimm, 1973; Grünwald, 1986; Jørum, 1988; Nielsen, 1974; Schauermann, 1973).

Qualitatively, the species composition present few surprises to the entomologist. At the time of sampling, some species were still considered quite unusual, e.g. *Xylechinus pilosus, Anthribus nebulosus* and *Cimberis attelaboides*. Those species are not really uncommon, but were still expanding their distributional ranges in Denmark following the introduction, expansion and delayed maturation of Norway spruce stands in Denmark (Bejer-Petersen & Jørum 1977; Viggo Mahler, pers. comm.). Our sampling efforts were directed towards quantitative sampling and were, thus, not directed towards providing rare species. Rather, the species composition reported here and in previous publications (cf. above) is likely to represent the typical and most abundant insect fauna species of the introduced tree species, Norway spruce, growing in planted, mature, well-managed and uniform single-species stands on poor acidic sandy soils in Denmark.

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Literature

Anon., 1996. Interpretation Manual of European Union Habitats. HAB 96/2 FINAL – EN, Version EUR 15. Europa Kommisionen 25. april 1996. 146 pp.

Bejer-Petersen, B. & P. Jørum, 1977. Danske barkbillers hyppighed og udbredelse (Coleoptera, Scolytidae). – *Ent. Meddr.* 45: 1-36.

Bílý, S. & O. Mehl, 1989. Longhorn Beetles (Coleoptera, Cerambycidae) of Fennoscandia and Denmark. – Fauna Entomologica Scandinavica 22. E.J. Brill, Leiden.

Fritzbøger, B., 1994. Kulturskoven. Dansk skovbrug fra oldtid til nutid. Gyldendal, Copenhagen.

Grimm, R., 1973. Zum Energieumsatz phytophager Insekten in Buchenwald. I. Untersuchungen an Populationen der Rüsselkäfer *Rhynchaenus fagi* L., *Strophosomus* (Schönherr) und *Otiorrhynchus singularis* L. – *Oecologia* 11: 187-262.

Grünwald, M., 1986. Ecological segregation of bark beetles (Coleoptera, Scolytidae) of spruce. – *J. Appl. Ent.* 101: 176-187.

Hansen, V., 1938. Biller X. Blødvinger, klannere m.m. Danmarks Fauna 44. Gad, København.

Hansen, V., 1945. Biller XII. Heteromerer. Danmarks Fauna 50. Gad, København.

Hansen, V., 1950. Biller XIII. Clavicornia 1. del. Danmarks Fauna 55. Gad, København.

Hansen, V., 1951. Biller XIV. Clavicornia 2. del og Bostrychoidea. Danmarks Fauna 56. Gad, København.

Hansen, V., 1956. Biller XVIII. Barkbiller. Danmarks Fauna 62. Gad, København.

Hansen, V., 1965. Biller XXI. Snudebiller. Danmarks Fauna 69. Gad, København.

Hansen, V., 1966. Biller XXIII. Smældere og pragtbiller. Danmarks Fauna 74. Gad, København.

Hansen, V., 1968. Biller XXV. Ådselbiller, stumpbiller m.m. Danmarks Fauna 77. Gad, København.

Jensen, T.S. & B. Bejer, 1985. Registrering og bekæmpelse af nonnen i Danmark 1978-84. – Dansk Skovforenings Tidsskrift 70: 182-205.

Jensen, T.S., 1988. Phenology and spatial distribution of *Cephalcia* (Hym., Pamphiliidae) imagines in a Danish spruce forest. – *J. Appl. Ent.* 106: 402-407.

Jørum, P., 1988. Billefaunaen på mor- og muldbund i Hald Egeskov. – Flora og Fauna 94: 35-45.

Koziol, M., 2000. Cono- and seminiphagous insects of Norway spruce *Picea abies* (L.) Karst. and their parasitoids in lower and upper montane zone of the Tatra National Park in Poland. – *J. Appl. Ent.* 124: 259-266.

Nielsen, B.O., 1970. Observations on the Hibernation of the Beech Weevil (*Rhynchaenus fagi* L.) in Denmark. – *Ent. scand.* 1: 223-226.

Nielsen, B.O., 1974. Insektfaunaen på bøg (*Fagus silvatica* L.) biologisk belyst. Unpublished report. Institute of Zoology and Zoophysiology, University of Aarhus. 74 pp.

Nielsen, B.O. & S. Toft, 1989. Undersøgelser over leddyrfaunaen i Sebstrup Sande 1989. Unpublished technical report for Skov- og Naturstyrelsen, Copenhagen. 38 pp.

Nielsen, B.O., 1994. Insektfaunaen i Vest-, Midt- og Sønderjyske skovbryn. Delprojekt 3 af projekt skovbryn. Miljøministeriet, Skov- og Naturstyrelsen, Copenhagen.

Nilssen, A.C., 1978. Development of a bark fauna in plantations of spruce (*Picea abies* (L.) Karst.) in North Norway. – *Astarte* 11: 151-169.

Otte, J., 1989a. Ökologische Untersuchungen zur Bedeutung von Windwurfflächen für die Insektenfauna (Teil I). – *Waldhygiene* 17: 193-247.

Otte, J., 1989b. Ökologische Untersuchungen zur Bedeutung von Windwurfflächen für die Insektenfauna (Teil I). – *Waldhygiene* 18: 1-36.

Palm, E., 1996. Nordeuropas Snudebiller. 1. Kortsnudede arter (Coleoptera: Curculionidae) – med særligt henblik på den danske fauna. Danmarks Dyreliv Bind 7. Apollo Books, Stenstrup.

Reddersen, J. & T.S. Jensen, 1991. The carabid fauna of a large Danish spruce forest. – *Ent. Meddr.* 59: 73-80.

Reddersen, J. & T.S. Jensen, 2002. The Syrphidae, Coccinellidae, and Neuroptera (s. lat.) of a large Danish spruce forest. – *Ent. Meddr.* 70: 113-127.
Rost, F.E., 1992. Karakteristik af et løv- og et nålebryn ud fra den epigæiske billefauna. Unpublished Master's Thesis. Institute of Biology, University of Aarhus. 64 pp.
Schauermann, J., 1973. Zum Energieumsatz phytophager Insekten in Buchenwald. II. Die produktionsbiologische Stellung der Rüsselkäfer mit rhizophagen Larvenstadien. – *Oecologia* 13: 313-350.
Schiegg, K., 2000. Are there saproxylic beetle species characteristic of high dead wood connectivity? – Ecography 23: 579-587.
Silvferberg, H. (ed.), 1979. Enumeratio Coleoptorum Fennoscandiae et Daniae. – Helsinki. 6 + 79 pp.
Skov, R., 2000. Skadevoldende snudebiller i danske bevoksninger – med særlig vægt på Strophosoma spp. – Unpublished Master's Thesis, Institute of Biology, Dept. of Zoology, University of Aarhus.
Southwood, T.R.E., 1978. Ecological methods with particular reference to the study of insect populations. Chapman & Hall, London.
Thiede, U., 1977. Untersuchungen über die Arthropodenfauna in Fichtenforsten (Populationsökologie, Energieumsatz). – *Zool. Jb. Syst.* 104: 137-202.
Weslien, J. 1992. The arthropod complex associated with Ips typographus (L.) (Coleoptera, Scolytidae): species composition, phenology and impact on bark beetle productivity. – *Entomol. Fennica* 3: 205-213.
Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan Publ. Co., New York.