

Canopy cover favours sporocarp-visiting beetles in spruce forest

Bjørn Økland

Økland, B. 2002. Canopy cover favours sporocarp-visiting beetles in spruce forest. *Norw. J. Entomol.* 49, 29-39.

Several studies conclude that sun-exposed habitats with sufficient supply of dead wood are essential for many saproxylic and mycetophagous beetle species in forests. This has induced Scandinavian foresters to leave artificial tall stumps on clear-cuts in spruce forests. In the present study of Norway spruce forest, habitat preferences during flight were studied for saproxylic and mycetophagous beetles recorded as sporocarp-visitors of *Fomitopsis pinicola* and *Fomes fomentarius*, using 690 randomly placed window traps in 69 sites covering three forest types: clear-cuts, young and oldgrowth stands. Many of the sporocarp-visitors showed a strong preference for oldgrowth forest, avoiding clear-cuts and young replantations. By stepwise linear multiple regression, presence of canopy cover appeared as a major factor while variables associated with sporocarps and dead wood were most often secondary in importance. The results indicate that sufficient canopy cover is important for many sporocarp-visiting beetles in Norway spruce forests.

Key words: Biodiversity, Coleoptera, dead wood, flight activity, microclimate, polypore fungi.

Bjørn Økland, Norwegian Forest Research Institute, Høgskoleveien 12, N-1432 Ås, Norway.

INTRODUCTION

In the last few years Scandinavian forestry has introduced several measures specifically aimed at conserving biodiversity. These practices imply large expenses for the forest companies. Since the measures are most often based on only scanty scientific evidence, it is necessary to scientifically evaluate their accuracy (Larsson & Danell 2001).

Insects associated with dead wood (saproxylic insects) and wood-inhabiting fungi (mycetophagous insects) are of special interest for maintenance of biodiversity in boreal forests (Dajoz 2000). In Sweden, more than a thousand of beetle species are dependant on dead trees (Ehnström 2001). Many species of these diverse insect groups are on red-lists (Gärdenfors 2000, Esseen et al. 1997, Direktoratet for Naturforvaltning 1999, Rassi et al. 1992). Due to their habitat preferences, they are in principle competitors with timber harvesting. To create artificial tall stumps and leave single dead trees on clear-cuts have become the

most common measures to meet the requirements of saproxylic and mycetophagous fauna in boreal forests of Fennoscandia. This measure, which easily can be combined with forestry practice, is particularly suited for species preferring sun-exposed dead wood (Kaila et al. 1997), in areas with a rich saproxylic fauna in the surrounding forest (Ehnström pers. comm.). However, it may be questioned to what extent all saproxylic and mycetophagous insects benefit from this practice, and whether microclimate or other factors are limiting dead-wood habitats of open environments.

Several authors conclude that density and quality of dead-wood substrates are of major importance for the saproxylic fauna (Ehnström & Waldén 1986, Økland et al. 1996, Esseen et al. 1997, Martikainen 2000, Martikainen et al. 2000, Siitonen & Saaristo 2000, Siitonen et al. 2000, Ehnström 2001). Particularly important for red-listed invertebrates are certain dead-wood elements, such as snags and logs (Berg et al. 1994) and dying

and dead aspen (Siitonen & Martikainen 1994, Siitonen et al. 1996). The abundance as well as species richness of saproxylic beetles may increase with the age of the stumps and logs (Irmeler et al. 1996). Habitat density seems to act at several spatial scales. Schiegg (2000a, b) found that fragmentation occurs at a local scale through isolation of single dead wood pieces, while other authors revealed a strong influence of dead wood at large scales (Siitonen 1994, Siitonen & Martikainen 1994, Økland et al. 1996). For insect diversity in sporocarps, the amount of dead wood at and near the sampling site also appears to be a major factor (Thunes et al. 2000). The concentration of fruiting bodies has been found to be important for beetle species (Rukke & Midtgaard et al. 1998, Rukke 2000). Substrate properties of the sporocarps are important for the inhabiting faunal composition, including tissue hardness and persistence (Paviour-Smith 1960, Lawrence 1973, Klopfenstein & Graves 1989, Økland 1995), size and water content (Willassen & Thunes 1996, Midtgaard 1998), and successional stage from start to full degradation (Ackerman & Shenefelt 1973, Thunes 1994, Økland & Hågvar 1994). Properties of the host tree influence the insect fauna of sporocarps, e.g. tree diameter and number of dead sporocarps on the tree (Nilsson 1997a, Sverdrup-Thygeson & Midtgaard 1998), whether the tree is standing or lying, and degree of contact between the tree and the ground (Nilsson 1997b).

Only few studies mention species with a preference for shaded sites and canopy cover; this may, however, determine whether artificial tall stumps on clear-cuts are utilised or not. Some saproxylic invertebrates, especially those living in the last successional stages (Jonsell et al. 1998), and some insects breeding in sporocarps of *Fomitopsis pinicola* and *Fomes fomentarius* (paper 1 in Jonsell 1999) are dependent on shaded sites. For species associated with oak in pasture woodlands, Ranius & Jansson (2000) found that only species using fruiting bodies of saproxylic fungi benefited from forest regrowth due to lacking management.

Sensitivity of canopy may possibly be found in more insect groups if the flying stage is studied. It is assumed that adaptations to prefer or avoid

characteristics of the surrounding forest environment are reflected in the flight behaviour during the search for suitable habitats. During flight, many insects show negative phototactic response or respond directly to other stimuli in the surrounding environment, such as moisture, temperature, wind and odour (Romoser 1981, Faldt et al. 1999).

The present study focuses on the additional effect caused by absence of canopy cover for saproxylic and mycetophagous insects visiting living sporocarps of *F. pinicola* and *F. fomentarius* in boreal spruce forest. A recent study gives a list of beetle species that have been recorded as visitors of living sporocarps of *F. pinicola* and *F. fomentarius* in the present study area (Hågvar 1999). Sporocarps and dead wood substrates used by these beetle species are found in all successional stages of spruce forest in the experimental area, making it possible to test the additional effect of canopy cover. Randomly placed flight interception traps were used to acquire information about preference and avoidance in this assemblage of beetles. Three forest types were compared: clear-cut, young spruce forest and oldgrowth spruce forest.

METHODS

All study sites were situated within an area of about 160 km² of continuous spruce-dominated forest in Østmarka (59°51'N 10°57'E, about 15 km south-east of Oslo city centre) with only slight variations in elevation (200 to 300 m above sea level). Flying beetles were trapped in 69 sites, each site placed in the centre of different spruce forest stands within *Eu-Piceetum myrtilletosum* vegetation type (Kielland-Lund 1973). Ten sites were located in *clear-cut stands* (clear-cut 2-3 years before, without artificial tall stumps), ten in *young stands* (plantations after clear-cutting 14-16 years ago, without artificial tall stumps), and 49 in *oldgrowth stands* (minimum 80 years old) with various densities of dead wood. There was a minimum distance of 200 m between the sites, and sites of the three forest categories were mixed within the study area. In each site, ten window traps were placed in a randomly centred circle (diameter 20 m) near the middle of the stand to secure random distances to sporocarps and dead

logs. The traps were operated from 22 April to 13 September 1991 and emptied four times. Window traps, catching flying individuals who hit a transparent window, are effective for capture of flying saproxylic and mycetophagous beetles (Siitonen 1994, Økland et al. 1996). The traps consisted of two vertical cobex plates (21 x 39 cm) mounted cross-wise above a 22 cm wide plastic funnel, hanging with the trapping surface 0.7–1.0 m above the ground. A cup with preservative (ethylene-glycol) was mounted below the funnel (photo of the trap is given as Fig. A in Økland 1996). Ecological variables associated with sporocarps and dead wood were recorded in a square of 40 by 40 meters around the site centres (Table 1).

Species recorded as sporocarp-visitors of *F. pinicola* and *F. fomentarius* in the same area (Hågvar 1999) were sorted out of the trapping material. These 42 species are referred in Table 2 using the nomenclature of Hansen (1996) supplemented by Silfverberg (1992) for a few species which are not included in Hansen's catalogue (1996). The second column in Table 2 shows the polypore species under which the beetle species in question has been recorded as a sporocarp-visitor by Hågvar (1999); however, the beetle species may visit various sporocarp species (Benick 1952, Nuss

1975). Based on information given in Hågvar (1999, Table 1), the species are described as: obligate saproxylic (species that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees, or upon wood-inhabiting fungi, or upon the presence of other saproxylics); facultative saproxylic (species that use the same kind of habitats as obligate saproxylics but may use alternative habitats); and mycetophil/mycetobiont (species requiring or associated with fungi).

Mean densities of sporocarps and dead wood in each of the forest categories are presented in Table 3. To avoid low-numbered species in the statistical treatment, only species with a minimum mean of five specimens per site in at least one forest category were tested. For these 27 species (Table 2), the mean numbers of individuals per site were compared between the three forest types (*clear-cuts*, *young forest* and *oldgrowths*) by means of Kruskal-Wallis One-Way Analysis of Variance (Freund 1992). Using the ranks, this method is not sensitive of deviations from normal distribution or the imbalanced numbers of sites between forest category. The *p*-level was adjusted to 0.005 to compensate for the multiple tests, giving a low chance of species turning out as significant by

Table 1. Ecological variables recorded in the study sites.

Variable	Explanation	Range
Number of sporocarp:		
SPOROCARP	No. of living sporocarps	0 - 232
PINICOL	No. of living <i>Fomitopsis pinicola</i> sporocarps	0 - 153
FOMENT	No. of living <i>Fomes fomentarius</i> sporocarps	0 - 50
Amount and quality of dead wood:		
WOOD	Dead wood (m ³)	0.09 - 21.76
DECID	Dead deciduous wood (m ³)	0.00 - 4.53
STUMPS	Dead wood of stumps (m ³)	0.02 - 4.73
BETULA	Dead birch wood (m ³)	0.00 - 3.27
Stand characteristics:		
CANOPY	1: presence of canopy cover 0: absence of canopy cover	0 - 1
CLEARCUT	1: clear-cut 0: covered with trees	0 - 1

chance (27 species \times 0.005 = 0.135 species). Either Kruskal-Wallis One-Way Analysis of Variance or Mann-Whitney U test were applied for testing differences between forest categories for sporocarps and dead wood variables (Freund 1992). The relationships between ecological variables (Table 1) and the abundance per site in single species ($n=69$) were tested by forward stepwise multiple linear regression up to two steps (Weisberg 1985) (Table 4). Due to deviations from normal distribution, abundance in single species was transformed by natural logarithm before entering as dependant variable in regression analyses. Pearson correlation between all possible predictors showed no strongly intercorrelated variables. All tests were performed by means of the statistical software Systat (SYSTAT 8.0).

Results

Altogether 14 species out of 27 tested showed significant differences in the variance analyses (Table 2). The majority (10) of these species were found in great numbers in oldgrowth, while they were completely absent or appeared to be rare in clear-cuts and young replantations. Most of the significant species (Table 2) are facultative saproxylic (*Cerylon ferrugineum*, *Leptusa pulchella*, *Oxypoda alternans*, *Quedius xanthopus*, *Quedius plagiatus*, *Rhizophagus dispar*, *R. nitidulus*, *R. parvulus*,

Sepedophilus littoreus) or obligate saproxylic (*Epuraea pygmaea*), and nearly all of them may be found in cortical or sub-cortical microhabitats (*C. ferrugineum*, *Agathidium nigripenne*, *Anisotoma humeralis*, *E. pygmaea*, *Salpingus ruficollis*, *L. pulchella*, *Anisotoma castanea*, *R. dispar*, *R. nitidulus*, *R. parvulus*). Four species have previously been reared from sporocarps (*L. pulchella*, *O. alternans*, *Q. plagiatus* and *R. dispar*) (Økland & Hågvar 1994, Thunes 1994), all of these being more abundant in oldgrowth (Table 2). Two species of the total material presented here are on red-lists in the Nordic countries. Even though their numbers appeared to be higher in oldgrowth, one species was too infrequent for testing (*Cis dentatus*) and the other was only close to the chosen significance level (*Dendrophagus crenatus*; $p=0.008$).

It could be suspected that a lower density of sporocarps is the reason for the small catches of many sporocarp-visiting beetles in clear-cuts and young plantations. However, the frequency of sporocarps was not significantly lower in clear-cuts than in oldgrowth (Mann-Whitney $U=188.5$, $p=0.252$), despite considerable variation between sites in both forest categories (Table 3). Accordingly, frequencies of sporocarps did not differ significantly between clear-cuts and oldgrowth stands for *F. pinicola* (Mann-Whitney $U=194.0$, $p=0.299$) and *F. fomentarius* (Mann-Whitney $U=216.0$, $p=0.510$) (Table 3).

Table 2. Mean number of individuals (per site, i.e. ten traps) of sporocarp-visiting species in three forest types (CLC = clear-cut, YNG = young stands, OLD = oldgrowth) and H and p values of Kruskal-Wallis One-Way Analysis of Variance between forest types; sign means $p < 0.005$ (see methods); visit = visitor records by Hågvar (1999); Ff = *Fomes fomentarius*; Fp = *Fometopsis pinicola*; b = both *Fomes fomentarius* and *Fometopsis pinicola*; hab = habitat; f = facultative saproxylic; o=obligate saproxylic; m=mycetophil or mycetobiont. For author names see methods.

Family	literal information			CLC (n=10)	YNG (n=49)	OLD	H	p
	visit	hab	(n=10)					
Aspidiphoridae								
<i>Aspidiphorus orbiculatus</i>	Ff	f; m	2.0	5.0	6.3	2.05		
Cerylonidae								
<i>Cerylon ferrugineum</i>	Ff		2.0	13.0	129.6	29.47	< 0.001	sign
Ciidae								
<i>Cis boleti</i>	Fp	m	25.0	45.0	51.6	3.52		
<i>Cis dentatus</i>	Fp	m	0.0	0.0	2.9			
<i>Cis glabratus</i>	b	m	2.0	0.0	6.3	7.24	0.027	
<i>Cis jacquemarti</i>	b	m	0.0	1.0	6.9	1.13	0.567	

Table 2. Continued.

Family	literal information			CLC (n=10)	YNG (n=49)	OLD	H	p
	Species	visit	hab (n=10)					
Corticariidae								
	<i>Cartodere nodifer</i>	Ff	m	0.0	1.0	0.4		
	<i>Enicmus rugosus</i>	Fp	m	1.0	1.0	0.8		
	<i>Enicmus testaceus</i>	b	m	0.0	0.0	0.4		
Cryptophagidae								
	<i>Cryptophagus abietis</i>	Ff	f	0.0	0.0	0.8		
Cucujidae								
	<i>Dendrophagus crenatus</i>	Fp	o	0.0	0.0	8.2	9.56	0.008
Erotylidae								
	<i>Triplax russica</i>	Ff		0.0	2.0	2.7		
Leiodidae								
	<i>Agathidium nigripenne</i>	Ff	m	1.0	4.0	20.0	10.43	0.005
	<i>Anisotoma castanea</i>	Ff		12.0	75.0	29.0	21.90	< 0.001
	<i>Anisotoma glabra</i>	Ff		29.0	14.0	12.9	6.25	0.044
	<i>Anisotoma humeralis</i>	b		21.0	47.0	224.5	35.99	< 0.001
Monotomidae								
	<i>Rhizophagus dispar</i>	b	f	4.0	4.0	72.9	35.51	< 0.001
	<i>Rhizophagus nitidulus</i>	Ff	f	0.0	13.0	79.6	27.82	< 0.001
	<i>Rhizophagus parvulus</i>	Ff	f	3.0	91.0	82.7	20.40	< 0.001
Nitidulidae								
	<i>Eपुरaea muehli</i>	Ff	o	1.0	1.0	4.9		
	<i>Eपुरaea pygmaea</i>	Ff	o	10.0	2.0	56.3	25.39	< 0.001
	<i>Eपुरaea silacea</i>	Ff	m	0.0	0.0	0.4		
	<i>Eपुरaea variegata</i>	b	f; m	3.0	5.0	7.3	2.54	0.281
	<i>Glischrochilus hortensis</i>	Ff	f	4.0	9.0	18.4	0.64	0.727
	<i>Glischrochilus quadripunctatus</i>	Ff	f	1.0	3.0	10.6	8.40	0.015
	<i>Pocadius ferrugineus</i>	Ff	f; m	1.0	0.0	1.0		
Salpingidae								
	<i>Salpingus ruficollis</i>	Ff		11.0	46.0	201.0	34.56	< 0.001
Scaphidiidae								
	<i>Scaphisoma agaricinum</i>	Fp	f; m	0.0	13.0	0.2	2.27	0.322
Staphylinidae								
	<i>Gyrophaena boleti</i>	b		12.0	115.0	36.5	8.70	0.013
	<i>Leptusa pulchella</i>	b	f	24.0	13.0	87.8	29.84	< 0.001
	<i>Lordithon lunulatus</i>	Ff	f; m	3.0	9.0	22.0	8.56	0.014
	<i>Lordithon trinitatus</i>	Ff	m	2.0	4.0	8.6	2.86	0.240
	<i>Oxypoda alternans</i>	Ff	f; m	2.0	4.0	18.8	16.34	< 0.001
	<i>Phloeonomus lapponicus</i>	Ff	f	0.0	0.0	1.2		
	<i>Phloeonomus monilicornis</i>	Ff	f	0.0	0.0	2.0		
	<i>Quedius plagiatas</i>	Ff	f	9.0	1.0	41.2	18.65	< 0.001
	<i>Quedius xanthopus</i>	Fp	f	2.0	10.0	52.0	32.95	< 0.001
	<i>Sepedophilus littoreus</i>	b	f; m	44.0	11.0	41.8	12.45	0.002
	<i>Stenus impressus</i>	Ff		2.0	1.0	1.0		
Tenebrionidae								
	<i>Bolitophagus reticulatus</i>	Ff	m	0.0	0.0	0.8		
Trogositidae								
	<i>Ostoma ferruginea</i>	Fp	f	2.0	3.0	3.3		
	<i>Thymalus limbatus</i>	b	f; m	0.0	0.0	0.2		

Table 3. Mean of sporocarps and dead wood per sampling site compared for three forest categories: clear-cut (n=10), young stands (12 – 14 years old; n=10) and oldgrowth stands (n=49). SE = standard error.

	No. of sporocarps		Sporocarps of <i>F. pinicola</i>		Sporocarps of <i>F. fomentarius</i>	
	Mean	SE	Mean	SE	Mean	SE
clear-cut	23.40	10.52	13.30	7.65	2.50	1.63
young stands	2.20	0.92	2.20	0.92	0.00	0.00
oldgrowth	27.24	5.62	13.36	2.88	2.76	0.77

	Dead wood (m ³)		Dead wood of stumps (m ³)		Dead wood of birch (m ³)	
	Mean	SE	Mean	SE	Mean	SE
clear-cut	4.88	0.70	2.97	0.33	0.02	0.01
young stands	4.95	0.08	1.76	0.08	0.04	0.02
oldgrowth	5.84	0.89	0.72	0.05	0.71	0.27

The amount of dead-wood substrates did not differ significantly between the forest types (Kruskal-Wallis $H = 0.271$, $df=2$, $p=0.873$). The amount of dead wood was nearly as abundant in clear-cuts as in oldgrowth, probably due to the larger abundance of stumps in clear-cuts (Table 3). *Dead birch wood* showed lower scores in clear-cuts than in oldgrowth (Table 3, $H = 12.876$, $df=2$, $p=0.002$). Even though dead birch is the main substrate for *F. fomentarius* in this area, the density of sporocarps of *F. fomentarius* was not significantly lower in clear-cuts than in oldgrowth (Table 3, Mann-Whitney $U=216.0$, $p>0.05$). Young forest showed a lower number of sporocarps compared to the other forest categories, both for sporocarps in general ($H = 10.973$, $df=2$, $p=0.004$) and for *F. pinicola* ($H = 7.676$, $df=2$, $p=0.022$) and *F. fomentarius* ($H = 6.281$, $df=2$, $p= 0.043$) (Table 3). The general amount of dead wood in young forest was not significantly lower (Kruskal-Wallis $H = 0.271$, $df=2$, $p=0.873$); however, a considerable fraction was older stumps, which are less suitable for *F. pinicola* and *F. fomentarius* (Table 3).

The combined influences of stand characteristics and the amount and quality of dead wood and sporocarps (all variables in Table 1) were tested for all species with high catches in oldgrowth by forward stepwise linear multiple regression. For all species tested (13) except for two, presence of a canopy cover was selected in first step and explained the major part of the variation in catches per site, and was the only selected variable for five of the species (Table 4). For the remaining two species *CANOPY* was selected in the second step. For two species, *CLEAR-CUT* was selected as a second negative variable after the selection of canopy cover (Table 4). Dead wood was selected in step one for the obligate saproxylic species *D. crenatus*, and in the second step for *C. ferrugineum* and *R. nitidulus*. *DECID* (amount of deciduous wood) was selected in step one for *A. nigripenne* and in the second step for *Q. plagiatus*, both species previously recorded from the deciduous-tree-living *F. fomentarius* (Ryvarden & Gilbertson 1993) (Table 4). *FOMENT* (no. of *F. fomentarius* per site) was a second variable for *E. pygmaea*, which is another beetle species previously recorded as visitor of this fungal species (Table 2).

Table 4. The influence of ecological variables on abundance in single species (ln) tested by stepwise forwards multiple regression up to two steps. F is given for each variable at entry into the model as well for the total model. p1 = significance value of F; T = T-value of slope; p2 = significance value of T; R2 = coefficient of determination (given as adjusted R2 for multiple models).

Species	F	p ₁	T	p ₂	R ²	R ² adj
<i>Cerylon ferrugineum</i>						
Step 1: CANOPY	48.118	0.000	6.937	<0.001	0.418	
Step 2: WOOD	9.007	0.004	3.001	0.004	0.488	
Model: 1.704CANOPY + 0.040WOOD + 0.126	31.438	0.000				0.472
<i>Dendrophagus crenatus</i>						
Step 1: WOOD	30.513	0.000	5.524	<0.001	0.313	
Step 2: CANOPY	7.083	0.010	2.661	0.010	0.380	
Model: 0.032WOOD + 0.295CANOPY - 0.155	20.183	0.000				0.361
<i>Agathidium nigripenne</i>						
Step 1: DECID	37.148	0.000	6.095	<0.001	0.357	
Step 2: CANOPY	3.644	0.061	1.909	0.061	0.390	
Model: 0.157DECID + 0.276CANOPY + 0.131	21.128	0.000				0.372
<i>Anisotoma humeralis</i>						
step 1: CANOPY	104.627	0.000	10.229	<0.001	0.610	
step 2: CLEARCUT	3.187	0.079	-1.785	0.079	0.628	
Model: 1.604CANOPY - 0.543CLEARCUT + 0.1380	55.615	0.000				0.616
<i>Rhizophagus dispar</i>						
Step 1: CANOPY	83.935	0.000	9.162	<0.001	0.556	
Step 2: None						
Model: 1.627CANOPY + 0.208	83.935	0.000			0.556	
<i>Rhizophagus nitidulus</i>						
Step 1: CANOPY	42.593	0.000	6.526	<0.001	0.389	
Step 2: WOOD	3.448	0.068	1.857	0.068	0.419	
Model: 1.446CANOPY + 0.023WOOD + 0.142	23.799	0.000				0.401
<i>Rhizophagus parvulus</i>						
Step 1: CANOPY	21.878	0.000	4.677	<0.001	0.246	
step 2: CLEARCUT	3.321	0.073	-1.822	0.073	0.282	
Model: 0.848CANOPY - 0.808CLEARCUT + 0.988	12.979	0.000				0.261
<i>Epuraea pygmaea</i>						
Step 1: CANOPY	35.713	0.000	5.976	<0.001	0.348	
Step 2: FOMENT	7.641	0.007	2.764	0.007	0.415	
Model: 1.144CANOPY + 0.027FOMENT + 0.237	23.447	0.000				0.398
<i>Salpingus ruficollis</i>						
Step 1: CANOPY	136.324	0.000	11.676	<0.001	0.670	
Step 2: None						
Model: 2.063CANOPY+ 0.809	136.324	0.000			0.670	
<i>Leptusa pulchella</i>						
Step 1: CANOPY	57.368	0.000	7.574	<0.001	0.461	
Step 2: None						
Model: 1.279CANOPY + 0.830	57.368	0.000				
<i>Oxypoda alternans</i>						
Step 1: CANOPY	20.039	0.000	4.476	<0.001	0.230	
Step 2: None						
Model: 0.675CANOPY + 0.194	20.039	0.000				

Table 4. Continued.

Species	F	p ₁	T	p ₂	R ²	R ² adj
<i>Quedius plagiatus</i>						
Step 1: CANOPY	19.991	0.000	4.471	<0.001	0.230	
Step 2: DECID	4.676	0.034	2.163	0.034	0.281	
0.825CANOPY + 0.089DECID + 0.314	12.882	0.000				0.259
<i>Quedius xanthopus</i>						
Step 1: CANOPY	75.430	0.000	8.685	<0.001	0.530	
Step 2: None						
Model: 1.348CANOPY + 0.309	75.430	0.000			0.530	

DISCUSSION

In the present study of sporocarp-visiting beetles, the density of dead wood and sporocarps was less important for beetle abundance than was canopy cover. However, it cannot be deduced from this that these substrates are unimportant for this fauna element. Window traps respond to faunal abundance on large scale since they capture the flying stage. Even though other factors than substrate densities may dominate locally, the latter are assumed to have a strong influence in the forest landscape. Compared to the present study, other studies based on window traps have shown a strong influence of dead-wood and wood-fungi variables at larger scales of 3 ha or more (Siitonen 1994, Økland et al. 1996, Martikainen et al. 2000, Siitonen et al. 2000).

It could be questioned if quality of dead wood substrates was an underlying factor for the differences in beetle captures between forest types in the present study, especially the lower amount of dead birch in clear-cuts and young forest. However, linear regression analyses and a closer examination of habitat preferences of the species did not support this. In multiple linear regression, amount of dead birch (BETULA) was not selected as an important factor for the ten species with significantly lower numbers in clear-cuts and young forest. The majority of these species are not known to have a special preference of dead birch. Three of them prefer or are more common on coniferous trees (*E. pygmaea*, *L. pulchella* and *Q. plagiatus*); five occur on both coniferous and deciduous trees or seem to be independent of tree species (*C. ferrugineum*, *A. humeralis*, *R. dispar*, *O. alternans* and *Q. xanthopus*); one is most frequent on aspen (*A.*

nigripennis); while one may be more common on birch (*R. nitidulus*) Palm 1951, Palm 1959, Ehnström pers.comm.).

It is not likely that differences in catchability should be the reason for the significantly lower numbers recorded in clear-cuts and young forest. The flight height of beetles during trivial flight (see definition in Kennedy 1985) is supposed to be nearly the same in clear-cut and oldgrowth forest. However, few studies deal with flight heights of insects in forests. Using suction traps on a TV-tower, Forsse (1989, see paper I and V) captured common bark beetle species (*Ips typographus*, *Hylastes* spp and *Pityogenes chalcographus*) at various heights on a clear-cut situated 100 m from spruce forest. Even in this open environment the majority were found to fly fairly close to the ground (2 m). Also, vertical flight patterns of dipterans inside forests showed a decrease from forest floor to canopy (Service 1973, Raabe et al. 1996). Flight heights in clear-cuts and closed forest were not investigated in the present study. However, if the species in question fly higher under canopy cover, the catches in clear-cuts should be higher and not the opposite as found here. Forsse and Solbreck found that catch efficiency of forest insects by window traps decreased at lower wind speeds (see paper IV in Forsse 1989). Similarly, higher temperatures due to more radiation in clear-cuts are expected to have a positive effect on flight activity and catchability. Lower catches in the clear-cuts did, however, not indicate an influence of wind or temperature on catchability of the present study.

The results indicate a positive influence of canopy cover on habitat preferences of several sporocarp-

visiting beetle species in boreal spruce forest. Increasing canopy cover was also found to be a positive factor for beetle species associated with saproxylic fungi on oak in pasture woodlands (Ranius & Jansson 2000). According to Jonsell et al. (1998), several red-listed saproxylic invertebrates, especially those living in the last successional stages of dead wood, prefer shady forest habitats. In colonisation experiments with insect species breeding in *F. pinicola* and *F. fomentarius*, *Cis* sp. were less successful colonisers of the sporocarps when they were forced to fly over open land (paper 5 in Jonsell 1999). In the present study, most *Cis* species were more numerous in old-growth than in the other forest categories; however, none of the species were significant when the level was adjusted for multiple tests ($p < 0.005$). The density of canopy cover is associated with microclimate and light conditions. Clear-cuts and other open forest habitats may present decisive stimuli for species with a negative phototactic response or to those who are sensitive to moisture, temperature and wind (Romoser 1981). Response to such cues appears to be adaptive, since the insect will save energy by being directed into an optimal forest habitat before the search for microhabitat. This hypothesis needs to be verified by more specific testing.

It is aimed to increase the amount of dead wood in order to improve the condition for saproxylic species in Fennoscandian forestry (Ehnström 2001). The quantity of dead wood in managed forests can be enhanced in many ways (Ehnström 2001). The most common method so far is to leave dead wood, especially tall stumps, on clear-cuts during the logging operation. This method has proved valuable for many saproxylic species preferring sun-exposed dead wood (Ahnlund 1992, Lindelöw et al. 1999, Schroeder et al. 1999), especially those adapted to natural disturbances in boreal forests (Kaila et al. 1997). Most of the artificial stumps are made from spruce attacked by root rot fungi. This method supports only a minor part of the deadwood communities, since many insects and lichens depend on other substrate types, such as the upper part of the stem and dead stems lying on the ground (Ehnström 2001).

Leaving dead wood on clear-cuts seems, however, to be of little help for several saproxylic and mycetophagous insects, who seem to avoid open forest habitats even when dead wood and sporocarps are present. Ehnström (2001) describes several additional methods to increase the amount of dead wood. Among these methods, species preferring shade could be favoured by increasing the rotation time between planting and cutting, and by cutting and leaving single trees every year. For many sporocarp-visitors, favourable management should provide an abundance of dead wood and wood-inhabiting fungi under a closed canopy, and prevent clear-cuts and young stands from becoming a too dominant proportion of the forest landscape.

Acknowledgements. I thank Torstein Kvamme, Anders Vik and Dr. Arne Fjellberg for identification of beetle species, Dr. Tore Skrøppa, Dr. Øystein Johnsen and Professor Jan F. Bjørnstad for comments on statistical presentations, and Cand. scient. Gry Alfredsen, Professor Erik Christiansen and Dr. Fred Midtgaard for comments on the manuscript. The study was supported by Norwegian Research Council and Norwegian Forest Research Institute.

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Received 12 November 2001,
accepted 18 February 2002