Saproxylic beetle fauna associated with living sporocarps of *Fomitopsis pinicola* (Fr.) Karst. in four spruce forests with different management histories

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Hågvar, S. & Økland, B. 1997. Saproxylic beetle fauna associated with living sporocarps of *Fomitopsis pinicola* (Fr.) Karst. in four spruce forests with different management histories. - Fauna norv. Ser. B 44: 95-105.

Trunk-window traps attached to living sporocarps of *Fomitopsis pinicola* (Fr.) Karst. caught a high number of saproxylic beetles. Comparison with free-hanging window traps showed that the sporocarps act as "attraction centra" for a number of species. Only one of these, *Gyrophaena boleti* (L.), regularly breeds in living sporocarps. The other ones probably visit sporocarps for feeding purposes (either as spore eaters or predators), and could be observed sitting on the hymenium of the sporocarps. As the visiting beetles were sometimes densely covered by fungal spores, we suggest that they may act as spore spreaders. *Gyrophaena boleti* and certain typical visiting species dominated the catches numerically in each of four spruce forest environments: (1) a small patch of little influenced "primeval forest", (2) a nature reserve with semi-natural forest, (3) a managed forest mature for cutting, and (4) a clear-cut area with small, 5 to 10-year-old planted trees. Due to the observed "baiting effect" of the sporocarps, only two sites with similar density of sporocarps and traps could be compared directly, the small patch of primeval forest and the nature reserve. Per trap, the primeval forest gave significantly more species of both saproxylic and red-listed beetles. Also, many species were more abundant in the primeval forest. It is noteworthy that fewest species were recorded in the clear-cut area.

Even some closely related species (e.g. within the genera *Cis, Anisotoma, Enicmus*) showed great differences in their relative catches between the four forest environments.

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INTRODUCTION

Nearly 700 Norwegian beetle species are obligate saproxylic, i.e. they depend on decaying wood or wood-inhabiting fungi for their development. More than 200 additional beetles are facultative saproxylic, i.e. they can also breed in alternative substrates (Stokland, pers. comm.). In Norway, Sweden and Finland, saproxylic beetles represent a large part of the red-listed insect species (Rassi et al. 1992, Størkersen 1992, Ehnstrøm et al. 1993).

Earlier studies of the saproxylic beetle fauna have often been based on destructive sampling procedures, especially by removing bark from decaying logs (e.g. Biström & Väisänen 1988, Väisänen, Biström & Heliovaara 1993, Siitonen 1994, Siitonen & Martikainen 1994). Because this method destroys the microhabitats, fails to catch wood-boring species, and is rather ineffective, Kaila (1993) proposed a "trunk-window trap" to collect insects which are active near dead wood. By placing such traps close to living sporocarps (fruiting bodies of wood-inhabiting fungi, Polyporaceae), he caught high numbers of saproxylic beetle species.

However, the catches depended on fungal and tree species. Also a study by Økland & Hågvar (1994) confirmed the great ability of this trap to collect saproxylic beetles. They suggested that living sporocarps act as "attraction centra" for certain saproxylic beetles, which were caught in high numbers.

In the present study, the trunk-window trap method was tested in four different spruce (*Picea abies* (L.) Karst.) forest environments. The polypore species used was *Fomitopsis pinicola* (Fr.) Karst., since this species is common both in managed and natural forests. We wanted to get more information about the role of living sporocarps as attraction centra for saproxylic beetles. In one locality (forest reserve), free-hanging window traps were operated simultaneously for comparison (Økland 1995, 1996), and direct observations were made about beetle species sitting on the underside of living sporocarps. Also, we wanted to evaluate whether the method is suitable for comparison of the saproxylic beetle fauna in different forest environments. Faunistic lists of saproxylic beetles are given, and the biology of some species is discussed.

MATERIAL AND METHODS

Study sites

All the four study sites were located in the Østmarka forest area, about 15 km SE of Oslo. They were placed within the dominant vegetation type (*Eu-Piceetum Myrtillus*), which is spruce forest with bilberry (*Vaccinium myrtillus* L.) in the field layer. In light open areas, *Deschampsia flexuosa* (L.) tends to dominate. UTM positions are given according to WGS84.

In the primeval forest and the forest reserve, sites with high density of dead wood were chosen. The amount of dead wood was measured in an area of 40x40 m.

1. A small "primeval forest" (PR) of about 0.1 km^2 was surrounded by managed forest in various successional stages. It was located in a valley named Styggvannsdalen, about 5 km north of the forest reserve. The absence of logging-related stumps, the occurrence of dead wood in all phases of decomposition, the heterogeneous age structure of the trees, and the difficult access to the site indicated a higher dead-wood continuity than in the forest reserve. Also certain indicator species of wood-inhabiting fungi and lichens were found (cf. Karström 1992, Bredesen et al. 1993, 1994). A lack of fire marks and a moist valley bottom may indicate that this site is a fire refuge (cf. Zackrisson & Östlund 1991). The forest was rather closed, with many high trees. The amount of dead wood in the sampling site was 109 m^3 per ha. Traps were separated by a mean distance of about 10 m. Sporocarps of *F. pinicola* occurred abundantly, on the mean every 1.3 meters. UTM position: PM 120424.

2. The reserve (RE), 12.5 km^2 large, was subjected to selective cutting until about 1930. The cutting has probably been rather intense along some parts of the watersheds, due to the possibility of timber floating. During World War II (1940-45), the amount of dead wood was reduced due to intensive firewood collection. Even though several parts of the reserve contain considerable amounts of dead wood today, there is a lack of continuity of dead wood in most of the area (Gauslaa 1994). Several of the hilltops have been subjected to forest fires. The traps were placed in the central part, and distributed in equal numbers on two plots (900 m apart) with high amounts of dead wood (372 m^3 per ha). The plots were half open due to many wind-felled trees 10-15 years ago. Some standing dead trees were probably killed by bark-beetles. Logs in more advanced states of decay occurred in the neighbouring area. The mean distance between traps was about 10 m. Sporocarps of *F. pinicola* were very abundant, on the mean every 0.8 meters. UTM position: PM 143367 and PM 141359.

3. The managed forest (MA) was situated close to site 1 and was largely mature for cutting. The density of decaying wood was on an average 3 m^3 per ha. The mean distance between traps was 125 m, with 79 m between sporocarps of *F. pinicola*. Some small clear-cut areas with a higher density of sporocarps (on stumps) occurred in the area, but these were avoided when placing traps. Because the traps had to be scattered over a large area, a wide spectrum of local forest habitats was included. UTM position: PM 116436.

4. The clear-cut area (CL) had been logged 5-10 years earlier, and contained small, planted spruce trees. It

covered about 0.06 km^2. While sporocarps (mainly on stumps) were rather abundant, on the mean every 21 meters, several grew so close to the ground that traps could not be attached to them. The mean distance between traps was about 40 m. Some remnants of dead wood after logging operations were present. UTM position: PM 088363.

Sampling of beetles

Trunk-window traps (Kaila 1993) consist of a window placed in a vertical split cut through a sporocarp, with a collecting funnel below. Our version (Økland et al. 1995, Økland 1996, Hågvar et al. 1995) was made of plastic, and had a roof to minimize rainwater and litter in the trap. Ethylene glycol with a small amount of detergent was used as preservative, and the traps were emptied monthly. Small holes halfway up in the wall of the collecting vial allowed surplus water to escape during heavy rain. For storage and identification the insects were transferred to 70 % alcohol. The size of the window was 20x20 cm, and the upper diameter of the collecting funnel 22 cm. The plastic funnel was adjusted so that it fitted closely to the trunk below the sporocarp. Most traps were placed 0.5-1.5 m above the ground, often on natural or man-made stumps. In each of the four habitats, 30 traps were operated from 28 April to 6 September 1992. Altogether, 15 387 individuals of obligate and facultative saproxylic beetles were collected.

Habitat ecology and nomenclature of the species

Information on the habitat ecology of the various beetle species was achieved from an extensive data base compiled by J. Stokland, based on both literature and personal communication.

Nomenclature is according to Silfverberg (1992), and we refer to this source concerning author names.

RESULTS

Faunal composition and baiting effects

Table 1 shows the catches of obligate and facultative saproxylic beetles among species represented by at least 20 individuals totally. In all four habitats, the catches were numerically dominated by "visiting species", i.e. certain species which were often observed sitting on living sporocarps, mainly on the underside. These species are marked with an asterisk in the table. Only one of these, *Gyrophaena boleti*, breeds in living sporocarps, having larvae in the pores.

The baiting effect of the sporocarps can be illustrated by comparing the catches with simultaneous catches in ordinary window traps placed about 0.7-1 m above the ground (Bakke 1975, Økland et al. 1995). Such comparisons, based on 30 traps of each type, have been performed in the reserve (cf. Økland 1996). Table 2 lists the most abundant saproxylic species from each trap type (minimum 10 individuals). Clearly, the beetle fauna swarming close to the sporocarps differs considerably from the general "air plankton". Only four species were common to the two lists. Several typical "visitor" species were poorly represented in the ordinary window traps. A closer statistical analysis of the differences in catches between the two methods has been made by Økland (1996).

The observed baiting effects makes it difficult to use the trunk-window traps in quantitative comparisons between habitats. Because several species actively search for sporocarps, the catches per trap will depend on the density of the sporocarps (i. e. the density of attraction centra). This can be clearly illustrated in *Gyrophaena boleti*, where all individuals aggregate on sporocarps during spring. Assuming that each trap collected a certain fraction of the individuals which were attracted to each sporocarp, the relative population size per area could be estimated by multiplying the catch per trap with the number of sporocarps per area. It turned out that the abundance per ha was highest in the two sites which had the lowest catches per trap (Figure 1). This was due to a very high density of sporocarps in the primeval forest and the reserve, so that the high number of beetle individuals per area was "diluted" over the many attraction centra. The data in Figure 1 were restricted to May, the month in which the overwintering adults colonize the

Table 1. Catches of obligate and facultative saproxylic species, trapped in at least 20 individuals. The species have been ranked according to total catches. Red-listed species (in Sweden or Norway) are underlined. Species observed sitting on living sporocarps are marked with an asterisk. MA=managed forest, PR=primeval forest, RE= reserve, CL=clearcut.

SPECIES	FAM**	MA	PR	RE	CL	SUM
Obligate saproxylic species:						
*Gyrophaena boleti**	STA	2375	1358	330	4556	8619
*Pteryngium crenatum**	CRY	238	194	72	58	562
*Cis glabratus**	CIS	243	131	21	109	504
Anisotoma axillaris	LEI	0	0	1	318	319
*Enicmus rugosus**	LAT	43	12	16	183	254
*Anisotoma humeralis**	LEI	39	93	12	44	188
*Rhizophagus dispar**	RHI	32	35	45	63	175
Hylastes cunicularius	SCO	145	15	6	0	166
*Enicmus testaceus**	LAT	60	48	51	2	161
*Atomaria alpina**	CRY	72	33	25	22	152
Anisotoma castanea	LEI	51	17	1	68	137
*Anisotoma glabra**	LEI	4	2	1	111	118
<u>*Cis quadridens**</u>	CIS	32	52	10	0	94
Anaspis rufilabris	ANA	12	21	27	4	64
Ptinus subpilosus	PTI	8	14	24	17	63
*Leptusa pulchella**	STA	22	17	9	5	53
*Hallomenus binotatus**	MELA	24	15	1	6	46
Nevraphes coronatus	SCY	0	37	3	2	42
Xylita laevigata	MELA	7	16	12	5	40
Dryocoetes autographus	SCO	4	32	4	0	40
Melanotus castanipes	ELA	11	11	7	6	35
Trypodendron lineatum	SCO	31	2	2	0	35
Crypturgus hispidulus	SCO	9	12	10	1	32
Hylurgops palliatus	SCO	18	11	1	0	30
Bolitochara mulsanti	STA	2	8	0	20	30
<u>*Ipidia quadriplagiata*</u>	NIT	13	13	3	0	29
Phloeonomus punctipennis	STA	13	6	3	7	29
*Thymalus limbatus**	TRO	7	9	8	5	29
Rhyncolus chloropus	CUR	4	4	10	4	22
*Ostoma ferruginea**	TRO	2	9	8	3	22
Bibloporus bicolor	PSE	10	4	5	2	21
Facultative saproxylic species:						
*Epuraea variegata**	NIT	128	83	44	454	709
*Lordithon lunulatus**	STA	201	52	164	86	503
*Scaphisoma agaricinum**	SCA	58	11	3	319	391
Bolitochara pulchra	STA	19	1	1	161	182
*Corticaria longicollis**	LAT	43	9	43	32	127
Lordithon thoracicus	STA	8	2	12	81	103
Gyrophaena affinis	STA	1	0	2	99	102
*Atomaria pulchra**	CRY	28	39	3	8	78
Quedius plagiatus	STA	26	39	10	0	75
Dienerella elongata	LAT	38	0	0	0	38
Sepedophilus testaceus	STA	9	2	1	26	38
Cychramus variegatus	NIT	12	13	7	0	32
Cryptophagus scanicus	CRY	6	8	17	0	31
Cryptophagus setulosus	CRY	7	2	0	11	20
*Sepedophilus littoreus**	STA	7	8	4	1	20

** Full family names are: Anaspidae, Cisidae, Cryptophagidae, Curculionidae, Elateridae, Latridiidae, Leiodidae, Melandryidae, Nitidulidae, Pselaphidae, Ptinidae, Rhizophagidae, Scaphidiidae, Scolytidae, Scydmaenidae, Staphylinidae, Trogositidae.

Table 2. Catches of saproxylic beetles from trunk-window traps and ordinary window traps in the same site (reserve, 30 traps of each type). Only the most abundant species (with ten or more individuals) are listed. O=obligate saproxylic, F=facultative saproxylic, *=species observed sitting on the underside of living sporocarps.

Trunk-window traps:				Window traps:			
O	*	*Gyrophaena boleti*	330	O	*	*Enicmus testaceus*	82
F	*	*Lordithon lunulatus*	164	O	*	*Enicmus rugosus*	36
O	*	*Pteryngium crenatum*	72	O		*Bibloporus bicolor*	36
O	*	*Enicmus testaceus*	51	F		*Cryptophagus abietis*	35
O	*	*Rhizophagus dispar*	45	O		*Crypturgus pusillus*	22
F	*	*Epuraea variegata*	44	O		*Dryocoetes autographus*	17
F	*	*Corticaria longicollis*	43	O		*Euplectus punctatus*	17
O		*Anaspis rufilabris*	27	O		*Dasytes niger*	15
O	*	*Atomaria alpina*	25	O	*	*Leptusa pulchella*	15
O		*Ptinus subpilosus*	24	F	*	*Henoticus serratus*	13
O	*	*Cis glabratus*	21	O		*Hylastes cunicularius*	12
F		*Cryptophagus scanicus*	17	O		*Melanotus castanipes*	12
O	*	*Enicmus rugosus*	16	O		*Ptinus subpilosus*	11
O	*	*Anisotoma humeralis*	12	O		*Anaspis rufilabris*	10
F		*Lordithon thoracicus*	12	O		*Atrecus pilicornis*	10
O		*Xylita laevigata*	12				
O		*Cerylon histeroides*	10				
O	*	*Cis quadridens*	10				
O		*Crypturgus hispidulus*	10				
F		*Quedius plagiatus*	10				
O		*Rhyncolus chloropus*	10				

sporocarps, in order to avoid inclusion of animals developed within the sporocarps.

Comparison between habitats

On this background, we have limited the statistical comparisons in Table 1 to the primeval forest and the reserve. These habitats had the same distance between the traps, and both had very high sporocarp densities. All significant differences ($p<0.05$) among obligate saproxylic species gave highest catches in the primeval forest (Pearson's chi square statistic for goodness of fit, according to Bhattacharyya & Johnson (1977)). This was found for the following species: *Cis glabratus, Cis quadridens, Pteryngium crenatum, Anisotoma castanea, Anisotoma humeralis, Hallomenus binotatus, Ipidia quadriplagiata, Dryocoetes autographus, Hylastes cunicularius, Hylurgus palliatus, Nevraphes coronatus, Bolitochara mulsanti, and Gyrophaena boleti.*

Even though Table 1 may misrepresent the relative abundance between habitats, we can observe that even closely related species may respond quite differently. Within the genus *Anisotoma, A. axillaris* and *A. glabra* were taken almost exclusively in the clear-cut area, while *A. humeralis* and *A. castanea* were also caught in the forest sites. *Cis quadridens* was absent in the clear-cut catches, but *C. glabratus* was taken in both types of environment. *Enicmus rugosus* was taken mainly in the clear-cut area, while *E. testaceus* was most often caught in the forested sites. Among the facultative saproxylic species, *Lordithon thoracicus* was taken abundantly only in the clear-cut site, while *L. lunulatus* was trapped frequently in all environments.

Table 3 shows the number of species trapped in the four habitats, distributed on three groups: obligate saproxylic, obligate plus facultative saproxylic, and red-listed species. The table also gives the mean number of species per trap for the same groups. Because the

Table 3. Catches of saproxylic beetles in four spruce forest environments: Total number of species and mean number of species per trap. MA=managed forest, PR=primeval forest, RE=reserve, CL=clearcut.

	Number of species:				*Species per trap:*			
Group	MA	PR	RE	CL	MA	PR	RE	CL
Obligate	92	105	83	70	14,2	15,8	11,4	11,0
Obligate + facultative	125	135	107	95	20,2	20,7	14,8	16,9
Red-listed	8	13	8	7	1,2	1,5	0,8	0,7

baiting effect may even have influenced the number of species, statistical comparisons have been limited to the primeval forest and the reserve. While no significant differences were found in total species number in the various groupings (Pearson's chi square), the primeval forest had significantly higher species numbers per trap in all three species groups (Fischer's least significant-difference test, Sokal & Rohlf (1981)).

Faunistical data

The catches of the less numerous saproxylic species are listed in Table 4. Clearly, a set of 30 trunk-window traps catches a large diversity of saproxylic species, but most species occur in low numbers. In total, 152 obligate and 47 facultative saproxylic species were trapped in the four habitats.

Sixteen red-listed species from Norwegian and Swedish lists have been underlined in Tables 1 and 4. Only one non-saproxylic red-listed species was recorded: one specimen of *Agonum mannerheimii* in the primeval forest. There were a total of 13 red-listed species in the primeval forest, 8 in the reserve, 8 in the managed forest, and 7 in the clearcut area.

DISCUSSION

Living sporocarps as attraction centra for saproxylic beetles

Trunk-window traps attached to living sporocarps of *Fomitopsis pinicola* and ordinary window traps in the same site yielded similar numbers of saproxylic beetle species, both among obligate and facultative species (Økland 1996). However, certain species were more abundant in the trunk-window traps (Table 2 and Økland 1996), and these dominated the catches numerically in all four environments (Table 1). Jonsell & Nordlander (1995) showed that the odour of chopped, living *Fomitopsis pinicola* attracts several saproxylic beetles, among them three of the typical "visiting species" in the present material: *Pteryngium crenatum, Cis glabratus and Cis quadridens.* There may be various reasons why living sporocarps act as attraction centra for saproxylic beetles:

1. *Breeding.* Only *Gyrophaena boleti* among the recorded species breeds in living, undamaged sporocarps of *Fomitopsis pinicola.* The larvae are spore-eaters and live in the pores (Ashe 1984). This species dominated the catches in all four habitats. *Cis glabratus* and *Cis quadridens* breed typically in dead sporocarps, although a few *Cis glabratus* have been extracted from living sporocarps (Økland & Hågvar 1994). Cisidae sometimes breed in weakened or dead parts of living sporocarps (Hågvar, unpubl.), and such "pioneer colonies" will have a good start when the sporocarp eventually dies.

2. *Feeding.* Among the other typical visiting species marked with an asterisk in Table 1, some are probably spore eaters, e.g. *Pteryngium crenatum, Atomaria alpina, Anisotoma humeralis,* and *Corticaria longicollis,* while some are predators, e.g. *Rhizophagus dispar* and *Quedius plagiatus* (Koch 1989-92). In addition to larvae of *Gyrophaena boleti,* the pores may contain dense populations of potential prey, especially Diptera larvae (Økland & Hågvar 1994) and white mites. Although these animals usually hide in the pores, they sometimes

Table 4. Catches of less common saproxylic species (less than 20 individuals in sum). To facilitate the overview, the families have been arranged in alphabetic order. Red-listed species are underlined. MA=managed forest, PR=primeval forest, RE=reserve, CL=clearcut.

Obligate saproxylic species:

Species	Fam*	MA	PR	RE	CL	Sum	Species	Fam*	MA	PR	RE	CL	Sum
Euglenes pygmaeus	ADE	0	0	0	1	1	*Dacne bipustulata*	ERO	0	1	0	0	1
Anaspis bohemica	ANA	1	0	0	0	1	*Xylophilus corticalis*	EUC	0	4	5	0	9
Anaspis flava	ANA	0	0	0	2	2	*Corticaria interstitialis*	LAT	2	2	0	0	4
Anaspis frontalis	ANA	7	0	0	0	7	*Enicmus fungicola*	LAT	1	2	0	0	3
Anaspis schilskyana	ANA	2	0	1	0	3	*Latridius hirtus*	LAT	0	1	0	0	1
Dorcatoma punctulata	ANO	2	3	4	10	19	*Agathidium nigripenne*	LEI	0	1	0	0	1
Hadrobregmus pertinax	ANO	0	0	2	1	3	*Anisotoma orbicularis*	LEI	0	0	1	1	2
Stagetus borealis	ANO	1	0	0	1	2	*Dictyoptera aurora*	LYC	6	2	6	1	15
Platystomus albinus	ANT	0	0	0	1	1	*Dictyoptera nigrorubra*	LYC	0	0	3	1	4
Anthaxia quadripunctata	BUP	0	0	2	0	2	*Lygistopterus sanguineus*	LYC	0	0	0	1	1
Absidia schoenherri	CAN	3	10	4	1	18	*Platycis minuta*	LYC	2	1	0	2	5
Malthodes brevicollis	CAN	7	6	1	0	14	*Hylecoetus dermestoides*	LYM	0	4	1	0	5
Malthodes crassicornis	CAN	4	1	0	5	10	*Hallomenus axillaris*	MELA	1	1	1	9	12
Malthodes flavoguttatus	CAN	0	1	0	0	1	*Dasytes niger*	MELY	3	8	2	0	13
Malthodes fuscus	CAN	6	4	4	1	15	*Curtimorda maculosa*	MOR	1	1	1	3	6
Malthodes marginatus	CAN	0	0	1	0	1	*Tomoxia bucephala*	MOR	0	0	1	1	2
Malthodes spathifer	CAN	3	0	0	1	4	*Epuraea bickhardti*	NIT	15	2	0	0	17
Alosterna tabacicolor	CERA	0	4	0	0	4	*Epuraea boreella*	NIT	2	0	2	0	4
Anoplodera maculicornis	CERA	0	4	4	0	8	*Epuraea laeviuscula*	NIT	1	0	0	0	1
Anoplodera rubra	CERA	0	0	0	4	4	*Epuraea pygmaea*	NIT	1	1	6	0	8
Evodinus borealis	CERA	0	1	0	0	1	*Epuraea silacea*	NIT	0	1	0	0	1
Judolia sexmaculata	CERA	1	1	0	0	2	*Glischrochilus hortensis*	NIT	1	0	1	12	14
Leptura melanura	CERA	2	0	0	8	10	*Glischrochilus quadripunctatus*	NIT	0	0	3	0	3
Oxymirus cursor	CERA	1	2	3	1	7	*Chrysanthia viridissima*	OED	0	0	0	3	3
Rhagium inquisitor	CERA	0	2	0	0	2	*Euplectus decipiens*	PSE	4	8	0	2	14
Rhagium mordax	CERA	0	1	0	0	1	*Pteryx suturalis*	PTI	2	6	4	4	16
Tetropium castaneum	CERA	2	1	1	0	4	*Rhizophagus cribratus*	RHI	0	1	0	0	1
Tetropium fuscum	CERA	1	0	0	0	1	*Rhizophagus depressus*	RHI	0	1	1	0	2
Cerylon fagi	CERY	6	1	0	2	9	*Rhizophagus ferrugineus*	RHI	3	0	0	0	3
Cerylon histeroides	CERY	0	3	10	0	13	*Rhizophagus parvulus*	RHI	1	0	0	0	1
Cis bidentatus	CIS	6	4	3	2	15	*Salpingus ruficollis*	SAL	2	2	3	0	7
Cis boleti	CIS	0	2	0	0	2	*Cryphalus abietis*	SCO	6	2	0	0	8
Cis fagi	CIS	0	9	0	0	9	*Crypturgus subcribrosus*	SCO	2	1	1	0	4
Cis hispidus	CIS	2	1	0	0	3	*Dryocoetes alni*	SCO	0	1	0	0	1
Cis lineatocribratus	CIS	0	2	1	3	6	*Hylastes brunneus*	SCO	3	0	0	0	3
Cis nitidus	CIS	0	2	0	1	3	*Ips typographus*	SCO	8	0	0	0	8
Cis punctulatus	CIS	0	0	1	0	1	*Pityogenes chalcographus*	SCO	9	2	8	0	19
Ennearthron cornutum	CIS	0	0	1	1	2	*Polygraphus poligraphus*	SCO	1	1	0	0	2
Ennearthron laricinum	CIS	4	0	8	0	12	*Trypodendron domesticum*	SCO	4	1	3	0	8
Hadreule elongatula	CIS	0	0	0	11	11	*Sphindus dubius*	SPH	1	1	0	5	7
Octotemnus glabriculus	CIS	0	1	0	0	1	*Anomognathus cuspidatus*	STA	0	0	1	0	1
Orthocis festivus	CIS	0	1	0	0	1	*Atrecus longiceps*	STA	1	1	2	0	4
Atomaria umbrina	CRY	0	3	0	0	3	*Atrecus pilicornis*	STA	0	2	0	0	2
Dendrophagus crenatus	CUC	0	1	0	1	2	*Dinaraea aequata*	STA	0	1	0	1	2

Table 4 (continued)

Obligate saproxylic species:

Species	Fam*	MA	PR	RE	CL	Sum	Species	Fam*	MA	PR	RE	CL	Sum
Silvanoprus fagi	CUC	0	1	0	0	1	*Dinaraea arcana*	STA	1	1	2	0	4
Hylobius abietis	CUR	4	0	0	0	4	*Euryusa castanoptera*	STA	0	2	0	0	2
Hylobius piceus	CUR	1	0	1	0	2	*Gabrius splendidulus*	STA	0	0	0	1	1
Hylobius pinastri	CUR	2	6	2	5	15	*Gyrophaena strictula*	STA	1	0	0	0	1
Pissodes pini	CUR	0	1	0	0	1	*Hapalarea linearis*	STA	4	6	1	0	11
Rhyncolus sculpturatus	CUR	0	0	1	0	1	*Leptusa fumida*	STA	6	2	0	0	8
Strophosoma capitatum	CUR	14	2	0	0	16	*Lordithon speciosus*	STA	0	0	3	0	3
Trachodes hispidus	CUR	1	0	0	5	6	*Oxypoda recondita*	STA	0	1	0	0	1
Ampedus balteatus	ELA	1	0	1	2	4	*Phloeonomus monilicornis*	STA	0	4	2	0	6
Ampedus nigrinus	ELA	5	3	1	2	11	*Phloeonomus pusillus*	STA	4	1	1	1	7
Ampedus pomorum	ELA	0	0	0	1	1	*Phloeonomus sjoebergi*	STA	0	1	1	0	2
Ampedus tristis	ELA	0	0	0	1	1	*Phymatura brevicollis*	STA	4	1	0	0	5
Dadobia immersa	ELA	1	0	1	2	4	*Placusa depressa*	STA	1	0	0	0	1
Denticollis linearis	ELA	0	1	0	0	1	*Placusa incompleta*	STA	1	0	0	0	1
Endomychus coccineus	END	0	0	1	0	1	*Placusa suecica*	STA	0	1	1	0	2
Triplax russica	ERO	1	2	0	1	4	*Bolitophagus reticulatus*	TEN	0	1	0	0	1

Facultative saproxylic species:

Species	Fam*	MA	PR	RE	CL	Sum	Species	Fam*	MA	PR	RE	CL	Sum
Dromius agilis	CAR	2	0	0	0	2	*Cychramus variegatus*	NIT	2	2	0	0	4
Anatis ocellata	COC	2	0	0	0	2	*Epuraea aestiva*	NIT	2	0	1	0	3
Orthoperus atomus	COR	1	0	1	0	2	*Epuraea binotata*	NIT	5	0	1	0	6
Atomaria contaminata	CRY	2	1	0	0	3	*Pocadius ferrugineus*	NIT	0	0	0	2	2
Cryptophagus abietis	CRY	11	5	1	0	17	*Tyrus mucronatus*	PSE	0	0	0	1	1
Gnathoncus buyssoni	HIS	0	1	1	0	2	*Phosphuga atrata*	SIL	0	0	0	1	1
Corticaria abietorum	LAT	1	0	0	2	3	*Arpidiphorus orbiculatus*	SPH	7	1	0	5	13
Corticaria serrata	LAT	0	1	0	0	1	*Acrulia inflata*	STA	3	7	0	2	12
Corticarina obfuscata	LAT	0	1	0	0	1	*Coryphium angusticolle*	STA	0	0	1	0	1
Latridius anthracinus	LAT	0	0	0	1	1	*Haploglossa villosula*	STA	6	1	1	0	8
Latridius minutus	LAT	3	0	0	0	3	*Ischnoglossa prolixa*	STA	0	1	0	0	1
Stephostethus rugicollis	LAT	1	0	0	0	1	*Mniusa incrassata*	STA	0	1	2	1	4
Agathidium badium	LEI	2	1	0	1	4	*Oxypoda vittata*	STA	0	0	0	3	3
Agathidium mandibulare	LEI	0	3	0	0	3	*Pachygluta ruficollis*	STA	0	0	0	4	4
Agathidium nigrinum	LEI	2	2	1	10	15	*Quedius maurus*	STA	0	1	0	0	1
Agathidium seminulum	LEI	5	2	6	6	19	*Quedius xanthopus*	STA	6	4	5	2	17

* Full family names are given at the bottom of Table 3, except for the following: Aderidae, Anobiidae, Anthribidae, Buprestidae, Cantharidae,Carabidae, Cerambycidae, Cerylonidae, Coccinellidae, Corylophidae, Cucujidae, Endomychidae, Erotylidae, Eucnemidae, Histeridae, Lycidae, Lymexylidae, Melyridae, Mordellidae, Oedemeridae, Ptilidae, Salpingidae, Silphidae, Sphindidae, Tenebrionidae.

emerge to the surface to change pore. The presence of these hidden groups may be demonstrated by putting the sporocarp into a tight-fitting plastic bag. When the oxygen concentration becomes low inside, both the Diptera larvae and the mites emerge from the pores,often in large numbers. The hymenium of the sporocarps may be a good hunting ground.

3. *Spore dispersal?* The fungus can probably afford to waste a fraction of the spores as insect food. Maybe the fungus attracts beetles for mutual benefit. Visiting beetles have often been observed with a white cover of fungal spores on their body. Since most of the visiting beetles will seek to dead wood to lay their eggs, they may be carriers of spores to new substrates.

4. *Kairomones?* Kaila (1993) suggested that saproxylic beetles might use the odour from sporocarps as orientation guides towards their breeding substrate, which in most cases is dead wood and not the sporocarp itself. It may even be favourable to breed in wood close to sporocarps, since many species use the wood-decomposing mycelium as their source of nutrition instead of the wood itself (Palm 1955).

Also living sporocarps of *Fomes fomentarius*, which usually grows on dead birch stems, act as attraction centra for saproxylic beetles. Kaila et al. (1994) obtained more species and individuals in traps attached to sporocarps than in traps attached to dead birch stems without sporocarps. Still fewer species were caught in traps placed on living birch stems. Just as for *Fomitopsis pinicola,* Jonsell & Nordlander (1995) found that chopped, living sporocarps of *Fomes fomentarius* attracted certain saproxylic beetles by odour. Some beetles were attracted to both fungal species, while some beetles preferred one of them.

We can conclude that living sporocarps may have a positive function for a larger number of saproxylic beetles than those few species which breed in them, at least as a source of food. A rich sporocarp flora will also indicate a good availability of dead wood substrates. Therefore, an attraction to sporocarp odours may automatically bring saproxylic beetles into a favourable breeding locality. Økland et al.(1995) found a positive relationship between the species number of obligatory saproxylic beetles and the density and species number of sporocarps (polypore fungi). This relationship, which was found at 1 and 4 km^2 area levels, might be helpful in mapping favourable sites for the saproxylic beetle fauna, since it is relatively easy to describe the community of polypore fungi. Other important factors for saproxylic beetles were dead wood of large diameter, and a high diversity of dead wood objects, including deciduous trees (Økland et al. 1996).

Comparisons between habitats

Because of the baiting effect connected with trunk-window traps, ordinary window traps screening the general "air plankton" are better for comparing the saproxylic beetle fauna in different habitats. However, this method requires a large-scaled sampling (Økland 1996). When trunk-window traps attached to sporocarps are used, the abundance of several species, and probably even the species number, will be underestimated with increasing sporocarp density. The reason for this is that there will be a higher number of attraction centra for the beetles to distribute themselves on, and even if a species has a high density per area, the catches per trap may be low (Figure 1).

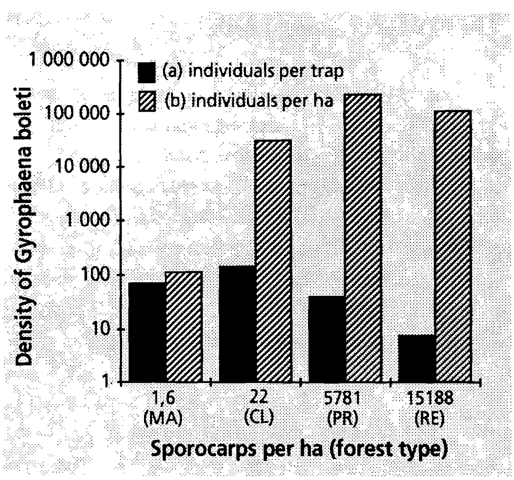

Figure 1
Relative densities of *Gyrophaena boleti* expressed as (a) the number of individuals per trap, and (b) the number of individuals per ha. MA=managed forest, CL=clearcut, PR=primeval forest, RE=reserve. The number of sporocarps per ha in each forest type has been given below.

Due to high sporocarp densities, the catches in the primeval forest and the reserve are probably underestimated compared to the clearcut area and the managed forest. This also indicates that the low species numbers recorded in the clearcut area (Table 3) may be a real trend. The clearcut area is the only habitat among the four which does not produce dead wood. The most overestimated species numbers in Table 3 are probably those from the managed forest, where there were both a greater distance between sporocarps and a large catching area which included a higher variety of forest environments. However, it is noteworthy that this habitat gave a rather high number of species, even if the density of dead wood was low. This indicates that even scattered dead wood substrates are localized and used by several species. Probably, any increase in dead wood in spruce forest will favour the saproxylic beetle community (cf. Økland et al. 1996, Hågvar et al. 1995).

The present material indicated higher populations of several species, and also higher numbers of species per trap, in the primeval forest compared to the reserve. The actual primeval forest also turned out to be a favourable habitat for Mycetophilidae (Diptera), with a high number of species (Økland 1994).

The biology of some species

It is interesting that closely related species within the genera *Anisotoma, Cis, Enicmus* and *Lordithon* responded quite differently to the four habitats (Table 1). This may reflect adaptations to different successional stages, from open areas to old forest. While some species were obviously very active on the clearcut area (e.g. *Anisotoma axillaris, Anisotoma glabra* and *Enicmus rugosus*), other species seemed to avoid the open area (e.g. *Cis quadridens* and *Enicmus testaceus*).

ACKNOWLEDGEMENTS

We thank Arne Kolerud, Torfinn Sæther and John Gunnar Dokk for technical assistance, Arne Fjellberg for species identification, Jogeir Stokland for access to a data base on the biology of Norwegian beetle species, and Alf Bakke and Torstein Kvamme for cooperation within the project "Forest Ecology and Multiple Use", financially supported by the Norwegian Research Council.

SAMMENDRAG

Biller fanget ved levende rødrandkjuker i fire ulike granskogsmiljøer

En finsk-konstruert vindusfelle festet til levende rødrandkjuker gav høye fangster av biller som utvikler seg i dødt trevirke. Samtidige fangster i ordinære, fritthengende vindusfeller viste at kjukene fungerte som "attraksjonssentra" for en rekke billearter. Kun en av disse, kortvingen *Gyrophaena boleti*, utvikler seg i levende rødrandkjuker. De andre "besøkerartene" trekkes trolig til kjukene for å ta til seg næring, enten som sporespisere eller som predatorer på insektlarver og midd, som kan forekomme i store tettheter i porene. Mange billearter kan observeres hyppig sittende på undersiden av levende rødrandkjuker. Da "besøkende" biller ofte var dekket av soppsporer, antas det at artene kan bidra til å spre sporer til annet død ved-substrat. *Gyrophaena boleti* og noen typiske besøkerarter dominerte fangstene i alle de fire undersøkte granskogsmiljøene: (1) et lite naturskogsparti med en viss kontinuitet, (2) Østmarka naturreservat med lite kontinuitet, (3) en hogstmoden kulturskog, og (4) en hogstflate med 5-10 år gamle trær. På grunn av kjukenes sterke tiltrekningsevne på mange arter, kunne direkte sammenligninger av fangstene bare foretas på to felter som hadde omtrent samme tetthet av kjuker og feller: naturskogspartiet og reservatet. Pr. felle hadde naturskogspartiet signifikant flest arter av både død ved -avhengige og rødlistede arter. Mange enkeltarter hadde også høyere individantall i naturskogens feller, sammenlignet med reservatet. Av alle de fire feltene ble færrest arter tatt på hogstflaten. Arter innen samme slekt (*Cis, Anisotoma, Enicmus*) kunne vise store forskjeller i deres relative fangster på de 4 lokalitetene. Det kan indikere at artene er knyttet til ulike suksesjonsstadier, fra flater til gammelskog.

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