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What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway

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The diversity in different groups of obligate saproxylic beetles was related to ecological variables at three levels of spatial scale in mature spruce-dominated forest. The variables were connected to: (i) decaying wood, (ii) wood-inhabiting fungi, (iii) the level of disturbance, (iv) landscape ecology, and (v) vegetational structure. Several strong relationships were found at medium (1 km^2) and large scales (4 km^2), while only weak relationships were found at a small scale (0.16 ha; 1 ha = 10^4 m^2). This may be explained by the local variations in habitat parameters and the high mobilities of many beetle species. Factors connected to decaying wood and wood-inhabiting fungi were clearly the most important factors at all scale levels. In particular, the variables *diversity of dead tree parts*, *number of dead trees of large diameter* and *number of polypore fungi species* increased the species richness of many groups and increased the abundance of many species. Eight species were absent below a certain density of decaying wood per 1 or 4 km^2. Former extensive cutting was a negative factor at large scale, probably because of decreasing recolonization with increasing distance to the source habitats. Thinning reduced the diversity of species associated with birch. The development of guidelines favouring the diversity of saproxylic beetles are discussed below.

Keywords: saproxylic; Coleoptera; spruce forest; spatial scale; conservation.

Introduction

The maintenance of biological diversity and the preservation of species are official goals of the Norwegian forestry (Miljøverndepartementet, 1992). The Council of Europe Committee of Ministers has recommended that the governments of their member states give particular consideration to the fauna and flora of saproxylic organisms (Fry and Lonsdale, 1991). However, we still have insufficient knowledge about how forests should be managed to reduce the risk of extinctions or local extirpations in species-rich groups, such as saproxylic beetles. Nearly 700 Norwegian beetle species are obligate saproxylic; that is, they depend on wood or wood-inhabiting fungi for their development. More than 200 additional beetle species are facultative saproxylic; that is, they can breed in alternative substrates (Palm, 1951, 1959; Koch, 1989–1992; Wilding *et al.*, 1989; J. Stokland, personal communication). A large number of the saproxylic beetle species are on the red lists of the Fennoscandian countries (Rassi *et al.*, 1991; Størkersen, 1992; Ehnström *et al.*, 1993).

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The faunas of various beetle groups from different parts of the world have been related to factors of decaying wood and forest structure (Gutowski, 1986; Chandler, 1987, 1991; Albrechts, 1991; Pfarr and Schrammel, 1991; Rauh and Schmitt, 1991; Chandler and Peck, 1992; Schmitt, 1992; Harding and Alexander, 1994; Kaila *et al.*, 1994; Möller, 1994). Essential factors for the invertebrate fauna in the boreal forests of Fennoscandia have been reviewed by Heliövaara and Väisänen (1984) and Esseen *et al.* (1992). Recently, a few Nordic studies have provided quantified information about how the saproxylic beetle fauna is related to forest characteristics. Siitonen (1994) compared two old, spruce-dominated forests with significant differences in the volume of decaying wood. The general species richness and the number of specimens of specialists on either spruce or birch wood were higher in the forest which had a larger supply of decaying wood. Siitonen and Martikainen (1994) collected beetles and flat bugs (Aradidae) from decaying aspen wood, and they found there was a significantly higher number of rare and threatened species in the Russian Karelia than in the Finnish Karelia. They attributed their findings to the differences in management history between these areas, which has resulted in a higher abundance and continuity of large, dead aspen on the Russian side. The subcortical beetle fauna in the primeval forest of the Pyhän-Häkki national park in Finland was compared with surrounding areas of managed forests (Biström and Väisänen, 1988; Väisänen *et al.*, 1993). Most species occurred in both primeval and managed forests, but the proportion of rare species (as a percentage of the specimens of each species in each forest type) was higher in the primeval forest. In Sweden, Ås (1993) found that there were no differences in the species richness of saproxylic beetles in large and small patches of deciduous forest. However, differences in species composition were observed. Ås concluded that the island biogeographic theory could not be applied in this case, since there was no clear border between the fragments of deciduous forest and the surrounding matrix.

Different forestry practices not only change the amount of decaying wood, they also change the quality and the spatial distribution of the saproxylic habitats. However, many forest characteristics have not been studied as potential factors for the fauna of saproxylic beetles. Beside decaying wood, several other factors may be important for the fauna of saproxylic beetles, for example, variables associated with wood-inhabiting fungi, the level of disturbance, landscape ecology and vegetational structure. The present study was made in localities with different levels of cultivation within a continuous spruce-dominated forest, and it included a number of variables which might be relevant to the beetle fauna. The main question was: What variables best explain the species richness, or the number of individuals of single species within selected guilds or groups of obligatory saproxylic beetles? The relationships were analysed at three levels of spatial scale, since the impact of the variables may depend on the scale of observation (Wiens, 1989; Kotliar and Wiens, 1990). General guidelines on how to favour the diversity of saproxylic beetles by forest management are discussed at the end of the article.

Methods

Study area

All the study sites were situated within an area of about 160 km^2 of continuous forest in Østmarka (59° 51′ N 10° 57′ E, about 15 km south-east of Oslo city centre). The landscape is intersected by many small north–south valleys with only slight variations in elevation

(200–300 m above sea level). Gneisses make up the bedrock. Most of the area is covered by spruce forest (*Picea abies*) with scattered deciduous trees (*Betula* sp., *Populus tremula*, *Salix caprea*, *sorbus aucuparia*, *Alnus incana*, *Prunus padus*), except for a dominance of pines (*Pinus sylvestris*) on ridges and hill tops.

None of the study areas have been untouched by forestry activities. However, the management history of the study areas differs significantly. The least forestry impact was found in Østmarka forest reserve (12.5 km^2), and in some small areas to the north of the reserve. According to older forest workers and managers, these areas have only been cut selectively; the most recent activity was 60 years ago. However, most of the areas within the reserve lacked a long continuity of large-diameter dead logs, and the zone close to some of the watercourses show signs of stronger logging activity due to earlier timber floating (Gauslaa, 1994). Measurements of single spruce trees within the reserve have shown ages up to 227 years (Hoel, 1993). The strongest impact was found on a property (7.5 km^2) to the south of the reserve, which supplied a pulp industry and match production in the period 1870–1900. According to historical descriptions, these areas were extensively cut and they consisted mostly of young trees at the beginning of this century.

Sampling methods

Saproxylic beetles were sampled in their flying phase by means of window traps made of two transparent cobex plates (21 × 39 cm^2) mounted above a 22 cm wide plastic funnel. A cup with preservative (ethylene–glycol) was mounted below the funnel. Each trap hung from a slanted bamboo pole with the trapping surface 0.7–1.0 m above the ground. This method was chosen because it yields large species numbers of saproxylic beetles at a small cost, and since other methods were considered inadequate for the purpose. Beetle samples reared or picked directly from dead-wood substrates are difficult to standardize, and even with a large sampling effort most species are too infrequent for statistical comparisons (Siitonen, 1994; own unpublished data). Bark peeling destroys much of the habitat and the species inside the wood are under-represented (Siitonen, 1994).

Due to the high mobility of many beetle species, the overall area encompassed by the study ('the extent'; Wiens, 1989) was as wide as possible, without bringing in undesirable factors, such as, disruptions of the forest by different landscape types (agricultural or urbanized), by variations due to elevation, by ocean/continent gradients, by bedrock, by forest and vegetation type.

The smallest units of observation in the landscape were 49 square 40 × 40 m^2 sites (0.16 ha sites, small scale). These were positioned in the landscape by stratified random sampling (Økland, 1990), using the following restrictions: (i) the spruce forest was at least 80 years old and it was within the *Eu-Piceetum myrtilletosum* vegetation type (Fremstad and Elven, 1987), (ii) different amounts of decaying wood and levels of disturbance were represented, and (iii) there was a minimum distance of 200 m between the sites. The other ecological variables (Table 1) varied randomly. Within each site, beetles were trapped by ten window traps. These were placed in a predetermined circle (diameter 20 m) around the centre to avoid the temptation to mount traps close to 'attractive' dead logs. The traps were operated from 22 April to 13 September 1991 and emptied four times.

The relationship between ecological and faunistic variables was studied at three levels of spatial scale: (i) small scale, sites of 0.16 ha; (ii) medium scale, combining sites within the same 1 km^2 square (there were 17 squares, each with two or three sites); and (iii) large scale, combining sites within the same 4 km^2 square (there were nine squares, each

Table 1. The Ecological variables

Variable	Registration
Decaying wood	
WOOD[a]	Dead wood in general (volume (m^3) per 1000 m^2)
CONIFER	Dead coniferous wood (volume (m^3) per 1000 m^2)
PICEA	Dead wood of *Picea abies* (volume (m^3) per 1000 m^2)
DECID[a]	Dead deciduous wood (volume (m^3) per 1000 m^2)
BETULA	Dead wood of *Betula* sp. (volume (m^3) per 1000 m^2)
POPULUS	Dead wood of *Populus tremulae* (volume (m^3) per 1000 m^2)
SP-DECID	Number of deciduous tree species within the site
DECAYING	Wood with decay deeper than 3 cm, but with a hard core (volume (m^3) per 1000 m^2)
DECAYED	Wood decayed right through (volume (m^3) per 1000 m^2)
BRYOCOV	Volume of dead wood covered by bryophytes (volume (m^3) per 1000 m^2)
LARGEDIA	Dead trees/logs with breast height diameter >40 cm (number per 1000 m^2)
HABITATD	'Habitat diversity', that is, the number of different types of dead tree parts within the site (distinguished according to tree species, level of degradation (see DECAYSTA), part of tree, lying or standing, class of breast height diameter: (i) <20 cm, (ii) 20–30 cm, (iii) 30–40 cm, (iv) >40 cm
DECAYSTA	Number of decay stages present within the site (stages: (i) firm surface, (ii) decay less than 3 cm deep, (iii) decay deeper than 3 cm, but with a hard core, (iv) decayed right through).
BRANCH	Percentage area of field layer dominated by branch/logwastes (diameter <10 cm)
STUMPS	Number per 1000 m^2 of human-made stumps
Wood-inhabiting fungi	
NO-POLY[a]	Polypore fruiting bodies (number per 1000 m^2)
SP-POLY	Polypore species within the site (40 × 40 m^2)
Level of disturbance	
CONT	Indications of long-time continuity for tree cover and dead-wood Substrates, based on fungal indicator species; there are four levels (see, Økland, 1994)
CUTTING	Former extensively cut/clear-cut (1), or never extensively cut/clear-cut (0)
THINNING	Former practice of thinning: (2) extensive, (1) medium, (0) none
Landscape ecology	
AREA	Area of seminatural forest surrounding the collection site
DISTSN	Distance to nearest big mainland of seminatural forest (forest reserve of 12.5 km^2)
DISTCLC	Distance to nearest clearcut (0–3 year since cutting)
DENSCLC	Density of clearcuts (percentage area of 1 km^2 at the medium scale and of 4 km^2 at the large scale)
DISTYNG	Distance to nearest young forest (about 10–40 years old)
DENSYNG	Density of young forest (percentage area of 1 km^2 at the medium scale and of 4 km^2 at the large scale)
EXPOSURE	Exposure towards the south, ranging from −100 at north to +100 at south
Vegetational structure	
BRYOPHYT	Percentage area of ground layer dominated by bryophytes
GRASS	Percentage area of field layer dominated by grass
HEATHER	Percentage area of field layer dominated by heather
FERNS	Percentage area of field layer dominated by ferns
LITTER	Percentage area of ground layer dominated by litter
ROCK	Percentage area of ground layer dominated by stones and rocks
SHRUB	Percentage area dominated by shrubs and smaller trees (2–5 m)
RELASCOPE	Spiegel relascope

[a]Variables recorded both within the 1600 m^2 sites and with a 500 m north–south transect through the sites.

containing 3–6 sites). The position of the sites within each square was assumed not to be significantly different from a distribution created by a randomized method. The small sites appeared to be quite representative for the forest within the 1 and 4 km^2 squares. The 1 and 4 km^2 squares covered sites with the same ownership or areas with similarities in management history, for example, the amount of decaying wood recorded in the sites within the same 1 or 4 km^2 square were significantly correlated with the amount of decaying wood recorded by 5 × 500 m transects (Spearman R_s = 0.70 and 0.75, respectively). At the same time, the forest characteristics varied considerably between the squares. The amount of decaying wood ranged from 1.8 to 221 $m^3 ha^{-1}$ at medium scales (1 km^2), and from 2.0 to 147 $m^3 ha^{-1}$ at large scales (4 km^2).

Ecological and faunistic variables

Altogether, 35 ecological variables were assessed within the sites (Table 1). Four of the variables were also recorded in a wider area by means of a 500 × 5 m north–south transect, with the trapping site in centre. The ecological variables were classified in five groups associated with: (i) different forms of decaying wood, (ii) wood-inhabiting fungi, (iii) the level of disturbance, (iv) the landscape ecology, and (v) the vegetational structure.

All saproxylic beetles were identified at the species level according to the catalogue of Silfverberg (1979). For all species which were present in at least five of the observation units, the number of individuals was tested against the ecological variables. According to this criterion, about half of the species occurred too infrequently for individual testing. However, all species were represented in the variables of species richness in the groups of: (i) Obligate saproxylic beetles in general, and obligate saproxylic beetles which may occur in decaying wood of (ii) *Picea*, (iii) *Populus*, (iv) *Betula*, (v) in deeply decayed wood, (vi) in wood-inhabiting fungi (both in the fruiting bodies and in the mycelium inside the wood), or (vii) species that are present on the Norwegian or Swedish Red List (Størkersen, 1992; Ehnström *et al.*, 1993).

Statistical methods

Spearman's rank correlation (Freund, 1992) was applied in the analyses of the relationships between the different ecological variables and between the ecological variables and the number of individuals in single species. The level of significance was adjusted for multiple tests by a Bonferroni correction (Weisberg, 1985).

The relationship between ecological variables and the species-richness variables was tested by a stepwise multiple regression (Weisberg, 1985). A maximum threshold for the number of explanatory variables in the multiple regressions was set at $(n - 5)/2$ (where n is the number of observations). The large number of first candidates in the stepwise regression were presented individually as simple linear regressions in the result tables (Tables 3–5). There was no significant heteroscedasticity due to the variation in the number of sites in the groups at the medium and large scales (Spearman's rank correlation).

Principal-component regression (PCR) analysis of the data was considered because of the collinearity between some of the most important ecological variables, but this method could not be used at the medium and large scales because the number of observations was low compared to the number of ecological variables. Further, the construction of principal components was not expected to give significant new information for the interpretation of the ecological variables. Alternatives to linear models in the regressions were evaluated, but they were rejected. Logarithmic transformations of dependent and independent

variables did not result in more significant variables being included in the multiple regression, and they did not improve the explanatory power of the variables.

Cause–effect relationships cannot be obtained directly from the regression and correlation results, since certain relationships may be spurious (Bhattacharyya and Johnson, 1977). In the present study, the assumption of cause–effect relationships was based on: (i) biological interpretations, and (ii) the fact that many of the statistical relationships pointed in the same direction.

Results

Relationships between the ecological variables

The ecological variables with the strongest intercorrelations at the medium and large scales are presented in Table 2. At both these scale levels the strongest correlations were found between some of the variables connected to decaying wood and wood-inhabiting fungi. Groups of strongly intercorrelated variables were: (i) WOOD–CONIFER–PICEA–LARGEDIA–HABITATD–NOPOLY–SPPOLY, and (ii) DECID–SPDECID–BETULA–POPULUS–DECAYING–BRYOCOV. Correlations between ecological variables at small scale ($40 \times 40\,m^2$) showed a similar pattern and strength to those at medium and large scales. However, they are not included in Table 2 due to their weak relationships with the faunistic variables.

Species richness

The complete material consisted of 34 914 individuals and 513 identified species of beetles. The present analysis was restricted to obligatory saproxylic species (23 258 individuals and 194 species).

The species richness and the number of red-listed species at each sampling site showed only weak relationships with the ecological variables measured at the immediate surroundings ($40 \times 40\,m^2$) (Table 3). Despite a positive and significant influence of saproxylic variables at this small scale, there was a large variation around the trends (low R^2). The inclusion of the $5 \times 500\,m^2$ transects did not improve the relationships. The explanatory power of the ecological variables was considerably improved at the medium ($1\,km^2$) and large scales ($4\,km^2$). This was also the case if the species were grouped according to the tree species (Table 4) or according to the degree of decay or affinity to fungi (Table 5). The small scale was excluded in Tables 4 and 5 because of the weak relationships at this scale.

For all groups of saproxylic beetles, the variables associated with dead wood and wood-inhabiting fungi proved to be the most important factors, and they were, with a few exceptions, the only significant explanatory variables for the species richness (Tables 3–5). The intercorrelation between the saproxylic variables (Table 2) made it difficult to identify the importance of each variable. However, some suggestions about the influence of single variables could be based on their tendency to be repeated in regressions with different groups of beetles (Tables 3–5). The amount of dead wood in general (WOOD) was amongst the most influential variables in many of the regressions, and it ranked top as the explanatory factor for the number of obligate saproxylic species at small and large scales. The diversity of dead tree parts (HABITATD) ranked near the top in most of the regressions. This variable even proved to be the strongest explanatory variable for the number of species associated with birch at the medium and large scales (Table 4), and for

Table 2. Spearman rank correlation between ecological variables at medium scale (lower triangle) and at large scale (upper triangle). The light-grey shading denotes significant correlation ($p < 0.05$ after a Bonferroni correction) and the dark-grey shading denotes strong correlations. ($\text{abs}(R_s) > 0.9$)

	WOOD	CONIFER	PICEA	DECID	BETULA	POPULUS	SPDECID	DECAYING	DECAYED	BRYOCOV	LARGEDIA	STUMPS	NOPOLY	SPPOLY	CUTTING	THINNING	AREA	DISTSN	DISTYNG	HABITATD	BRANCH	GRASS	HEATHER
WOOD	–	100	100	68	73	71	62	73	67	70	85	−63	98	87	−50	−68	74	−54	77	98	38	32	−50
CONIFER	97	–	100	68	73	71	62	73	67	70	85	−63	98	87	−50	−68	74	−54	77	98	38	32	−50
PICEA	97	100	–	68	73	71	62	73	67	70	85	−63	98	87	−50	−68	74	−54	77	98	38	32	−50
DECID	74	60	60	–	95	92	74	92	73	90	55	−67	73	78	−23	−84	74	−71	58	73	90	−3	−50
BETULA	74	66	66	83	–	87	85	97	77	92	63	−70	80	68	−16	−79	61	−54	60	80	78	−12	−38
POPULUS	60	48	48	84	60	–	71	89	75	87	64	−84	77	79	−52	−86	87	−65	64	77	74	24	−73
SPDECID	56	46	46	84	65	85	–	79	54	76	44	−65	69	46	−12	−75	41	−24	39	69	64	11	−38
DECAYING	77	74	74	74	74	69	61	–	90	95	75	−78	82	68	−23	−78	67	−56	60	82	69	−5	−48
DECAYED	57	54	54	58	60	46	34	71	–	87	85	−75	75	63	−27	−64	68	−56	53	75	47	3	−53
BRYOCOV	80	74	74	77	67	66	56	93	62	–	65	−82	80	73	−30	−71	74	−47	70	80	73	2	−58
LARGEDIA	89	90	90	58	66	55	43	74	67	67	–	−68	87	67	−47	−59	66	−51	60	87	17	23	−48
STUMPS	−47	−45	−45	−48	−48	−34	−38	−58	−53	−50	−49	–	−73	−58	70	73	−74	25	−58	−73	−46	−40	82
NOPOLY	94	95	95	64	63	57	51	77	68	75	93	−42	–	85	−50	−70	75	−49	80	100	43	28	−55
SPPOLY	92	86	86	79	77	66	58	71	47	72	78	−32	85	–	−54	−67	92	−75	80	85	59	33	−65
CUTTING	−49	−49	−49	−33	−14	−34	−27	−22	−7	−34	−45	49	−43	−37	–	44	−72	17	−51	−50	−6	−77	84
THINNING	−70	−65	−65	−63	−66	−41	−49	−50	−31	−59	−48	33	−52	−63	33	–	−72	67	−30	−70	−75	−36	65
AREA	65	64	64	51	38	50	39	50	50	49	58	−49	65	62	−60	−55	–	−70	71	75	57	50	−87
DISTSN	−52	−46	−46	−53	−42	−61	−48	−37	−35	−27	−47	9	−52	−69	17	43	−74	–	−29	−49	−63	−10	39
DISTYNG	61	72	72	23	21	17	21	43	30	47	57	−43	67	46	−72	−41	68	−26	–	80	30	12	−47
HABITATD	95	94	94	74	78	63	63	73	61	70	90	−44	95	89	−47	−64	67	−59	63	–	43	28	−55
BRANCH	53	43	43	79	57	69	67	48	31	47	38	−26	47	71	−20	−41	47	−73	15	55	–	−8	−39
GRASS	38	40	40	8	16	−13	−8	8	8	15	35	−31	29	21	−53	−42	51	−10	47	34	0	–	−75
HEATHER	−50	−42	−42	−60	−36	−49	−56	−41	−34	−48	−44	63	−45	−38	68	39	−59	26	−43	−52	−43	−46	–

Table 3. The influence of ecological variables on the species richness of (a) obligate saproxylic beetles and (b) Red-Listed saproxylic beetles, at three levels of spatial scale. Alternative first candidates in the stepwise multiple regression are listed as simple linear regressions, ranked according to their strength of R^2, t and p, where T and p are the test indicator and significance value for the slope, R^2 is the coefficient of determination (adjusted). The variables are defined in Table 1

Group	Small scale (0.16 ha)		Medium scale (1 km^2)		Large scale (4 km^2)	
(a) Obligate saproxylic species						
	Simple regression		Simple regression		Simple regression	
	Y = 0.94WOOD + 51.07	T = 4.43 p = 0.000 R^2 = 0.28	Y = 2.19LARGEDIA + 51.42	T = 4.93 p = 0.000 R^2 = 0.59	Y = 0.85WOOD + 51.51	T = 3.36 p = 0.008 R^2 = 0.61
	Y = 1.09CONIFER + 51.30	T = 4.21 p = 0.000 R^2 = 0.26	Y = 1.09WOOD + 51.01	T = 4.30 p = 0.001 R^2 = 0.52	Y = −9.40CUTTING + 58.00	T = −3.59 p = 0.009 R^2 = 0.60
	Y = 0.59HABITATD + 48.11	T = 4.02 p = 0.000 R^2 = 0.24	Y = 1.18CONIFER + 51.12	T = 3.99 p = 0.001 R^2 = 0.48	Y = 1.01CONIFER + 51.57	T = 3.58 p = 0.009 R^2 = 0.60
	Y = 1.57LARGEDIA + 52.53	T = 3.93 p = 0.000 R^2 = 0.23	Y = 0.11NOPOLY + 52.00	T = 3.54 p = 0.003 R^2 = 0.42	Y = 0.08NOPOLY + 52.36	T = 3.30 p = 0.013 R^2 = 0.55
	Y = 0.08NOPOLY + 52.90	T = 3.22 p = 0.002 R^2 = 0.16	Y = 0.63HABITATD + 47.95	T = 3.52 p = 0.003 R^2 = 0.42	Y = 1.81LARGEDIA + 52.09	T = 3.28 p = 0.014 R^2 = 0.55
	Y = 2.50DECID + 53.51	T = 2.84 p = 0.007 R^2 = 0.13	Y = 3.58DECID + 52.92	T = 3.30 p = 0.005 R^2 = 0.42	Y = 0.05DISTYNG + 50.18	T = 3.13 p = 0.017 R^2 = 0.52
	Y = 2.12SPPOLY + 51.13	T = 2.71 p = 0.009 R^2 = 0.12	Y = 2.62SPPOLY + 50.40	T = 2.93 p = 0.010 R^2 = 0.32	Y = 0.52HABITATD + 49.15	T = 3.01 p = 0.020 R^2 = 0.50
	Y = 0.56AREA + 53.01	T = 2.27 p = 0.028 R^2 = 0.08	Y = 13.71DECAYED + 53.07	T = 2.79 p = 0.014 R^2 = 0.30	Y = 2.43SPPOLY + 50.70	T = 2.94 p = 0.022 R^2 = 0.49
					Y = 3.97DECID + 52.41	T = 2.70 p = 0.031 R^2 = 0.44
	Multiple regression		Multiple regression		Multiple regression	
			Y = 2.14LARGEDIA + 0.15GRASS + 48.26	R^2 = 0.67	Y = 0.56WOOD − 6.12CUTTING + 54.46	R^2 = 0.81
			T/p 4.80/0.000 2.10/0.055		*T/p* 2.96/0.025 – 2.89/0.028	
					Y = 0.70WOOD − 0.10HEATHER + 57.34	R^2 = 0.74
					T/p 3.43/0.014 – 2.11/0.08	
(b) Red-listed saproxylic species						
	Simple regression		Simple regression		Simple regression	
	Y = 0.46SPPOLY + 2.11	T = 4.82 p = 0.000 R^2 = 0.32	Y = 0.11HABITATD + 1.64	T = 5.14 p = 0.000 R^2 = 0.61	Y = 0.11HABITATD + 1.57	T = 4.67 p = 0.002 R^2 = 0.72
	Y = 0.08HABITATD + 2.10	T = 3.71 p = 0.001 R^2 = 0.21	Y = 0.14WOOD + 2.89	T = 4.57 p = 0.000 R^2 = 0.55	Y = 1.52SPDECID + 1.32	T = 4.00 p = 0.005 R^2 = 0.65
	Y = 0.11WOOD + 2.53	T = 3.60 p = 0.001 R^2 = 0.20	Y = 0.48SPPOLY + 2.00	T = 4.54 p = 0.000 R^2 = 0.55	Y = 0.26SHRUB + 0.87	T = 3.46 p = 0.011 R^2 = 0.58
	Y = 0.011NOPOLY + 2.67	T = 3.49 p = 0.001 R^2 = 0.19	Y = 0.18CONIFER + 2.31	T = 4.14 p = 0.001 R^2 = 0.50	Y = −1.10THINNING + 3.53	T = −3.31 p = 0.013 R^2 = 0.56
	Y = 0.13CONIFER + 2.57	T = 3.39 p = 0.002 R^2 = 0.18	Y = 0.016NOPOLY + 2.41	T = 4.09 p = 0.001 R^2 = 0.50	Y = 0.74DECID + 2.39	T = 2.58 p = 0.036 R^2 = 0.42
	Y = 0.18LARGEDIA + 2.71	T = 3.15 p = 0.003 R^2 = 0.16	Y = 0.29LARGEDIA + 2.45	T = 3.81 p = 0.002 R^2 = 0.46	Y = 0.014NOPOLY + 2.45	T = 2.42 p = 0.046 R^2 = 0.38
	Y = 0.11SHRUB + 2.15	T = 2.86 p = 0.006 R^2 = 0.13	Y = 0.56DECID + 2.56	T = 3.72 p = 0.002 R^2 = 0.45	Y = 0.13WOOD + 2.34	T = 2.38 p = 0.049 R^2 = 0.37
	Y = 0.29BRYOCOV + 2.71	T = 2.74 p = 0.009 R^2 = 0.12	Y = 0.45BRYOCOV + 2.46	T = 3.28 p = 0.005 R^2 = 0.38	Y = 0.41SPPOLY + 2.16	T = 2.33 p = 0.053 R^2 = 0.36
	Multiple regression		Multiple regression		Multiple regression	
	Y = 0.41SPPOLY + 0.79SHRUB + 1.56	R^2 = 0.37	Y = 0.09HABITATD + 0.09SHRUB + 1.16	R^2 = 0.69	Y = 0.08HABITATD + 0.14SHRUB + 0.90	R^2 = 0.81
	T/p 4.40/0.000 2.32/0.025		*T/p* 4.25/0.001 2.17/0.048		*T/p* 3.11/0.021 2.08/0.083	

the number of species associated with deeply decayed wood tested at large scale (Table 5). At the medium scale, the number of dead trees of large diameter (LARGEDIA) ranked top as the explanatory variable in all of the groups, except for the group of red-listed species and the species associated with birch (Tables 3–5). Decaying wood of aspen (POPULUS) was the most important variable for the number of species associated with aspen at the large scale, while this variable was less important at the medium scale. Several other saproxylic variables showed a strong influence without ranking top in any of the groups tested, for example, the variables CONIFER, PICEA, DECID, BETULA, NOPOLY, SPPOLY, DECAYING and DECAYED.

Two of the variables associated with disturbance, CUTTING and THINNING, showed a negative influence on the species richness at the large scale (Tables 3 and 4), but they did not contribute significantly at the medium and small scales. At the large scale, CUTTING was the strongest variable for the beetles associated with spruce, and it was the second strongest variable for the obligate saproxylic beetles in general (Tables 3 and 4). THINNING was the second strongest explanatory variable for the number of species associated with birch at the large scale. Most of the area in two of nine 4 km^2 squares has been subject to extensive cutting in the past, while five of the squares included areas with different degrees of thinning.

At the large scale, the area of seminatural forest surrounding the sample plots (AREA) was the third strongest explanatory variable for the number of species associated with *Populus* (Table 4). This variable was significantly correlated with many of the variables associated with decaying wood and wood-inhabiting fungi (Table 2), and it had no significant contribution when combined with selected variables (Table 4). The distance to the nearest large mainland of seminatural forest (DISTSN) was a negative variable for species associated with fungi at the medium scale, for species associated with birch at the large scale, and for species in deeply decayed wood at both the medium and large scales (Tables 4 and 5). However, the actual substrate variables of these beetle groups were also negatively correlated with DISTSN, for example there was a significant decrease of polypore fungi species with increasing distance from a large mainland of seminatural forest (Table 2). The distance to clearcuts (DISTCLC) and the density of clearcuts and young forests (DENSCLC and DENSYNG) were not significant variables. The distance to the nearest young forest (DISTYNG) showed a significant influence on the species richness in some of the groups at the large scale (Tables 3–5). However, the variable DISTYNG was significantly correlated with the most important saproxylic variables (WOOD, HABITATD), and it did not contribute significantly when combined with one of these variables.

Among the variables associated with vegetational structure, GRASS and HEATHER were the most important. GRASS showed positive relationships and (or) HEATHER showed negative relationships with the number of species associated with: (i) *Picea*, (ii) *Populus*, (iii) *Betula*, and (iv) obligate saproxylic beetles in general (Tables 3 and 4). However, GRASS and HEATHER were significantly correlated with CUTTING (Table 2), and they did not contribute significantly in combination with this variable. The influence of the variable GRASS and HEATHER on species richness motivated a separate regressional test of their influence on the number of flower-visiting species. However, no significant influence was found.

The collection of saproxylic beetles contained 21 red-listed species (Størkersen, 1992; Ehnström *et al.*, 1993), including 18 obligate saproxylic species. Most of these species

(17) are classified as care-demanding, while four species are vulnerable according to at least one of the red lists in Sweden and Norway. The majority of the red-listed species are known from fungal habitats in dead wood (including both fruiting bodies and mycelia inside the wood), and a large proportion of the species is associated with deciduous tree species (Koch, 1989–1992).

The number of red-listed saproxylic species was best explained by the diversity of dead tree parts (HABITATD), both at the medium and large scales (Table 3). The number of deciduous tree species (SP-DECID) was the second-best variable at the large scale while several other saproxylic variables showed explanatory power, for example, WOOD, SPPOLY, NOPOLY, LARGEDIA, DECID and BRYOCOV. The number of red-listed species was positively related to the coverage by shrubs (SHRUB), and it was negatively related to thinning (THINNING). At the large scale, the combined variables HABITATD and SHRUB together explained more than 80% of the variation in the number of red-listed species.

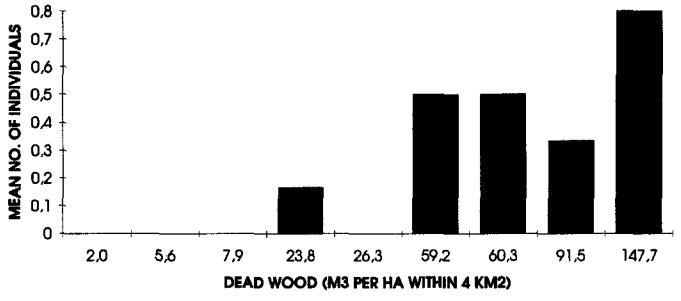
Abundance in single species

A sufficient frequency for individual testing was found in 103 species at the medium scale and in 99 species at the large scale (these species were represented in at least five of the observation units). At the small scale ($40 \times 40\ m^2$), only a few of the correlations between single species and the ecological variables were significant. The highest number (65) of significant correlations was found at a large scale, and a somewhat lower number (43) was found at the medium scale (Appendices 1 and 2).

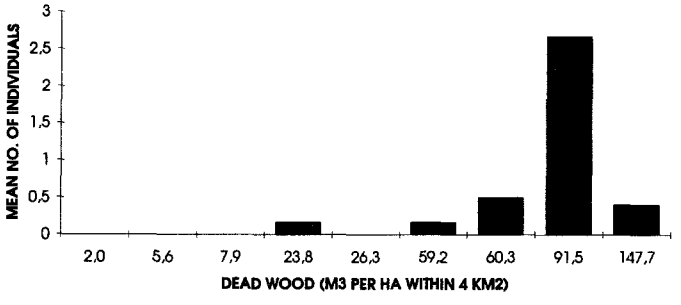
Table 6 shows how many significant correlations were found between ecological variables and the number of individuals in single species. The variables associated with dead wood and wood-inhabiting fungi were ranked top. The amount of dead wood in general (WOOD) was correlated with the largest number of single species both at the medium and at the large scale. The number of polypore species (SPPOLY) and the number of dead trees of large diameter (LARGEDIA) ranked near the top at the large scale, while these variables were correlated with relatively few species at the medium scale. The variable CUTTING was negatively correlated with a large number of species at the large scale, but it was correlated with only a few species at the medium and small scales. Some species were significantly correlated with more than one ecological variable; for example, the amount of decaying wood of spruce (PICEA) was correlated with exactly the same species as dead wood in general (WOOD) at the large scale (Appendix 2). Among the vegetational variables, GRASS and HEATHER were correlated with the largest number of species (Appendices 1 and 2). Also, GRASS and HEATHER were correlated with CUTTING (Table 2), but they had few correlated species in common with this ecological variable (Appendices 1 and 2). The significant tests of single species included five of the Red-Listed species (Appendices 1 and 2): at the large scale, *Xylophilus corticalis* was most strongly correlated with the variables BETULA, DECAYING and BRYOCOV; and it was negatively correlated with the variables STUMPS and THINNING. LARGEDIA was the most strongly correlated variable with *Dendrophagus crenatus* at the medium scale, and with *Ipidia quadriplagiata* at the large scale. *Euryusa castanoptera* was positively correlated with the cover of grass (GRASS), and *Hapalarea linearis* with the number of deciduous tree species (SPDECID) at a large scale.

Altogether, eight species were not trapped in areas below a certain density of decaying wood (Fig. 1). Five species were absent below 23.8–28.5 $m^3\ ha^{-1}$ of decaying wood within an

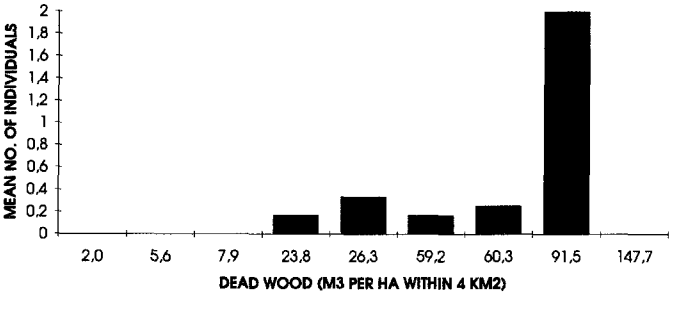
(a) Anaspis frontalis



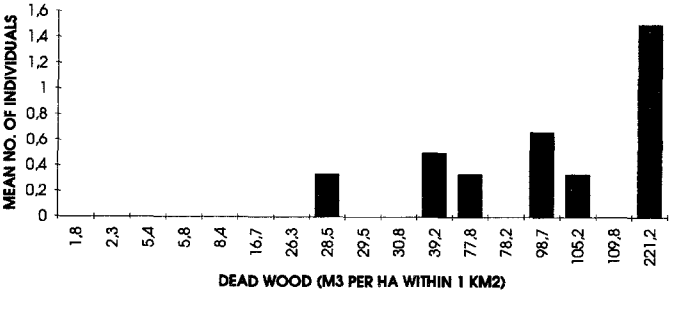
(b) Anoplodera maculicornis



(c) Octotemnus glabriculus



(d) Placusa suecica



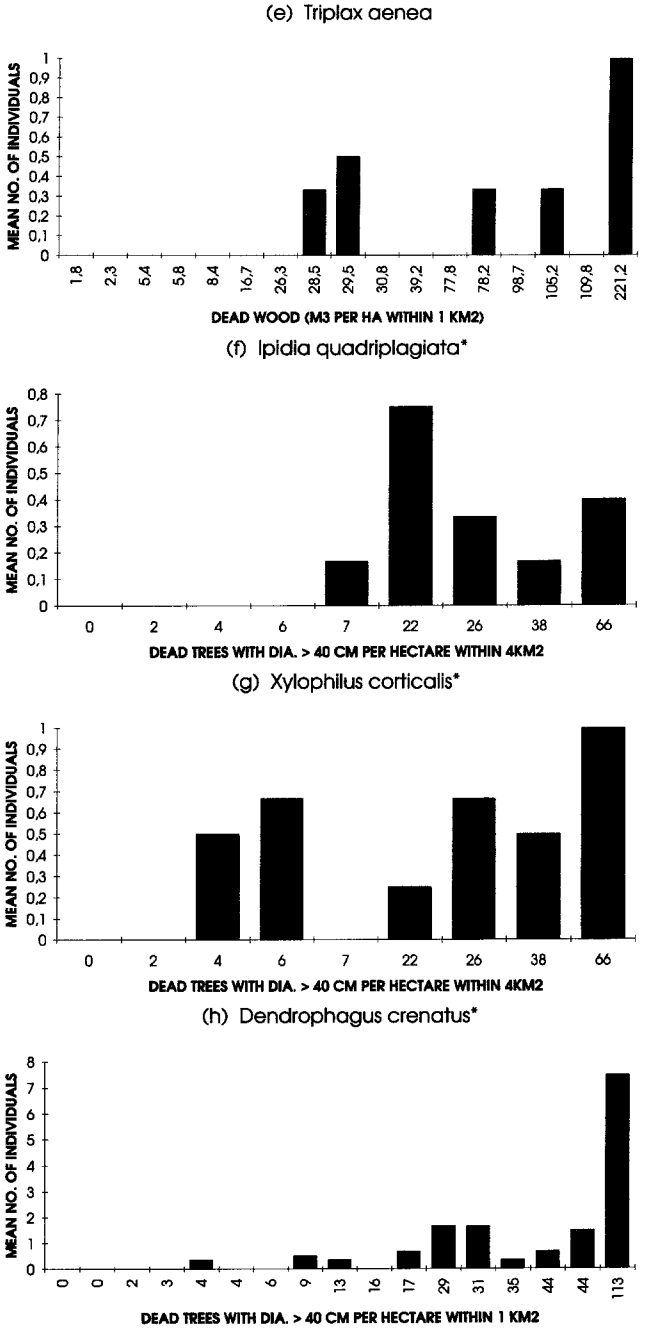


Figure 1. Species absent in areas below a certain density of general decaying wood: (a) *Anaspis frontalis*, (b) *Anoplodera maculicornis*, (c) *Octotemnus glabriculus*, (d) *Placusa suecica*, and (e) *Triplax aenea*, and species absent below a certain density of large-diameter trees. (dbh > 40 cm): (f) *Ipidia quadriplagiata*, (g) *Xylophilus corticalis*, and (h) *Dendrophagus crenatus*. The abundance values for the species are given as an average of the sites within the same 1 or 4 km^2 square. Red-listed beetle species are denoted with asterisks.

Table 4. The influence of ecological variables on the species richness of obligate saproxylic beetle species associated with (a) *Picea*, (b) *Populus* and (c) *Betula*, at the medium and large spatial scales. Alternative first candidates in the stepwise multiple regression are listed as simple linear regressions, ranked according to their strength of R^2, t and p. T and p are the test indicator and significance value for the slope, respectively; R^2 is the coefficient of determination (adjusted). The variables are defined in Table 1

Guild	Medium scale (1 km^2)		Large scale (4 km^2)	
(a) Species in *Picea*				
	Simple regression		Simple regression	
	Y = 1.42LARGEDIA + 38.84	T = 3.29 p = 0.005 R^2 = 0.38	Y = −7.10CUTTING + 43.59	T = −3.71 p = 0.042 R^2 = 0.62
	Y = 0.78PICEA + 38.60	T = 2.89 p = 0.011 R^2 = 0.31	Y = 0.17GRASS + 37.33	T = 2.49 p = 0.055 R^2 = 0.39
	Y = 0.21GRASS + 36.65	T = 2.75 p = 0.015 R^2 = 0.29	Y = 0.61PICEA + 39.35	T = 2.30 p = 0.055 R^2 = 0.35
	Y = 0.06NOPOLY + 39.40	T = 2.33 p = 0.034 R^2 = 0.22		
	Multiple regression		Multiple regression	
	Y = 1.18LARGEDIA + 0.16GRASS + 35.30	R^2 = 0.55	Y = −8.35CUTTING −0.27LITTER + 46.45	R^2 = 0.75
	T/p 3.11/0.008 2.58/0.022		*T/p* −5.13/0.002 −2.23/0.068	
	Y = 1.47LARGEDIA − 0.23ROCK + 42.21	R^2 = 0.52		
	T/p 3.89/0.002 −2.34/0.034			
(b) Species in *Populus*				
	Simple regression		Simple regression	
	Y = 1.38LARGEDIA + 27.71	T = 5.12 p = 0.000 R^2 = 0.61	Y = 5.31POPULUS + 28.86	T = 3.38 p = 0.012 R^2 = 0.57
	Y = 0.41HABITATD + 25.38	T = 3.91 p = 0.001 R^2 = 0.47	Y = 0.033DISTYNG + 27.04	T = 3.01 p = 0.020 R^2 = 0.50
	Y = 1.82SPPOLY + 26.69	T = 3.63 p = 0.002 R^2 = 0.43	Y = 0.39AREA + 28.76	T = 3.00 p = 0.021 R^2 = 0.49
	Y = 3.04POPULUS + 29.64	T = 1.95 p = 0.070 R^2 = 0.15	Y = 1.56SPPOLY + 27.33	T = 2.92 p = 0.022 R^2 = 0.48
			Y = 0.54FERNS+28.48	T = 2.89 p = 0.023 R^2 = 0.48
			Y = 0.33HABITATD + 26.40	T = 2.88 p = 0.024 R^2 = 0.48
	Multiple regression		Multiple regression	
	Y = 1.23LARGEDIA + 0.09GRASS + 25.82	R^2 = 0.68	Y = 4.96POPULUS + 0.09GRASS + 26.53	R^2 = 0.74
	T/p 4.98/0.00 2.09/0.06		*T/p* 4.07/0.007 2.43/0.051	
(c) Species in *Betula*				
	Simple regression		Simple regression	
	Y = 0.54HABITATD + 29.33	T = 4.82 p = 0.000 R^2 = 0.58	Y = 0.48HABITATD + 30.09	T = 3.47 p = 0.010 R^2 = 0.58
	Y = 1.60LARGEDIA + 32.91	T = 4.66 p = 0.000 R^2 = 0.57	Y = −5.10THINNING + 38.63	T = −3.35 p = 0.012 R^2 = 0.56
	Y = 2.23SPPOLY + 31.48	T = 3.72 p = 0.002 R^2 = 0.44	Y = −0.001DISTSN + 39.75	T = −2.64 p = 0.033 R^2 = 0.43
	Y = 3.47BETULA + 34.55	T = 3.11 p = 0.007 R^2 = 0.35	Y = 1.44LARGEDIA + 33.29	T = 2.64 p = 0.033 R^2 = 0.43
			Y = 3.17BETULA + 34.61	T = 1.25 p = 0.25 R^2 = 0.07
	Multiple regression		Multiple regression	
	Y = 0.49HABITATD + 0.13GRASS + 26.87	R^2 = 0.70	Y = 0.38HABITATD + 0.13GRASS + 27.86	R^2 = 0.75
	T/p 4.97/0.000 2.60/0.021		*T/p* 3.33/0.016 2.37/0.055	

area of 1 or 4 km^2. Predators and fungivores were both included, and all of these species are known from different tree species. Another three species were not trapped in areas below 4–7 dead trees of large diameter (>40 cm dbh) per hectare (Fig. 1). These three species are present on the red lists in Sweden and Norway, and they are classified as vulnerable according to the Swedish red list. Out of these species, *Dendrophagus crenatus* and *Ipidia quadriplagiata* have earlier been described as species mainly found in forests with trees of large dimension (Palm, 1959; Ehnström and Waldén, 1986).

Discussion

General evaluation of the spatial scale

The small scale (40 × 40 m^2) seems to be too small for the study of the relationship between the ecological variables and the fauna of flying saproxylic beetles. In Finland, Siitonen

Table 5. The influence of ecological variables on the species richness of obligate saproxylic beetle species associated with (a) deeply decayed wood, and (b) fungi, at the medium and large spatial scales. Alternative first candidates in the stepwise multiple regression are listed as simple linear regressions, ranked according to their strength of R^2, t and p. T and p are the test indicator and significance value for the slope, respectively; R^2 is the coefficient of determination (adjusted). The variables are defined in Table 1

Guild	Medium scale (1 km^2)	Large scale (4 km^2)
(a) Species in deeply decayed wood		
	Simple regression	Simple regression
	Y = 1.68LARGEDIA + 31.75 T = 5.34 p = 0.000 R^2 = 0.63	Y = 0.48HABITATD + 28.68 T = 3.58 p = 0.009 R^2 = 0.60
	Y = 0.54HABITATD + 28.32 T = 4.78 p = 0.000 R^2 = 0.58	Y = 1.57LARGENDIA + 31.65 T = 3.22 p = 0.015 R^2 = 0.54
	Y = 2.4SPPOLY + 30.1 T = 4.29 p = 0.001 R^2 = 0.52	Y = 2.20SPPOLY + 30.25 T = 3.22 p = 0.015 R^2 = 0.54
	Y = 10.32DECAYED + 33.06 T = 2.84 p = 0.013 R^2 = 0.31	Y = 0.044DISTYNG + 30.00 T = 3.08 p = 0.018 R^2 = 0.51
		Y = −0.002DISTSN + 38.40 T = −2.81 p = 0.026 R^2 = 0.46
	Multiple regression	
	Y = 1.44LARGEDIA −0.001DISTSN + 33.93 R^2 = 0.69	
	T/p 4.59/0.000 −1.93/0.075	
(b) Saproxylic species in fungi		
	Simple regression	Simple regression
	Y = 1.25LARGEDIA + 23.85 T = 5.78 p = 0.000 R^2 = 0.67	Y = 0.54WOOD + 23.53 T = 4.83 p = 0.002 R^2 = 0.74
	Y = 0.59WOOD + 23.50 T = 5.39 p = 0.000 R^2 = 0.64	Y = 1.17LARGEDIA + 23.85 T = 4.87 p = 0.003 R^2 = 0.71
	Y = 0.39HABITATD + 21.50 T = 4.72 p = 0.000 R^2 = 0.57	Y = 0.056NOPOLY + 24.02 T = 4.48 p = 0.003 R^2 = 0.70
	Y = 1.80SPPOLY + 22.61 T = 4.69 p = 0.000 R^2 = 0.57	Y = 0.34HABITATD + 21.85 T = 4.29 p = 0.004 R^2 = 0.69
	Y = 2.29DECID + 24.47 T = 4.58 p = 0.000 R^2 = 0.56	Y = 1.63SPPOLY + 22.84 T = 4.28 p = 0.004 R^2 = 0.69
		Y = 0.032DISTYNG + 22.75 T = 3.67 p = 0.008 R^2 = 0.61
	Multiple regression	Multiple regression
	Y = 1.09LARGEDIA − 0.001DISTSN + 25.46 R^2 = 0.73	Y = 0.42WOOD + 0.27FERNS + 23.15 R^2 = 0.86
	T/p 5.13/0.000 −2.13/0.051	*T/p* 4.34/0.005 2.64/0.038

(1994) found no significant correlation between the species richness of saproxylic beetles and the amount of decaying wood very close to the traps (100 m^2). In the present study, the different sites formed a very marked gradient in the amount of decaying wood at the small scale (ranging from 0.6 to 372 m^3 ha^{-1} of decaying wood). Even then, only a weak influence of the saproxylic variables was found, both on the number of species and on the abundance of single species. The most simple explanation for these findings would be a high mobility in many of the species. The faunistic variables in the local sites were not better explained by recording the ecological variables in a somewhat wider range (transects of 500 × 5 m). Even sites close to each other with similar scores in ecological variables could show considerable differences in the species richness and abundance of single species. Besides variations in behaviour and flight patterns between the species, this faunistic variation may be a product of many factors which may be difficult to quantify, for example variations in microclimate and air currents because of topography and forest structure, and heterogeneous distributions of breeding substrates.

Generally, the relationships between ecological and faunistic variables were improved by increasing the spatial scale of the sampling to the medium (1 km^2) and large scales (4 km^2) with the strongest being found at the level of 4 km^2. Some variables were only important at large scale, for example, the volume of dead aspen (POPULUS, Table 3), former extensive cutting (CUTTING, Tables 2 and 3), and the number of deciduous tree species (SPDECID, Table 2). Improvements resulting from increasing the scale may be ascribed to: (i) a better correspondence with the mobility and activity ranges in the majority of the species, (ii) less influence of local heterogeneity, and (iii) a better

Table 6. The ecological variables ranked according to their number of significant correlations with abundance in single species (Spearman R_s with $p < 0.05$ after a Bonferroni adjustment for multiple tests). Number is the total number of significant correlations. Neg. is the number of significantly negative correlations. The variables are defined in Table 1

Small scale (1.6 ha)	Number	neg	Medium scale (1 km^2)	Number	neg.	Large scale (4 km^2)	Number	neg.
NOPOLY	5	0	WOOD	12	2	WOOD	15	3
WOOD	3	0	NOPOLY	7	0	CONIFER	15	3
SPPOLY	2	0	THINNING	7	0	PICEA	15	3
AREA	2	0	PICEA	6	0	SPPOLY	14	3
HABITATD	2	0	DECAYED	6	1	LARGEDIA	13	3
DECAYING	1	0	STUMPS	6	0	CUTTING	13	13
BRYOCOV	1	0	AREA	6	3	AREA	13	2
CONT	1	1	HABITATD	6	3	NOPOLY	12	1
CUTTING	1	1	GRASS	6	0	HABITATD	12	1
DISTSN	1	1	CONIFER	5	0	GRASS	11	1
GRASS	1	0	RELASCOP	5	5	POPULUS	10	2
HEATHER	1	1	DISTYNG	5	1	HEATHER	10	9
EXSPOSUR	1	0	DECID	4	2	DECAYED	9	2
DECID	0	0	BETULUS	4	0	DECAYING	8	3
SPDECID	0	0	SPDECID	4	2	THINNING	8	5
DECAYED	0	0	LARGEDIA	4	0	DENSCLC	8	6
LARGEDIA	0	0	BRANCH	4	3	DISTYNG	7	1
STUMPS	0	0	LITTER	4	0	DECID	7	3
THINNING	0	0	SHRUB	4	1	BETULA	7	2
DECAYSTA	0	0	DECAYING	3	0	SHRUB	7	2
BRANCH	0	0	SPPOLY	3	2	BRYOCOV	6	0
BRYOPHYT	0	0	CUTTING	3	2	DISTSN	6	3
FERNS	0	0	DISTSN	3	1	FERNS	6	1
LITTER	0	0	DECAYSTA	3	2	RELASCOP	6	6
ROCK	0	0	ROCK	3	3	DISTCLC	6	3
SHRUB	0	0	POPULUS	2	1	SPDECID	5	2
RELASCOP	0	0	BRYOCOV	2	1	STUMPS	5	4
			HEATHER	2	1	BRYOPHYT	4	2
			EXSPOSUR	2	0	ROCK	4	3
			DISTCLC	1	0	EXSPOSUR	4	2
			DENSYNG	1	0	LITTER	3	2
			BRYOPHYT	0	0	DECAYSTA	2	0

correspondence between the spatial scale of sampling and the spatial scale of ecological differences within the study area.

Large-scaled ecological differences of saproxylic environments have been demonstrated between the Russian and Finnish Karelia due to the management history. Higher numbers and abundances of rare and threatened saproxylic species on the Karelian side were ascribed to these large-scaled differences (Martikainen *et al.*, 1994; Siitonen and Martikainen, 1994). The importance of increasing the spatial scale of ecological differences

is obvious when the temporal scale is included. For example lack of certain habitats within one area may reduce the fauna dependent on those habitats. If the conditions are improved, recovery of the fauna will probably be very dependent on the extent to which the surrounding areas are lacking in the actual habitats.

Decaying wood and wood-inhabiting fungi

Of all the ecological variables recorded, those associated with decaying wood and wood-inhabiting fungi were clearly the most important factors for the species richness of different beetle groups and the abundances in single species. Furthermore, their influence was best expressed at the medium and large scales.

Even though the saproxylic variables described different aspects of decaying wood and wood-inhabiting fungi, many of these variables were strongly intercorrelated. Some variables are assumed to be mathematically connected, for example the volume of dead wood and the number of dead trees of large diameter and the diversity of dead tree parts. The volume of dead wood and the diversity of dead tree parts could be two independent factors; however, they are probably covariant in empirical data. Strong correlations between these variables may also be ascribed to effects of forest management. The highest values of these variables were all found in the areas with the lowest level of exploitation.

Many of the saproxylic variables are also interconnected in their biological function. A large number of the species are fungivorous, or predacious on other invertebrates. The number of polypore species and fruiting bodies often belonged to the most influential variables. These variables are first of all important for the fungivorous beetles, but they may also impact on the predators because of the high number of prey in the fungal microhabitats. The diversity of dead tree parts (HABITATD) and the number of dead trees of large diameters (LARGEDIA) were important substrate variables for the species richness and for the abundance of both polypore fungi and saproxylic beetles. The presence of a wider assortment of microhabitats appears to be associated with a higher species richness in both groups. Habitat heterogeneity is an important factor for wood-boring insects (Stevens, 1986), for land snails (Nilsson *et al.*, 1988) and within many other groups of organisms (Bell *et al.*, 1991; Naeem and Colwell, 1991). The species composition of fungi in the trunks is related to the diameter. Høiland and Bendiksen (1992) found that the diversity of fungus species was positively correlated with the diameter of fallen spruce trunks, and each fungus species may prefer different ranges of tree diameter (Bredesen *et al.*, 1994).

Siitonen and Martikainen (1994) assumed that the survival of rare species on aspen was ultimately dependent on metapopulation dynamics (Hanski, 1991; Hanski and Gilpin, 1991): if the distance between suitable habitats becomes too great, then the colonization rate of newly appeared habitats becomes too low to compensate for the extinction rate in old and disappearing habitats. A consequence of this model is that every species has some lower limit of how scattered their substrate can be before their populations collapse. In this respect, species may be rankable according to their tolerances. In the present study, eight species were absent under a certain density of decaying wood, including three red-listed species which were absent in areas with a low density of dead trees of large diameter (Fig. 1). These species probably do not tolerate a reduced availability of habitats even within relatively small areas. However, whether the mathematical criteria of the metapopulation

model are satisfied in this case or whether other related models are more suitable (for example, 'mainland-island' or 'patchy population' (Harrison, 1991)) cannot be judged.

Level of disturbance

The variable for extensive cutting (CUTTING) had a negative influence on the species richness and on the abundance of single species of obligate saproxylic beetles at a large scale (4 km^2), but it had little influence at small and medium scales. The lowest species numbers at the large scale were recorded in a forest area which was extensively cut for industrial purposes in the period 1870–1900. At the end of this period, only smaller trees were scattered in an area of 7.5 km^2, and the climatic conditions may have been comparable to the dry and sun-exposed clearcuts introduced in Scandinavian forestry during a later period. These findings are interpreted as follows: at smaller clearings scattered in seminatural forests, the distances to source habitats are generally small, which implies that most kinds of organisms may have a fairly high probability of recolonization after regrowth of the forest. With extensive cutting, above some area limit, many species are probably not able to recolonize for a long time, because of the longer distances to areas with a high density of source habitats. This model implies that the logging method is of secondary importance, rather it is a question of how large a continuous area has been converted into young forest within a short period. The diversity of species would probably be reduced if the area of 7.5 km^2 had been logged patch by patch, or if the whole area had been extensively logged in all parts at the same time, during a period of 30 years.

Long-lasting, negative effects of extensive cutting have also decreased species numbers of fungus gnats (Mycetophilidae, Diptera) (Økland, 1994). However, for this latter group of insects, the differences were even expressed at a small spatial scale of sampling (0.16 ha). Such scale differences between insect groups may have many possible explanations including: (i) significant differences in the spatial patterns of migratory and trivial flights (Johnson, 1969), (ii) variations in life-cycle strategies and in the duration of oviposition (Rankin *et al.*, 1986; Solbreck, 1978), or (iii) differences in ecological requirements and in the dispersal abilities of certain host organisms.

Thinning has been a common practice in young coniferous forests in order to favour spruce or pine at an early stage. Deciduous trees are strongly reduced by the most extensive form of thinning (Børset, 1986). The negative influence of thinning in the present study is assumed to be explained by the reduced availability of dead deciduous trees, since such relationships were only found in groups which have many species associated with deciduous trees, such as species associated with birch, and red-listed species.

Landscape ecology and vegetational structure

It could not be proved that the distance to, or the size of, the seminatural forest had a separate effect beyond the influence of the saproxylic variables. However, the substrate conditions of certain beetle groups (for example, species associated with wood-inhabiting fungi, deeply decayed wood and decaying wood of *Betula*) were optimal within a large area of seminatural forest, and they decreased with increasing distance from this area. Thus, large areas of seminatural forests (several square kilometres) may be important for the regional persistence of species associated with these habitats, and they may be important sources for colonizations when such habitats are few and are scattered in the landscape.

Several of the recorded species occurred in young forest and in new clearcuts within the study area, and some of these species were even more numerous in these forest types

(unpublished data). Due to the apparently high mobility of many species, the present samples in mature forests might have been influenced by the distance to clearcuts and young forests, or by the fraction of these forest types in the surrounding area. However, in the cases of significant influence by these variables, species richness (Tables 3–5) or the abundance of single species (Table 6) most often increased with increasing distance from clearcuts or from young forests, or they were negatively influenced by an increase in the density of these forest types. A positive relationship between DISTYNG and the species richness in many of the groups may be indirectly explained by the saproxylic variables due to its positive correlation with these variables.

GRASS and HEATHER showed the strongest influence among the variables related to the vegetational structure. An increased dominance of grasses was recorded in the parts of the seminatural forests which had open patches created by windfalls and by broken trees. On the other hand, an increased dominance of heather was found within the more even-aged forest which had been extensively cut in the past. It might be expected that flower visitors among the saproxylic beetles might gain from an increased number of patches which are richer in grass and herbs. However, the variables GRASS and HEATHER had no significant influence on the species richness of flower visitors. Further, none of the single species which positively correlated with GRASS or which negatively correlated with HEATHER are classified as flower visitors.

Since GRASS and HEATHER were significantly correlated with CUTTING, the influence of these variables may be spurious and indirectly explained by the factors of recolonization suggested under the discussion of the variable CUTTING.

Management implications

Modern forestry has brought about considerable changes in the structure of forests over large areas (Haila *et al.*, 1994). Some of the most characteristic changes of Swedish boreal forests in the 19th and 20th centuries have been in the decrease of old-growth forest, of trees with large diameters and in the amount of decaying wood (Linder and Östlund, 1992). Guidelines to favour diversity in the various groups of saproxylic beetles may be derived from two main sources: (i) ecological studies which identify the critical requirements in different taxa, and (ii) studies of the structure and processes found in less-disturbed forests (Hunter, 1990; Syrjänen *et al.*, 1994).

Generally, a high availability of mature forests with a high density of decaying wood and wood-inhabiting fungi is favourable for the diversity of saproxylic beetles. It is assumed that an increase in these factors not only enhances the local species richness, but it also minimizes the risk of local extirpations by increasing the population size of single species. The maintenance of large populations may give a lower risk of local extirpations due to ecological or stochastic factors, or because of detrimental losses of genes during long-lasting bottlenecks (Brakefield, 1991). In a German study of oak and spruce forests, it was suggested that 5–10 m^3 of dead wood per hectare is sufficient to provide an adequate environment for the saproxylic beetles, including faunistically important species (Hilt and Ammer, 1994). However, in the present study certain species were absent below 23.8–28.5 m^3 of decaying wood per hectare within an area of 1–4 km^2. In a Swedish study, the average density of standing dead trees in unexploited mature spruce forests was 12–13 m^3 of decaying wood per hectare (Linder and Östlund, 1992), and in the Pechora region (Russia) it was 10–14% of the standing crop (Syrjänen *et al.*, 1994). According to Albrechts (1991), the volume of decaying wood in virgin and seminatural forest ranges

from 50 to 200 m^3 per hectare. The more specific variables (than the general amount of decaying wood) 'dead trees of large diameter' and 'diversity of dead tree parts' were the most important factors in the present study. Three of the species classified as vulnerable were absent in areas with less than 4–7 dead trees of large diameter per hectare.

Monitoring of decaying wood may be a useful tool in the management of saproxylic insects, and it could be integrated into regular forest inventories. In addition to the general amount of wood, the variables LARGEDIA, HABITATD, DECID, SPDECID, NOPOLY and SPPOLY are important since they were strongly related to the species richness and to the species abundance within the red-listed beetles and within many ecological groups of saproxylic beetles. The importance of decaying wood seems to increase with increasing spatial scale. A minimum level of 1 km^2 for such surveys is indicated by the present study. Surveys at a regional scale ($\geq$100 km^3) are recommended because of the results found in the comparisons of Russian and Finnish Karelia given by Siitonen and Martikainen (1994).

Certain saproxylic environments are often poorly represented in cultivated spruce forests, for example, habitats with large amounts of polypore fungi, deeply decayed wood and decaying deciduous wood. Large areas of seminatural forests (several square kilometres) are assumed to increase the regional persistence of species associated with these habitats, and they may be important sources for colonizations when such habitats are few and are scattered in the landscape.

Extensive cutting over large, continuous areas should be avoided due to its long-lasting, negative effect on the saproxylic insect fauna. The size of single clearcuts is not the only important factor. It is equally important to avoid converting large areas (several square kilometres) into young forest within a time shorter than one tree generation. As a guideline, a considerable part of a larger area (4 km^2) should always contain old forest (that is, older than the harvesting age).

Extensive thinning with the removal of deciduous trees, in particular of *Betula* and *Populus*, should be avoided. A negative effect on the saproxylic insect fauna of large-scaled thinning and removal of deciduous tree species was indicated in both the present study, and in studies from the Karelia (Martikainen *et al.*, 1994; Siitonen and Martikainen, 1994). Studies of large areas with uncultivated spruce forests in climatic climax showed that the density of deciduous trees was normally as high as 15% of the standing crop (Syrjänen *et al.*, 1994). It is recommended that a high proportion of deciduous trees are saved during thinning, in order to imitate the species composition of trees in uncultivated spruce forests. For the same ecological reasons, the use of chemicals to kill all deciduous trees in forest plantations should be avoided (for example, the use of glyphosphate).

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Appendix 1

Significant correlations between single species and ecological variables at the medium scale (Spearman R_s with $p < 0.05$ after a Bonferroni adjustment for multiple tests). Red-Listed species are denoted by asterisks.

FAMILY/SPECIES	WOOD	CONIFER	PICEA	DECID	BETULA	POPULUS	SPDECID	DECAYING	DECAYED	BRYOCOV	LARGEDIA	STUMPS	NOPOLY	SPPOLY	CUTTING	THINNING	AREA	DISTSN	DISTCLC	DISTYNG	DENSYNG	HABITATD	DECAYSTA	BRANCH	BRYOPHYT	GRASS	HEATHER	FERNS	LITTER	ROCK	SHRUB	RELASCOP	EXSPOSUR
Anaspidae:																																	
Anaspis frontalis	0.73	–	–	–	0.68	–	0.68	0.68	0.72	–	–	0.67	–	–	–	0.63	–	–	–	–	–	–	–	–	–	–	–	0.60	–0.61	0.60	–0.61	–
Anaspis rufilabris	–	–	–	–	0.62	0.71	–	–	–	–	–	–	0.68	–	–	0.61	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cerambycidae:																																	
Anoplodera maculicornis	0.63	–	–	–	–	–	–	0.65	–	–	–	–	–	–	–	0.67	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leptura melanura	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.64	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cerylonidae:																																	
Cerylon ferrugineum	0.62	–	–	–	–	–	–	–	–	–	–	0.72	–	–	–	0.69	–	0.59	–	–	–	–	–	–0.61	–	–	–	–	–	–	–	–	–
Cisidae:																																	
Cis glabratus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.60	0.63	–	–	–	–	–	–	–	–	–	–	–	–
Cucujidae:																																	
*Dendrophagus crenatus**	0.71	0.78	0.78	–	–	–	–	–	–	–	0.82	–	0.78	–	–	–	0.61	–	–	0.66	–	0.75	–	–	–	0.61	–	–	–	–	–0.63	–
Elateridae:																																	
Ampedus nigrinus	–	–	–	–	–	–	–	–	–	–	–	0.71	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.65	–	–	–	–	–	–
Eucnemidae:																																	
*Xylophilus corticalis**	–	–	–	–	–	–	–	–	–	–	–	–	0.64	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.66	–	0.66	–	–
Leiodidae:																																	
Agathidium nigripenne	0.62	–	0.65	–	–	–	–	–	0.61	–	–	0.68	–	–	–	0.61	–	–	–	–	–	–	–	–	–	–	–	0.61	–	0.61	–	–
Anisotoma castanea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anisotoma glabra	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.66	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lycidae:																																	
Dictyoptera nigrorubra	–	–	–	–	0.77	–	0.66	–	0.70	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitidulidae:																																	
Epuraea angustula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.61	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Epuraea bickhardti	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.76
Epuraea laeviuscula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.64	–	–	–	–	–	–	–	–	–
Epuraea muehli	–0.66	–	–	–0.62	–	–	–	–	–0.62	–	–	–	–	–0.63	–	0.64	–0.69	–	–	–	–	–0.63	–	–	–	–	–	–	–	–	–	–
Epuraea oblonga	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.68	–	–	–	–	–	–
Epuraea pygmaea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.60	–	–	–	–	0.69	–	–	–	–	–	–	–	–	–	–	–	–
Glischrochilus hortensis	0.60	0.60	0.60	–	–	–	–	–	–	–	0.62	–	0.60	–	–	–	–	–	–	–	–	0.64	–	–	–	–	–	–	–	–	–	–
G. quadripunctatus	0.70	0.66	0.66	–	–	–	–	–	–	–	0.71	–	0.60	0.69	–	–	0.60	–	–	–	–	0.70	–	–	–	–	–	–	–	–	–	–
*Ipidia quadriplagiata**	0.61	0.68	0.68	–	–	–	–	–	–	–	0.66	–	0.61	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.72	–
Pityophagus ferrugineus	–	–	–	–	–	–	–	–	–	–0.60	–	–	–	–	–	–	–	–	–	–	–	–	–0.64	–	–	–	–	–	–	–	–	–
Pselaphidae:																																	
Euplectus punctatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.62	–	–	–	–	–	–	–	–	–
Rhizophagidae:																																	
Rhizophagus ferrugineus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.70	–	–	0.66	–	–	–	–	–	–	–
Rhizophagus nitidulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.62	–0.60	–	–	–	–	–	–
Scolytidae:																																	
Cryphalus abietis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.71	–	–	–	–
Dryocoetes autographus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.68	–	–	–	–	–	–
Dryocoetes hectographus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.72	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.64	–
Hylastes cunicularius	–0.65	–	–	–0.69	–	–0.67	–0.66	–	–	–	–	–	–	–0.76	–	–	–	0.63	–	–	–	–0.63	–	–0.61	–	–	–	–	–	–	–	–
Hylurgops glabratus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.60	–	–	–	–	–	–	–	–	–	–
Ips typographus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.64	–	–	–
Pityogenes quadridens	–	–	–	–	–	–	–	–	–	–	–	0.68	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pityophthorus micrographus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.66	–	–
Polygraphus poligraphus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.66	–	–	–	–	–	–	–	–	–	–	–	–

Appendix 1. (*Continued*)

FAMILY/SPECIES	WOOD	CONIFER	PICEA	DECID	BETULA	POPULUS	SPDECID	DECAYING	DECAYED	BRYOCOV	LARGEDIA	STUMPS	NOPOLY	SPPOLY	CUTTING	THINNING	AREA	DISTSN	DISTCLC	DISTYNG	DENSYNG	HABITATD	DECAYSTA	BRANCH	BRYOPHYT	GRASS	HEATHER	FERNS	LITTER	ROCK	SHRUB	RELASCOP	EXSPOSUR
Staphylinidae:																																	
Arrecta piliformis	0.64	0.63	0.63																														
Dadobia immersa							−0.63																										
Dinaraea arcana				0.69																													
Leptusa fumida					0.67																												
Phloeonomus monilicornis																																	
Phloeonomus punctipennis																																	
Placusa suecica	0.59			0.79				0.60	0.68			0.66			0.67	0.68			0.63													0.59	
Placusa tachyporoides					0.67				0.59																							−0.60	

Appendix 2

Significant correlations between single species and ecological variables at the large scale (Spearman R_s with $p < 0.05$ after a Bonferroni adjustment for multiple tests). Red-Listed species are denoted by asterisks.

FAMILY/SPECIES	WOOD	CONIFER	PICEA	DECID	BETULA	POPULUS	SPDECID	DECAYING	DECAYED	BRYOCOV	LARGEDIA	STUMPS	NOPOLY	SPPOLY	CUTTING	THINNING	AREA	DISTSN	DISTCLC	DENSCLC	DISTYNG	DENSYNG	HABITATD	DECAYSTA	BRANCH	BRYOPHYT	GRASS	HEATHER	FERNS	LITTER	ROCK	SHRUB	RELASCOP	EXSPOSUR
Anaspidae																																		
Anaspis frontalis	0.86	0.86	0.86	–	–	–	–	–	–	–	0.81	–	0.86	0.81	–0.71	–	0.79	–	–	–	0.77	–	0.86	–	–	–	–	–	–	–	–	–0.82	–
Anaspis rufilabris	–	–	–	0.87	0.93	0.84	0.90	0.92	0.72	0.80	–	–	0.70	–	–	–0.83	–	–	–	–	–	–	0.70	–	–	–	–	–	–	–	0.70	–	–0.70
Cerambycidae																																		
Anoplodera maculicornis	0.85	0.85	0.85	–	–	–	–	–	–	–	0.75	–	0.80	0.86	–0.71	–	0.84	–	–	–	0.71	–	0.80	–	–	–	–	–	–	–	–	–	–
Judolia sexmaculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.79	–	–	–	–
Oxymirus cursor	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.76	–	–	–	–	–	–	–	–	–	–	–	–	–
Cerylonidae																																		
Cerylon ferrugineum	0.70	0.70	0.70	–	–	–	–	–	–	–	–	–	–	0.83	–	–	0.76	–	0.70	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cisidae																																		
Cis boleti	–	–	–	–	0.72	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cis dentatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.73	–	–	–	–	–	–	–	–	0.77	–	–
Octotemnus glabriculus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.80	–	–
Orthocis alni	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.82	–	–	–	–	–	–
Cucujidae																																		
*Dendrophagus crenatus**	0.82	0.82	0.82	–	–	–	–	–	–	–	0.74	–	0.79	0.80	–	–	–	–	–	–	0.82	–	0.79	–	–	–	–	–	–	–	–	–	–	–
Curculionidae																																		
Hylobius pinastri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.75	–	–	–
Magdalis carbonaris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.71	–	–	–
Pissodes gyllenhali	–0.71	–0.71	–0.71	–	–	–	–	–	–	–	–0.73	–	–	–	–	0.70	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.80	–	0.80
Elateridae																																		
Ampedus nigrinus	–	–	–	–	–	–	–0.74	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Denticollis linearis	0.75	0.75	0.75	–	–	–	–	–	–	–	–	–	0.72	0.73	–	–	–	–	–	–	–	–	0.72	–	–	–	0.76	–	–	–	–	–	–	–
Eucnemidae																																		
*Xylophilus corticalis**	0.76	0.76	0.76	0.77	0.84	0.76	0.82	0.84	0.72	0.84	–	–0.85	0.82	–	–	–0.83	–	–	–	–	–	–	0.82	–	–	–	–	–	–	–	–	0.75	–	–
Leiodidae																																		
Agathidium nigripenne	0.80	0.80	0.80	0.72	–	0.79	–	–	0.72	–	0.76	–	0.79	0.93	–	–	0.93	–0.84	–	–0.71	–	–	0.79	–	–	–	–	–	0.82	–	–	–	–	–
Anisotoma humeralis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.74	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lycidae																																		
Dictyoptera aurora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.71	–	–	–	–	–	–	–	–	–	–
Dictyoptera nigrorubra	–	–	–	–	0.75	–	–	0.85	0.83	0.73	0.80	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.75
Melandryidae																																		
Hallomenus binotatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.75	–	–	–	–	–	–	–	–	–	–	–	0.81	–0.76	–	–	–	–	–	–
Xylita laevigata	–	–	–	–	–	–	–	–	–	–	0.70	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitidulidae																																		
Epuraea bickhardti	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.75	–	–	–	–	–	–	–	–	–	–	–	0.92	–0.73	–	–	–	–	–	–
Epuraea biguttata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.78	–	–
Epuraea muehli	–	–	–	–0.71	–	–0.86	–	–0.70	–0.76	–	–0.71	0.71	–	–0.79	–	0.77	–0.92	0.77	–	–	–	–	–	–	–	–	–	0.83	–0.94	–	–	–	–	–
Epuraea oblonga	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.72	–	–	–	–	–	–	–	–	–	–	–	0.79	–	–	–	–	–	–	–
Epuraea pygmaea	–	–	–	–	–	0.75	–	0.70	0.70	0.70	–	–0.92	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.70	–
Glischrochilus hortensis	0.76	0.76	0.76	–	–	–	–	–	–	–	–	–	0.71	0.74	–	–	–	–	–	–	0.81	–	0.71	–	–	–	–	–	–	–	–	–	–	–
G. quadripunctatus	0.75	0.75	0.75	–	–	0.74	–	–	0.72	–	0.83	–	0.75	0.83	–0.71	–	0.91	–	–	–	–	–	0.75	–	–	–	–	–0.75	0.80	–	–	–	–	–
*Ipidia quadriplagiata**	–	–	–	–	–	–	–	–	–	–	0.81	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.80	–	
Pityophagus ferrugineus	–	–	–	–	–0.77	–	–	–0.82	–0.79	–	–0.83	–	–0.71	–	–	–	–	–	–	–	–	–	–0.71	–	–	–	–	–	–	–	–	–	–	0.80
Oedemeridae																																		
Calopus serraticornis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.72	–	–	–	–	–	–	–	–	–	–	0.71	–	–	–	–	–

Appendix 2. (*Continued*)

FAMILY/SPECIES	WOOD	CONIFER	PICEA	DECID	BETULA	POPULUS	SPDECID	DECAYING	DECAYED	BRYOCOV	LARGEDIA	STUMPS	NOPOLY	SPPOLY	CUTTING	THINNING	AREA	DISTSN	DISTCLC	DENSCLC	DISTYNG	DENSYNG	HABITATD	DECAYSTA	BRANCH	BRYOPHYT	GRASS	HEATHER	FERNS	LITTER	ROCK	SHRUB	RELASCOP	EXSPOSUR
Pselaphidae																																	
Bibloporus bicolor	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.87	–	–	–	–	–	–
Euplectus decipiens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.78	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Euplectus punctatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.85	0.74	–0.76	–	–	–	–	–	–	–	–	–	–	–	–	–
Ptinidae																																	
Ptinus subpilosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.90	–	–	–	–	–	–	–	–	–0.76	–	–	–
Rhizophagidae																																	
Rhizophagus cribratus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.78	–	–
Rhizophagus dispar	–0.73	–0.73	–0.73	–	–	–	–	–	–	–	–	–	–	–0.85	–	–	–	0.81	–0.71	0.78	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizophagus nitidulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.77	–0.72	–	–	–	–	–
Rhizophagus parvulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.82	–	–	–	–	–	–	–
Salpingidae																																	
Rabocerus foveolatus	0.77	0.77	0.77	–	–	0.79	–	0.73	0.77	0.78	0.78	–0.95	0.83	0.72	–0.77	–0.71	0.83	–	–	–	–	–	0.83	–	–	–	–	–0.87	–	–	–	–	–0.77	–
Salpingus ruficollis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.77	–	–	–	–	–	–	–
Scolytidae																																	
Cryphalus abietis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.75	–	–	–
Crypturgus hispidulus	–	–	–	–	–	–	–	–	–	–	–	–	–	0.78	–	–	0.70	–	0.73	–0.82	–	–	–	–	–	–	–	–	–	–	–	–	–
Crypturgus pusillus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.82	–	–
Crypturgus subcribrosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.71	–	0.72	–	–	–0.86	–	–	–	–	–	–0.72	–	–	–	–	–	–	–
Dryocoetes aeni	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.71	–	–	–	–	–
Dryocoetes autographus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.78	–	–	–	–	–	–	–	–	–	–	–	0.82	–	–	–	–	–	–
Dryocoetes hectographus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.84	–	–	–	–	–	–	–	–	–	–	–	0.70	–	–	–	–	–0.87	–
Hylastes cunicularius	–0.72	–0.72	–0.72	–0.73	–	–	–	–	–	–	–	–	–	–0.88	–	–	–0.74	0.86	–0.73	0.77	–	–	–	–	–	–	–	–	–	–	–	–	–
Hylurgops glabratus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.79	–	–	–	–	–	–	–
Hylurgops palliatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.80	–	–	–	–
Pityogenes quadridens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.88	–	–
Trypodendron lineatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.78	–	–	–	–	–	–	–	–	–	–	–	0.86	–0.76	–	–	–	–	–
Staphylinidae																																	
Atrecus pilicornis	–	–	–	–	–	0.72	–	–	–	–	–	–0.83	–	–	–0.84	–	0.87	–	–	–	–	–	–	–	–	–	–	–0.98	0.70	–	–	–	–
Dadobia immersa	–	–	–	–0.78	–0.75	–0.73	–0.80	–0.72	–	–	–	–	–	–	–	0.92	–	–	–	–	–	–	–	–	–0.80	–	–	–	–	–	–	–	–
Dinaraea arcana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.77	–	–	–	0.72	–	–	–	–	–	–	–0.78	–	–	–	–	–
*Eurytusa castanoptera**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.83	–	–	–	–	–	–
*Hapalarea linearis**	–	–	–	–	–	–	0.75	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leptusa fumida	–	–	–	0.75	0.79	–	–	–	–	0.70	–	–	–	–	–	–	–	–	–	–	–	–	–	0.91	0.77	–	–	–	–	–	–	–	–
Leptusa pulchella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–0.77	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phloeonomus punctipennis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.74	–	–	–0.75	–	–	–	–	–	–	–	–	–	–	–	–	–
Placusa tachyporoides	0.90	0.90	0.90	–	–	0.70	–	–	–	–	0.80	–	0.86	0.75	–	–0.78	–	–	–	–	–	–	0.86	–	–	–	–	–	–	–	–	–	–0.74	–
Trogositidae																																	
Ostoma ferruginea	0.70	0.70	0.70	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.80	–	–	–	–	–	–	–	–	–	–	–	–