

Ground beetle (Coleoptera, Carabidae) diversity in Finnish arable land

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Carabid data compiled from six independent studies, consisting of 97 799 individuals trapped by pitfalls from Finnish agricultural fields and identified to 111 species were analyzed. Shannon-Wiener H' diversity index was typically around 2.5 and expected species number rarefied to 600 trapped individuals was typically around 30 species. The five most abundant species accounted for 42% of the total catch, and the thirty most abundant species made up 98% of the total catch. Percentage similarities among the assemblages by PS-index were from 16% to 48%. In comparison to published data about carabid diversity in boreal forests, which form the dominating habitat matrix in which Finnish farmland is embedded as relatively small patches, arable fields harbor more species rich assemblages, with more even rank-abundance distributions but variable species composition. Importance of landscape (regional) level, instead of spatial level of crop fields, in understanding carabid diversity in farmland is discussed. Inclusion of carabids into monitoring schemes of agro-biodiversity at landscape level is suggested.

Key words: Carabid fauna, agricultural fields, species richness, evenness, similarity, agro-biodiversity, monitoring

Introduction

Ground beetles (Coleoptera, Carabidae) are ground dwelling, polyphagous or predatory insects, abundant in many kinds of terrestrial habitats. The larvae are subterranean predators. Carabids may be collected in large numbers using pitfall traps, and due to their abundance and species richness (more than 40 000 species described) they are popular objects of study. They are abundant in agricultural fields all over the world and may be important natural enemies of agricultural pests. Thiele (1977) investigated the carabids associated with European agricultural crops. For Fennoscandia and Denmark, a comprehensive key for identification, with short descriptions of biology, is available from Lindroth (1985, 1986). Our aim is not to present a review of the extensive literature of agro-carabidology. Among many excellent reviews, see e.g. Lövei and Sunderland (1996), or Kromp (1999).

In 1956, Wishart et al. estimated that predatory beetles destroyed 70% of cabbage root fly eggs, and Hughes (1959) confirmed that carabids were mainly responsible for this. Potts and Vickerman (1974) suggested that polyphagous predators such as carabids (but also some rove beetles (Staphylinidae) and many spiders) are important predators of aphids in cereal ecosystems. In decades following these reports, applied research into the role of carabids in agroecosystems has proliferated. Kromp (1999) concludes his review on this aspect by asking for more studies that would quantify predation and pest control in open-field conditions, and emphasizing that carabids are only one component in the natural enemy complexes in crop fields. Most of the studies from which our data originates were originally motivated by the beneficial role of carabids.

In Finland, Varis and colleagues initiated agro-carabidology by studying egg predation on cabbage root flies (Varis 1982), and abundance and seasonal occurrence of adult carabids in some crops in southern Finland (Varis et al. 1984). She and her students then continued with

studies on various applied aspects: studies on trapping methods (Holopainen and Varis 1986, Holopainen 1992), on predation of root flies (Varis 1989) and cereal aphids (Helenius 1990, Holopainen and Helenius 1992), on abundance and reproduction (Helenius et al. 1995, Helenius 1995), and on pollution effects (Holopainen et al. 1995) in agroecosystems. Vasarainen and Kurppa (1996) and Huusela-Veistola (1996, 2000) continued with studies into effects of cultivation techniques and pesticide use on carabids. All these studies serve in describing carabid diversity, but Kinnunen (1999, see also Kinnunen et al. 1996, Kinnunen and Tiainen 1999, Kinnunen et al. 2001) was the first who focused into understanding the patterns, especially in relation to spatial scales, in communities of carabids in Finnish farmland.

Apart from what is listed above, we do not know of other studies that would deal with diversity of carabids in agricultural fields in Finland. As only 9% of the land cover is in agricultural use, and practically all the rest is under forest cover, Finnish biologists have traditionally focused into forest systems. However, Kinnunen's (1999) work now provides a landmark for further studies on community ecological aspects of carabid diversity in agricultural land in Finland.

In this report we do not aim into a community ecological analysis. The basic idea of this study was to pull together our various pitfall data on carabids in many regions and over a 17 years time span in Finnish agroecosystems, in order to provide a reference for future surveys of species diversity (along the lines of Duelli et al. 1999). We believe that such reference, even if unperfected in many respects, may be useful especially for future studies monitoring biodiversity and agroecosystem change in Finland.

Material and methods

Study areas, data sets and trapping methods

All data were from pitfall trapping studies. Altogether 23 subsets of data from 1978 until 1994 were used, and the pooled (total) number of pitfall samples was 21344. These studies covered a geographic area ranging from the Southwest to the Northeast of Finland (Table 1, Fig. 1).

Regional range is from hemiboreal to southern boreal phytogeographical zones (Ahti et al. 1968) and from 1.25 to 0.95 k°C DD above 5°C in the length of the thermal growing season.

Pitfall traps varied moderately in design (Table 2). All studies used circular cups, in which the diameter range was 80 to 100 mm. The most common collecting fluid was water with detergent and sometimes NaCl as preservative added. In one study, ethylene glycol, and in another, formalin solution was used. A lid to shade the trap was sometimes used (Table 2). Traps

Table 1. Data sets and study sites (from North to South, see also Fig. 1). Windows of Day Degrees are indicated, and the total catch of carabids given, for the sub-sets of the data.

Data set	Author	Year	Trapping period	DD range ¹	Total number of specimens
Siilinjärvi	Holopainen	1991	4 June – 20 August	74.3– 876.9	8722
Outokumpu	Pokki	1990	9 May – 20 July	76.3– 580.6	3062
		1991	15 May – 21 July	20.2– 556.7	2315
		1993	12 May – 1 July	87.7– 375.0	1057
		1994	18 May – 39 June	66.0– 322.2	726
		Total	.	20.2– 580.6	7160
Jokioinen	Kurppa	1991	31 May – 24 September	66.7–1087.5	2442
		1992	5 May – 26 August	18.8–1106.9	3666
		1993	7 May – 1 September	102.2–1076.2	3018
		1994	6 May – 25 August	51.0–1047.3	1534
		Total	.	18.8–1106.9	10660
SW Finland	Huusela-Veistola	1991	17 June – 5 July	81.9– 510.9	11860
Viikki-I	Helenius	1983	26 May – 21 July	132.3– 792.4	5675
		1984	18 May – 20 July	58.3– 757.4	3703
		1985	30 May – 5 September	66.5–1160.3	1102
		1986	29 May – 7 August	189.4–1040.7	2595
		1988	13 May – 22 September	52.3–1533.8	2812
		1989	23 May – 19 June	152.6– 394.5	555
		1990	9 May – 16 September	144.1–1320.9	11346
		1991	13 May – 4 August	40.7– 807.7	8551
		Total	.	40.7–1533.8	36339
Viikki-II	Varis	1978	17 May – 14 September	29.4–1195.5	8348
		1979	10 May – 12 September	8.1–1362.4	9170
		1982	31 May – 20 August	134.0– 982.7	5633
		1984	11 June – 26 July	359.4– 815.1	570
		1985	2 June – 27 July	160.6– 715.8	997
		Total	.	8.1–1362.4	24718
Total	.	.	.	99459	

¹ Range of Day Degrees accumulated from the start to end of the trapping period, obtained from the nearest meteorological station as accumulation of degrees above 5°C from the onset of the thermal growing season.



Fig. 1. Map of sampling locations for the six data sets of the study.

were emptied at intervals of two days to two weeks. Trapping effort is expressed as the total number of trap-days cumulated from the onset to the emptying of the last trap for each of the data sets (Table 2).

The Siilinjärvi data (63°03' N, 27°39' E) are from the study by Holopainen et al. (1995) who conducted pitfall trapping from 15 spring barley fields and one oat field in the Siilinjärvi municipality. The original aim in this study was to relate carabid diversity to soil properties and to foliar fluoride content. Holopainen (1992) described details of the trapping method, and an independent analysis of species diversity was given by Holopainen et al. (1995).

The 1990–1991 subset of Outokumpu data are from an unpublished M.Sc. study by Pokki (Pia Pokki, unpublished MSc thesis, University of Helsinki 1992), which aimed to describe the local diversity of carabids in arable land. Pit-

fall trapping was conducted in 8 spring barley fields in the neighboring municipalities of Outokumpu (3 fields; 62°42' N, 29°05' E), Liperi (2 fields; 62°36' N, 29°14' E), Joensuu (one field; 62°36' N, 29°34' E), and Kontiolahti (2 fields, 62°45' N, 29°49' E). In each field, three trap stations of two traps 2 m apart were established at 30 m intervals. The 1993–1994 subset of Outokumpu data is from an unpublished study by Pokki and Helenius, in which the effect on carabid activity-density of undersowing with clover or ryegrass was investigated. Trapping was conducted in spring barley fields in Outokumpu (4 fields) and in Liperi (4 fields). The trapping method was the same as for the 1990–1991 Outokumpu data.

The Jokioinen data are from a study by Kurppa and Vasarainen (Vasarainen and Kurppa 1996), in which activity densities of carabids were compared between various crop rotations and between organic and conventional production. All the data are from Yöni-farm in Jokioinen (60°48' N, 23°28' E), from 14 fields. In these fields, according to the crop rotation scheme, the crops were spring barley (either with or without next year's ley undersown), winter rye, an oat-pea mixture (traditional 'mixed cereal'), ley, open fallow, or a weedy field uncultivated since the late 1980s. In the middle of each field, five pitfall traps in 10 m intervals were emptied every two weeks.

The SW-Finland data are from an unpublished study by Kurppa and Huusela-Veistola. In this study, 127 arable farms in around South and Southwest of Finland were sampled, and pitfall trapping conducted in cereal fields on 43 farms, in sugar beet fields on 49 farms, and in spring rape fields on 35 farms (Fig. 1). Each field was sampled by 10 traps. These were in two sets of five traps, each of the five at 10 m intervals in a row. The traps were run for a two week period. The trapping periods were set to weeks 23 to 25 in cereal fields, 25 to 27 in sugar beet fields and to weeks 26 to 28 in spring rape fields.

The Viikki-I data are from studies on epigeal predators (Helenius 1990) in spring-sown cereal or seed legume crops on Viikki Experimental

Table 2. Details of pitfall trapping.

Data set	Year	Effort (trap-days)	Diameter (mm)	Collecting fluid	Lid on trap
Siilinjärvi	1991	1155	90	water+detergent	Aluminium
Outokumpu	1990	3108	100	water+detergent+salt	no
	1991	2814	“	“	“
	1993	2016	“	“	“
	1994	1692	“	“	“
	1991	5060	“	water+detergent+salt	Plastic foil
Jokioinen	1992	6335	“	“	“
	1993	6055	“	“	“
	1994	5590	“	“	“
	1991	17780	95	“	“
SW Finland	1983	8064	80	water+detergent	no
	1984	1608	“	“	“
	1985	720	68	50% ethylene glycol	“
	1986	1680	80	water+detergent	no
	1988	4848	100	“	“
	1989	800	“	water+detergent+salt	no
	1990	3808	“	“	no
	1991	1664	“	“	no
Viikki-II	1978	7680	80	dry / 2% formalin+det.	Plastic foil
	1979	4000	“	“	“
	1982	2916	“	water+detergent	no
	1984	1104	“	“	“
	1985	1320	“	“	“
Total		91817 trap days			

Farm (60°13' N, 25°02' E) in Helsinki. For summaries see Helenius (1991a). In the 1983 experiment, the crops were oats, an oat-faba bean mixture and faba bean alone, in which pitfall trapping was conducted in 8 plots, with 16 traps per plot. Half of the traps were operated within 5 m × 5 m enclosures, enclosed by steel strip 200 mm high, buried 50 mm into the soil (see Helenius 1990). In the 1984 experiment, the crops were also monocrops or mixtures of oats and faba bean. Pitfall trapping was conducted in 24 plots, one trap per plot. One half of the traps were operated within egress-only plots, and the other half within plots surrounded by ingress-only trenches (ca. 8 cm deep trenches, Helenius 1990).

In the 1985 experiment, the crops were oats and an oat-faba bean mixture. Trapping was conducted in 12 plots, 2 traps per plot. A quarter of

the traps were in open plots, another quarter in plots enclosed by an egress-only trench (trenches as in 1984) for the whole period, a further quarter in plots enclosed by egress-only trenches until June 24, and the rest in plots trenched after June 24. In the 1986 experiment, the crops were oats and an oat-faba bean mixture, and the trapping was conducted in 12 plots, 2 traps per plot as in 1985. Half of the traps were operated within isolators 57 cm in diameter, 30 cm high, buried 20 cm deep into the soil, covered with an insect net (see Helenius 1991b for description and for some results from oats).

In the 1988 to 1991 experiment, one hectare of spring barley, as a monocrop or undersown with ryegrass or clover (1988 to 1991), or spring wheat, was used for studying the possibility of enhancement of carabids by undersowing in ce-

reals (Holopainen and Helenius 1992, Helenius and Tolonen 1994, Helenius 1995, Helenius et al. 1995). Altogether, 48 traps in 1988, 32 traps in 1989 (half of which were within plots of 2 m × 3 m enclosed by plastic sheet, 10 cm high, buried 2 cm into the soil), and 32 traps in 1990 and 1991 were operated.

The Viikki-II data of 1978 and 1979 are from a faunistic study by Varis et al. (1984) and by Holopainen and Varis (1986). One cabbage field, one sugar beet field, and one timothy field in Viikki Experimental Farm were included. Each field was sampled by 64 traps (4 × 16 trap set) in 1978 and by 32 traps (4 × 8 trap set) in 1979. Every fourth trap was filled with a formalin medium; otherwise dry traps were used. The traps were emptied every two to four days. Half of the traps were operated inside 10 m × 10 m plots (16 traps per plot in 1978 and 8 traps per plot in 1979) surrounded by 35 cm high and 15 cm deep plastic barriers in order to restrict the movement of carabids into and from the plots (for details, see Varis et al. 1984, and Holopainen and Varis 1986).

The Viikki-II data of 1982, 1984 and 1985 are from studies by Varis and Tolonen (unpublished M.Sc. thesis by Timo Tolonen, University of Helsinki 1990), in which carabids were studied as predators of cabbage root flies in Viikki Experimental Farm. The crops were monocropped white cabbage or white cabbage undersown with subterranean clover. The carabids were trapped in 1982 in 6 plots, and in the other years in 4 plots by 6 traps per plot. In 1984 and 1985 half of the traps were within enclosures of steel strips 10 cm high, 5 cm deep into soil.

Identification of species

Identification keys by Lindroth (1985, 1986) were used, and the nomenclature follows the enumeration by Silfverberg (1992). Only adult specimens were included. The members of the research teams did taxonomic work. Coleoptera specialists were consulted in a few unclear cas-

es. For the Jokioinen data, specimens of the genus *Amara* were not identified to species level, and for the SW Finland data, only *A. aulica*, *A. eurynota* and *A. plebeja* were identified to species level. Authors of the scientific names of the species are given in Appendix 1.

Meteorological data

Cumulative day degrees (DD, in °C above 5°C) were calculated as thermal windows of trapping (Table 1). By definition (Finnish Meteorological Institute) the accumulation of DD starts in spring as the mean daily temperature at 2 m height above ground is permanently above 5°C, and the snow cover is less than 50%. We used the standard DD statistics from the Finnish Meteorological Institute. The DD data for each pitfall study was obtained from a meteorological station closest to the site. The stations do not measure heat sums at ground level, which would be more directly interpreted as conditions experienced by the carabids. However, the thermal windows are better related to phenology of poikilotherms than calendar dates, especially for comparison of sites latitudinally far from each other (e.g. snow melts a month later in the most northern sites than in the most southern sites).

Data analysis

The data are from several independent studies, with variable pitfall trapping methods, in variable crops and 14 variable growing seasons in several widely distributed locations. Each of these factors is confounded with all or many of the other factors. From the first to the last study, a period of 17 years is covered. No assumptions are made concerning possible trends in diversity during this time. As a consequence of this heterogeneity, the data are used only to obtain an overall picture of the diversity of ground beetles in Finnish arable land, rather than to attempt to deepen our understanding about their ecology and function in agroecosystems.

Ranks of the species abundances were calculated as means over the relative (%) catches in the six data sets. Among the top 30 species in rank abundance, rank frequencies were compared. These were calculated as ranks in the incidence, or occurrence in the samples of the pooled data. For further comparison, abundance ranks based on total catch of the species in the pooled data were also calculated. Estimate of Gamma (γ) diversity is the total number of species caught (S).

Shannon-Wiener H' (see Southwood 1978) was used as a robust and general Alpha (α) diversity index for the local assemblages represented by the six sets of data:

$$(1) \quad H' = \sum p_i \ln p_i,$$

where p_i is N_i/N (N stands for total catch of individuals) for species i . H' was calculated in three different ways, first with *Amara*-specimens identified to species level, then with *Amara* excluded, and finally, with *Amara* sp. at genus level. The last two allowed calculation of the index also for the Jokioinen and the SW Finland data sets. Interpretation of H' in this study must be done bearing in mind that the 'local assemblage' refers to ground beetle communities sampled in each of the individual studies. Thus, due to pooling in each of the data sets, H' s do not refer to ecologically meaningful entities (which would be assemblages, or communities, at the same time in the same site). Evenness associated to H' , was calculated as J' ($= H'/\ln S$).

Rarefaction (Simberloff 1978, see also Kouki and Haila 1985, Duelli et al. 1999) was used to further study the structure of the assemblages: this method models how species are accumulated with increasing number of individuals caught in the trapping. For any sample size (n) smaller than the original sample N ($n < N$), the expected number of species $E(S_n)$ is calculated as:

$$(2) \quad E(S_n) = \sum_{i=1}^S \left\{ 1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right\}$$

where N_i is the number of individuals of species i in the original sample. It should be noted that neither rarefaction curves nor H' use identities of species: in an extreme case, two samples rarefied to the same number of individuals may have the same number of species, but none of the same species. Similarly, two samples may have the same H' , without sharing the same species.

For comparison of similarities between the different data sets at the level of species' identities, two Beta (β) diversity indices were calculated (Wolda 1981). Jaccard index is indicative of similarity of the species lists only, ignoring the evenness component. Thus, this index is sensitive to species numbers, to the chance event of getting a high number of low frequency species in the catch:

$$(3) \quad C_j = j/(a + b - j)$$

where j is the number of species common to the two samples, and a and b are respectively the total number of species in each sample (Southwood 1978). The other index, Czekanowski-Sørensen-Renkonen's (subsequently referred to as Renkonen's index) percentage similarity PS is not dependent on species numbers, being sensitive to the evenness component of α -diversity:

$$(4) \quad PS = \sum \min(p_{1i}, p_{2i})$$

where p_i is the proportion of the species i in the total catch in data sets 1 and 2 (Wolda 1981). For all the diversity indices, Viikki I data were sorted to exclude samples from the plots in which beetle movement had been experimentally manipulated, giving 62 species from a catch of 31934 specimens in this sub sample. This precaution reduced the estimated value of H' , for example, by only 0.01 to 0.02 units.

C_j and PS were also calculated from sub-sets of data within the same thermal window of DD-range 20.2–580.6°C, set by the narrowest window of the data sets, that of Outokumpu. This was done in order to allow phenologically more realistic comparison than the comparisons be-

tween the original data sets with variable trapping times and variable thermal periods.

Results

Altogether, 111 species of Carabidae were identified from the total of 97799 specimens determined to species level, in the total catch of 99459 beetles (Table 3, Appendix 1). This gives an average catch rate of 1.08 ground beetles per trap day.

Order of H' values were not sensitive to the inclusion or exclusion of *Amara* sp. at the genus level. The values of H' ranged from 2.32 to 2.97 in the three data sets with all species identified (Table 3). The highest alpha-diversity H' , but with relatively low evenness J' values, were from cabbage and sugar beet crops of Viikki II data (Table 3).

Number of species in the data sets ranged from 45 to 82. As a cautious, conservative rule of thumb (in judging from the rarefaction curves), Finnish crop fields typically harbor carabid communities of *at least* 30 to 40 species. Rarefied to sample size of 600 individuals

Table 4. Expected number of species E(S) of carabids rarefied to sample size of 600 individuals. Examples from northern and southern spring cereal fields, and southern row crop fields. (SD standard deviation)

Sub-set of data	field crop	E(S)	SD
Outokumpu 1990	barley	30.6	2.12
Outokumpu 1991	barley	32.2	2.11
Viikki I 1990	barley	25.6	1.78
Viikki I 1991	barley	23.2	1.86
Viikki II 1978	cabbage	34.8	1.84
Viikki II 1979	cabbage	33.9	2.12
Viikki II 1978	sugar beet	37.7	1.82
Viikki II 1979	sugar beet	29.2	1.15

(which is sufficiently small sample to include all our data sets), expected species number was in every case over 20 species (Fig. 2). Expected species number at 600 individuals in northern (Outokumpu) barley crops was 31 and 32 species, 5 and 9 species more than in southern (Viikki) barley crops in 1990 and 1991, respectively (Table 4, Fig. 2a–b). With this sampling effort, highest expected species number was found from Viikki cabbage and sugar beet (Fig. 2c) crops in 1978 and 1979 (Table 4).

The five most abundant species accounted for 41.96% of the total catch in the pooled data

Table 3. Number of Carabidae species, number of identified specimens, total catch, α -diversity index H' , and evenness index (J'). Because for two of the data sets (Jokioinen and SW Finland), no data of *Amara* at species level were available, H' and J' are calculated in three versions: first, with *Amara* species included, then by excluding the genus, and last, by including the genus. (The data sets are in approximate order from North to South: Siilinjärvi-Outokumpu-Jokioinen-SW Finland-Viikki I-Viikki II.)

Summary statistics	Data set						Total
	Sii	Out	Jok	S-W Fi	Viik-I	Viik-II	
Number of species	45	51	n.a.	n.a.	65	82	111
(excluding <i>Amara</i> species)	(33)	(39)	(27)	(39)	(47)	(61)	(84)
No. of specimens identified to species	8722	7160	9844	11453	35908	24712	97799
Total catch	8722	7160	10660	11860	36339	24718	99459
Shannon-Wiener H' (and J' for row 1.)							
1. with <i>Amara</i> identified	2.32	2.67	n.a.	n.a.	2.53	2.97	.
(evenness J')	(0.34)	(0.37)	n.a.	n.a.	(0.31)	(0.33)	.
2. with <i>Amara</i> excluded	2.28	2.57	2.41	2.59	2.40	2.77	.
3. with <i>Amara</i> at genus level	2.30	2.62	2.53	2.67	2.49	2.78	.

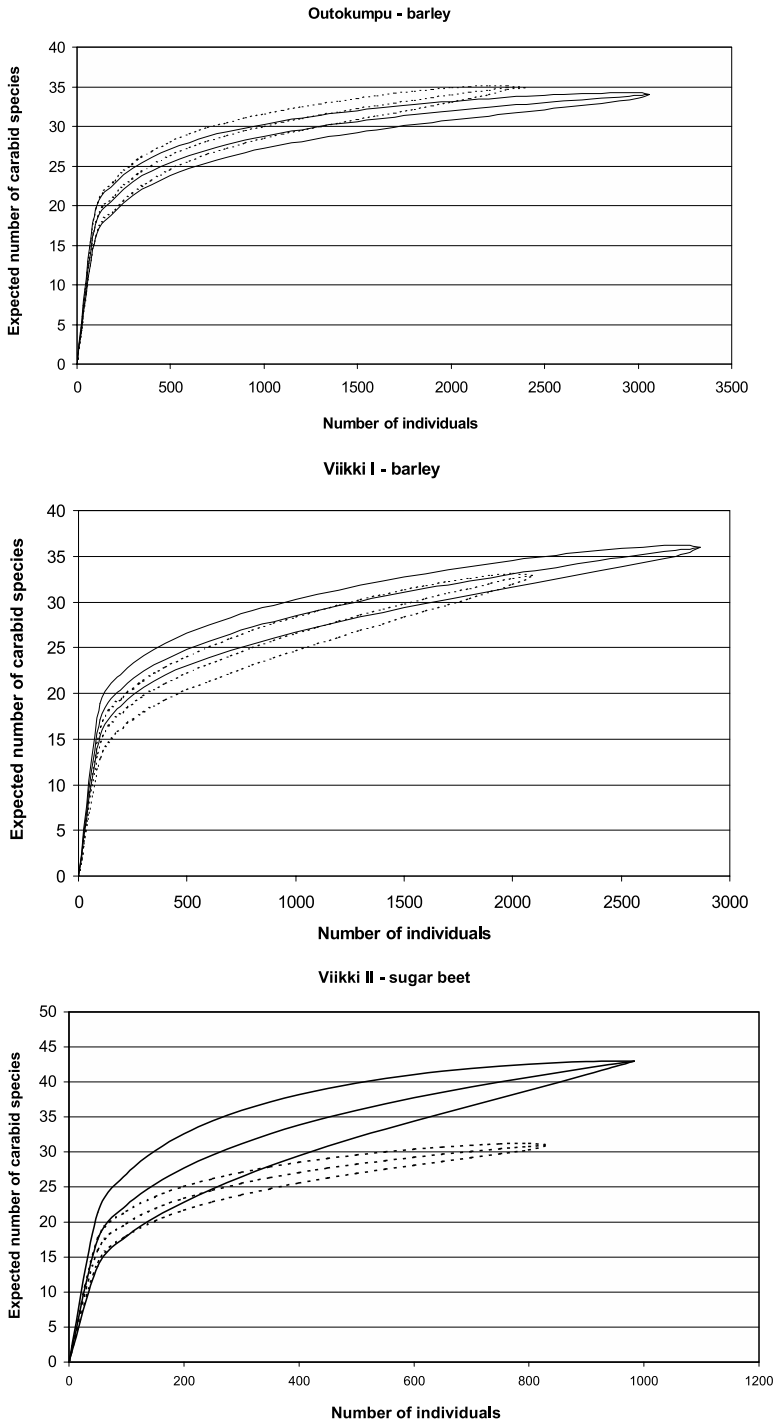


Fig. 2. Expected (rarefied) species number against number of individuals caught in pitfalls in Outokumpu and Viikki I spring barley crops (solid line 1990, dashed line 1991), and in Viikki II sugar beet (solid line 1978, dashed line 1979). (The middle line is the mean, and the upper and lower lines are + and – SD, respectively).

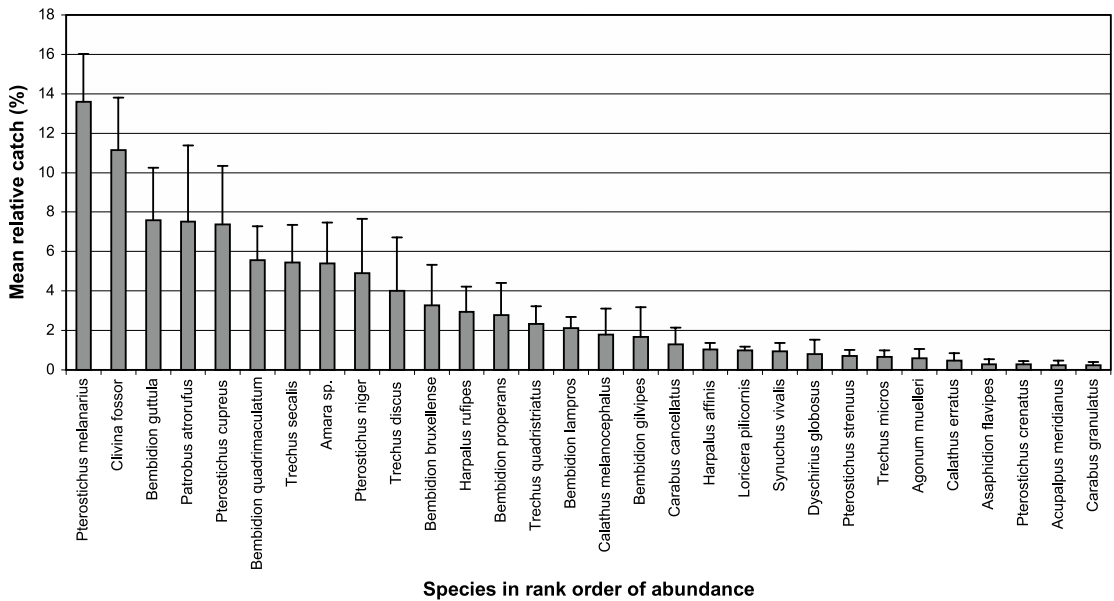


Fig. 3. Relative abundance (% in catch), as mean of the proportions of total catches in pitfalls over the six data sets, against rank in the mean relative abundance. (Thirty most abundant species. Error bars: SE).

(Fig. 3). These were, in terms of means of the relative catch over the data sets, in rank order *Pterostichus melanarius*, *Clivina fossor*, *Bembidion guttula*, *Patrobus atrorufus*, and *Pterostichus cupreus* (Table 5). *Trechus secalis* and *T. discus* ranked among the top five in abundance in the pooled data, but not quite in terms of mean relative abundance. They were numerous in the large data set (high total catch) of Viikki I. These species were all included in the list of only 17 species that were shared by all the data sets. The 17 species (numbered 1–10, 12–15, 19–21, 23 in Table 5) were also among the thirty most abundant species. Among the top 30 species, two species were present in the two northern data sets only. These were *Carabus cancellatus* and *Agonum muelleri*. Another two species were missing from both northern data sets: these were *Trechus micros* and *Acupalpus meridianus*. Top 30 species made up 97.86% of the total catch (Table 5, Fig. 3).

The most frequently collected species was *C. fossor* (Table 5), which was found in 11.7% of samples of the pooled data. The ranks in fre-

quencies roughly followed the ranks in mean relative abundance (Fig. 4). Notably more frequent than numerous, i.e. common but not abundant species within the top 30 were *Harpalus rufipes* and *T. micros*. Among the numerous but not as frequent species were *P. atrorufus*, *P. cupreus*, *P. niger*, *B. bruxellense*, *B. gilvipes*, *Agonum muelleri* and *P. crenatus*, in order of rank in abundance (Fig. 4).

Percentage similarities (PS) of the species assemblages ranged from 48.4% between the two Viikki data sets, to only 16.4% between the northern Siilinjärvi data from cereals and the very southern (coastal) Viikki II data including row crops. Jaccard's C_j of similarity between species lists varied less, and ranged from 0.39 between the previous two data sets, to 0.55 between the two northern sets from cereals, namely Siilinjärvi and Outokumpu. Notably, as for PS, C_j was also high between the two Viikki data sets (Table 6). Positive correlation between C_j and PS was weak ($R^2 = 0.54$, $P = 0.095$). Phenologically more realistic comparison (subsets of data from the same early season thermal win-

Table 5. Thirty most abundant species numbered in rank order of mean relative pitfall catch calculated over the data sets (first two columns, see also Fig. 3). Ranks in the data sets (in approximate order from north to south) Siilinjärvi-Outokumpu-Jokioinen-SW Finland-Viikki I-Viikki II, and mean over these ranks (nc stands for 'not caught', i.e. absent from the data set) (middle columns). Species' share in the total catch (pooled data) and rank in this share (two columns next to the last column). Ranks in frequency (presence-absence) in pitfall samples at level of the pooled data (last column). Note: *Amara* sp. at genus level, due to incomplete data of species in two of the subsets of data (Jokioinen and SW Finland).

Top 30 species in rank order of mean relative abundance	Abundance ranks in the data sets	mean rank	Total catch: %	rank	Ranks in frequency
1. <i>Pterostichus melanarius</i>	2-4-3-2-1-10	3.7	13.38	1.	3.
2. <i>Clivina fossor</i>	6-1-11-1-3-2	4.0	12.64	2.	1.
3. <i>Bembidion guttula</i>	11-6-2-4-4-36	10.5	6.74	5.	4.
4. <i>Patrobus atrorufus</i>	1-7-14-3-14-12	8.5	4.90	7.	11.
5. <i>Pterostichus cupreus</i>	4-5-1-7-22-46	14.2	4.30	10.	15.
6. <i>Bembidion quadrimaculatum</i>	15-3-9-6-10-7	8.3	4.84	8.	7.
7. <i>Trechus secalis</i>	14-22-8-5-5-3	9.5	7.27	3.	5.
8. <i>Amara</i> sp.*	16-11-5-10-7-1	8.3	6.61	6.	2.
9. <i>Pterostichus niger</i>	3-21-6-9-15-22	12.7	3.23	12.	16.
10. <i>Trechus discus</i>	8-20-19-13-2-19	13.5	7.10	4.	8.
11. <i>Bembidion bruxellense</i>	5-2-nc-14-29-24	.	1.65	16.	20.
12. <i>Harpalus rufipes</i>	23-18-13-11-6-6	12.3	4.56	9.	6.
13. <i>Bembidion properans</i>	28-12-21-21-8-4	15.7	4.08	11.	10.
14. <i>Trechus quadristriatus</i>	21-34-7-15-9-8	15.7	2.82	14.	9.
15. <i>Bembidion lampros</i>	17-10-15-8-16-9	12.5	2.04	15.	13.
16. <i>Calathus melanocephalus</i>	27-28-nc-23-13-5	.	2.88	13.	12.
17. <i>Bembidion gilvipes</i>	nc-24-4-18-nc-41	.	1.08	20.	25.
18. <i>Carabus cancellatus</i>	7-9-nc-nc-nc-nc	.	0.63	23.	22.
19. <i>Harpalus affinis</i>	25-17-17-12-17-13	16.8	1.15	17.	18.
20. <i>Loricera pilicornis</i>	13-13-12-20-18-16	15.3	0.84	21.	19.
21. <i>Synuchus vivalis</i>	10-30-24-17-11-18	18.3	1.39	17.	17.
22. <i>Dyschirius globosus</i>	nc-8-26-24-25-35	.	0.38	25.	23.
23. <i>Pterostichus strenuus</i>	19-15-10-16-35-30	20.8	0.45	24.	24.
24. <i>Trechus micros</i>	nc-nc-22-19-12-17	.	1.12	19.	14.
25. <i>Agonum muelleri</i>	9-16-nc-nc-nc-nc	.	0.30	28.	34.
26. <i>Calathus erratus</i>	nc-35-28-28-19-11	.	0.70	22.	21.
27. <i>Asaphidion flavipes</i>	30-14-nc-27-29-46	.	0.14	35.	28.
28. <i>Pterostichus crenatus</i>	12-19-nc-25-26-46	.	0.16	31.	35.
29. <i>Acupalpus meridianus</i>	nc-nc-nc-34-24-14	.	0.35	26.	30.
30. <i>Carabus granulatus</i>	24-30-15-nc-38-41	.	0.14	34.	29.
Total			97.86%		
* of which the most abundant:					
<i>Amara bifrons</i>	42.79				
<i>A. apricaria</i>	9.18				
<i>A. plebeja</i>	5.17				
<i>A. communis</i>	3.96				
<i>A. aulica</i>	3.64				
<i>A. municipalis</i>	2.69				
In all from total of <i>Amara</i> sp.	67.42%				

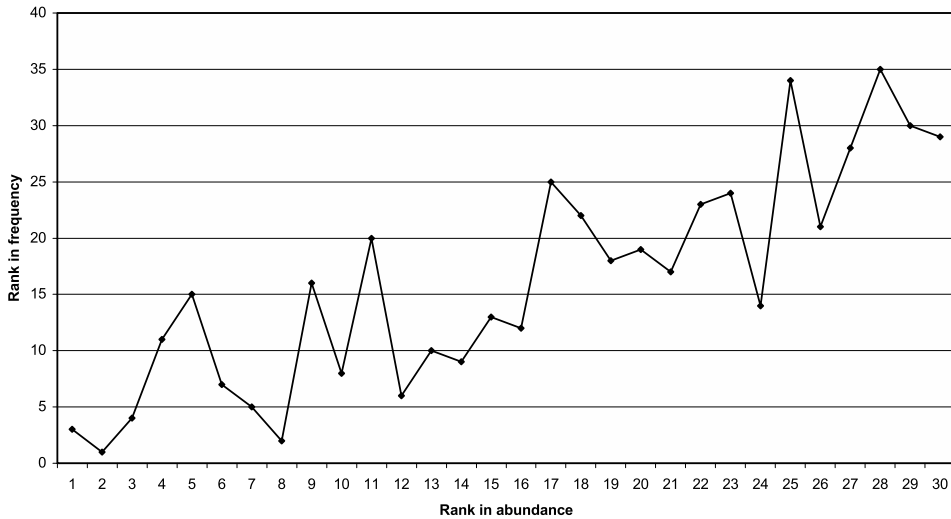


Fig. 4. Rank in frequency (occurrence or incidence in samples) against rank in mean relative abundance of the thirty most abundant species in the pooled data. (Species' order as in Fig. 3, and in Table 5.)

Table 6. Similarity (beta-diversity) indices of Jaccard (Cj: above the diagonal) and Renkonen (PS-%: below the diagonal) for the data sets (including only the sets for which all the specimens, including *Amara* sp., were identified to species level). For a phenologically adjusted comparison, index values are also given for early season sub-sets of data set by Outokumpu day-degree (DD) window (in parentheses: including catches at DD range 20.2–580.6)

Data set:	Siilinjärvi	Outokumpu	Viikki I	Viikki II
Siilinjärvi	-----	0.55	0.40	0.39
Outokumpu	44.3	-----	0.44 (0.45)	0.39 (0.46)
Viikki I	35.7	44.2 (48.2)	-----	0.54 (0.58)
Viikki II	16.4	33.7 (39.1)	48.4 (52.7)	-----

dow defined by DD sums) increased PS values by a mean of 4.6%-units (SD 0.85), and Cj values by 0.04 (SD 0.03) (Table 6), but did not change the order in the comparison.

Discussion

For a reliable diversity estimate, sampling should access all species equally and in proportion of their population densities. Pitfall trapping meas-

ures a combination of density and activity of the individuals, and even trappability may vary between species and be sensitive to slight modifications of the trap design (see e.g. Greenslade 1964, Holopainen 1992, Sundarland et al. 1995). On the other hand, pitfall trapping is cheap and effective in collecting large numbers over short periods of time. Most importantly, pitfall trapping is by far the most frequently used method in even ecological studies of ground beetles (Kromp 1999), its shortcomings are known, and in many cases, activity density is exactly what is needed, especially for studies concerning func-

tional diversity of this family. In estimating spider diversity by four different methods, Coddington et al. (1996) found that each method collected clearly different set of species. Future studies of carabid diversity would benefit from such a comparison of sampling methods. Here, we discuss our results keeping in mind that the estimates are specific to pitfall sampling.

Our estimate of regional (or Gamma) diversity of farmland carabids in Finland was 111 species. Six more species would be added from a total pitfall sample of 36675 beetles from farmland around Lammi Biological Station in southern Finland in 1991–1996, analyzed by Kinnunen et al. (1996, 2001), and Kinnunen and Tiainen (1999). The 117 species is 40% of carabid species found in Finland, including forests and all other habitats (Lindroth 1985, 1986).

The alpha-diversities calculated from our data (from pooled samples) do not refer to genuine local communities in one place and time. However, the H' values may be used as rough indices of richness and evenness of the assemblages sampled. We present these in order to allow comparison to possible further monitoring studies, which may conveniently be based on meta-analysis of several data sets, as in this study.

Using rarefaction, we came up with an estimate of at least 30 to 40 species in an ordinary agricultural field in Finland. This would include all species from the early season ones (adult overwinterers) to late season ones (larval overwinterers). Duelli et al. (1999), using sophisticated extrapolation from rarefaction curves, report estimates of 37.9 ± 5.6 (SD) and 43.1 ± 6.8 species in winter wheat and maize in Switzerland. They sampled by funnel-type pitfalls, which are more efficient than cup type ones (Obriest and Duelli 1996). Their estimates as well as the rarefaction curves they present are remarkably close to the ones we report here. We consider these estimates being conservative rather than liberal. Exhaustive sampling would result in higher estimates: Kinnunen et al. (Heidi Kinnunen, Seppo Rekolainen and Maximillian Posch, manuscript: see Kinnunen 1999) trapped

18724 carabid beetles with 900 pitfalls in 45 days in a one hectare plot within a bare fallow field, and caught 60 species.

Boreal coniferous forests dominate Finnish landscapes. Fields are embedded in the taiga. In comparison to rarefaction curves for carabid beetle assemblages in the southern Finnish taiga, provided by Niemelä et al. (1990), the curves for the assemblages in the agricultural fields indicate more species rich and more even communities. For a sample of 100 individuals from a forest community, ca. 10 species were found (Niemelä et al. 1990), whereas in our samples from agricultural land, the same effort would yield twice as many species. Rarefied species number for 600 individuals ranged from 16.6 ± 0.5 species to 20.6 ± 0.6 species in forests (Niemelä et al. 1990), again almost only half of the values in our data. Why should agricultural fields have higher diversity than successional mature, relatively stable and undisturbed forests? Although the analysis is outside the scope of this paper, we suggest the contemporary disturbance (non-equilibrium) theory to be applicable. It explains how richness may peak at intermediate level of disturbance frequency (Bagon et al. 1996, p. 813–827, 908–912 and references therein. See also Pachevsky et al. 2001). Agricultural fields are not in a succession and they are predictable habitats. Although ‘disturbed’, the disturbance pattern is rather stable irrespective of crop rotation (‘same procedure as last year’, concerning ploughing, sowing etc.).

Percentage similarities measured by Renkonen PS among the data sets were in every case lower (always less than 50%) than those reported from forest communities (usually 50% or higher: Niemelä et al. 1990). Assemblages are more variable in fields than in forests. This is in agreement with Kinnunen (1999, p. 10), who concludes: “*In forests (...) communities of nearby sites were very similar. The fields instead seem to support less predictable communities.*” Again, the disturbance theory provides a way to understand the pattern.

Communities of carabids in surrounding forest patches provide a source of immigrants into

fields. 24 (70.6%) of the 34 species found by Niemelä et al. (1990) were also included in our list. Effect of drawing from a same regional pool may best (and in agreement with disturbance theory and the patch-dynamics concept) explain why relatively high similarity (by both Cj and PS) was associated with regional closeness (the two northern data sets, vs. the two southern data sets), rather than to same or similar (as a habitat) agricultural crops. Our data are only indicative in this respect, but in full agreement with Kinnunen et al. (2001) who found that carabid communities varied significantly among patches of farmland but not between fields of different crops within the patches. This and formerly published research strongly suggest that it is the landscape level of spatial hierarchy at which carabids form communities, and at field or crop level, patterns are less clear and the carabids appear as random assemblages (Thiele 1977, Burel 1989, Burel and Baudry 1995, Östman et al. 2001, see also Kromp 1999, Kinnunen 1999).

Carabids are a species rich family in farmland. Their activity-densities are high throughout growing season. As generalists they are not

dependent on any pest species as prey: they are always present in the fields, and may contribute to natural control of pests as a buffer against invaders. Economic significance of the group would become obvious only if carabids were missing from the crop fields (see Helenius 1990 for a result of ca. 20% yield reduction in oats, following only partial removal of carabids).

Because of their diversity and potential role as beneficials, we suggest including carabids into monitoring of biodiversity in agroecosystems. In designing such schemes, we suggest landscape level sampling frames, rather than randomly choosing individual fields for sampling. Pitfall sampling has an advantage of being much used, which eases comparisons to earlier studies.

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SELOSTUS

Maakiitäjäisten lajimonimuotoisuus suomalaisilla peltoviljelmillä

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Maakiitäjäisten lajimonimuotoisuutta suomalaisilla peltoviljelmillä selvitettiin kuudesta toisistaan riippumattomasta tutkimuksesta, joista vanhin oli vuodelta 1978 ja uusin vuodelta 1994. Kuoppa-ansapyynnillä koottu aineisto käsitti 97 799 maakiitäjäisyksilöä, jotka määritettiin 111 lajiin. Shannonin-Wienerin diversiteetti-indeksin H' arvo oli tyypillisesti noin 2,5. Kuudensadan yksilön otoskokoon rarefoitu, odotettavissa oleva lajimäärä yksittäiseltä peltolohkolta oli noin 30 lajia. Viisi runsainta lajia muodostivat 42 % ja 30 runsainta lajia 98 % koko yksilömäärästä. Lajimäärän ja runsaussuhteet huomioon ottava Renkosen prosentuaalisen samankaltaisuuden indeksi PS sai arvoja 16 % samankaltaisuudesta aina 48 % samankaltaisuuteen osa-aineistojen välillä. Samalta maantieteelliseltä alueelta pyydytetyt aineistot olivat kasvustotyyppistä riippumatta samankaltaisempia kuin eri alueilta pyydytetyt aineistot.

Suomessa pellot ovat tyypillisesti ainakin osittain metsien ympäröimiä. Verrattuna metsälajistosta julkaistuihin tietoihin, peltomaiden maakiitäjäisyhteisöt ovat lajirikkaampia, ja niissä lajien väliset runsaussuhteet ovat tasaisempia kuin metsien maakiitäjäisyhteisöissä. Tarkastelemme tätä yhteisöekologisen häiriöteorian valossa, jonka mukaan yhteisöjen lajiversiteetit ovat korkeimmillaan kohtuullisesti (keskinkertaisen usein) häirityissä elinympäristöissä.

Tuloksemme korostavat viljelyalueen (alue-ekologisen tason) merkitystä lohkotason tai viljelykasvilajin sijasta, pyrittäessä ymmärtämään viljelymaiden maakiitäjäisdiversiteetin vaihtelua paikasta toiseen. Ehdotamme, että maakiitäjäislajistot otetaan mukaan maatalousympäristön biodiversiteetin seurantaan, ja että seuranta näiden osalta järjestettäisiin viljelyalueiden mittakaavassa.

AGRICULTURAL AND FOOD SCIENCE IN FINLAND

Appendix 1

Species of Carabidae and their total catch using pitfall-traps. Thermal window of Day Degrees (DD, above 5°C) of trapping, as well as DD range in which the species was trapped. The DD range gives an indication of thermal activity range, but is artificially limited by the period of pitfall trapping (see also Table 1). (Note: '0' denotes not caught, '-' denotes not identified).

Species	Sii	Out	Jok	SW Fin	Viik I	Viik II	DD range:	
	74.3- 876.9	20.2- 580.6	18.8 -1106.9	81.9 510.9	40.7 1533.8	8.1 1362.4	min	max
<i>Acupalpus meridianus</i> (Linnaeus)	0	0	0	6	14	332	66.5	849.3
<i>A. parvulus</i> (Sturm)	0	0	0	0	5	28	87.4	529.9
<i>Agonum fuliginosum</i> (Panzer)	41	0	0	0	0	3	74.3	876.9
<i>A. gracile</i> Sturm	0	0	0	13	0	0	231.5	483.3
<i>A. micans</i> Nicolai	1	0	0	0	0	0	74.3	876.9
<i>A. muelleri</i> (Herbst)	245	53	0	0	0	0	32.7	876.9
<i>A. piceum</i> (Linnaeus)	0	9	0	0	0	0	69	400.7
<i>A. sexpunctatum</i> (Linnaeus)	47	16	0	0	0	0	74.3	876.9
<i>Amara aenea</i> (Degeer)	5	7	-	-	0	9	74.3	1007.3
<i>A. apricaria</i> (Paykull)	3	14	-	-	480	106	56.6	1320.9
<i>A. aulica</i> (Panzer)	3	4	-	5	73	154	74.3	1160.3
<i>A. bifrons</i> (Gyllenhal)	14	8	-	-	236	2554	8.1	1257.1
<i>A. brunnea</i> (Gyllenhal)	0	0	-	-	0	1	970.8	1028.4
<i>A. communis</i> (Panzer)	3	21	-	-	3	233	8.1	1127
<i>A. consularis</i> (Duftschmid)	0	0	-	-	29	50	168.3	1238
<i>A. convexiuscula</i> (Marsham)	0	0	-	-	0	16	413.5	1040.2
<i>A. curta</i> Dejean	0	1	-	-	3	0	85.6	807.7
<i>A. cursitans</i> Zimmermann	0	0	-	-	0	1	1136.6	1169.7
<i>A. equestris</i> (Duftschmid)	0	0	-	-	7	2	168.3	965.1
<i>A. eurynota</i> (Panzer)	1	0	-	23	115	33	61.6	1320.9
<i>A. famelica</i> Zimmermann	2	2	-	-	20	0	74.3	883.1
<i>A. familiaris</i> (Duftschmid)	0	17	-	-	7	3	88	715.4
<i>A. fulva</i> (Müller)	0	0	-	-	8	110	134	1195.5
<i>A. gebleri</i> Dejean	0	1	-	-	0	0	231.2	313.5
<i>A. ingenua</i> (Duftschmid)	0	0	-	-	2	172	193.9	1227.4
<i>A. littorea</i> Thomson	0	0	-	-	0	1	1136.6	1169.7
<i>A. lunicollis</i> Schiödte	0	8	-	-	1	2	102.2	764
<i>A. majuscula</i> (Chaudoir)	0	0	-	-	7	39	115.8	1205.4
<i>A. montivaga</i> Sturm	0	0	-	-	1	2	58.3	444
<i>A. municipalis</i> (Duftschmid)	0	0	-	-	1	176	328.7	1257.1
<i>A. nitida</i> Sturm	1	0	-	-	0	0	74.3	876.9
<i>A. ovata</i> (Fabricius)	2	0	-	-	1	2	74.3	876.9
<i>A. plebeja</i> (Gyllenhal)	23	101	-	9	207	0	35.9	1257.1
<i>A. quenseli</i> (Schönherr)	1	0	-	-	0	0	74.3	876.9
<i>A. similata</i> (Gyllenhal)	2	6	-	-	0	5	35.9	952
<i>Amara sp.</i>	0	0	745	293	371	5	18.8	1533.8
<i>Anchomenus dorsalis</i> (Pontoppidan)	0	0	0	1	53	132	58.3	1197.8
<i>Anisodactylus binotatus</i> (Fabricius)	0	1	0	0	0	0	313.5	400.7
<i>Asaphidion flavipes</i> (Linnaeus)	1	110	0	18	6	3	20.2	876.9
<i>A. pallipes</i> (Duftschmid)	0	12	0	0	1	162	135.1	1040.2
<i>Badister bullatus</i> (Schränk)	0	0	0	0	0	1	328.7	358.5
<i>B. lacertosus</i> Sturm	0	0	0	0	1	0	152.6	206.9
<i>Bembidion biguttatum</i> (Fabricius)	0	0	0	2	0	0	287.1	472.8
<i>B. bruxellense</i> Wesmaël	390	928	0	202	6	111	20.2	970.8
<i>B. femoratum</i> Sturm	6	0	0	0	0	75	74.3	1147.9

continued on the next page

AGRICULTURAL AND FOOD SCIENCE IN FINLAND

Appendix 1

continued from the preceding page

Species	Sii	Out	Jok	SW Fin	Viik I	Viik II	DD range:	
	74.3- 876.9	20.2- 580.6	18.8 -1106.9	81.9 510.9	40.7 1533.8	8.1 1362.4	min	max
<i>B. gilvipes</i> Sturm	0	12	976	79	0	5	18.8	1106.9
<i>B. guttula</i> (Fabricius)	112	668	1938	1019	2957	11	18.8	1320.9
<i>B. lampros</i> (Herbst)	53	227	121	393	363	874	8.1	1533.8
<i>B. nigricorne</i> Gyllenhal	0	0	0	0	3	0	180.6	395.8
<i>B. properans</i> (Stephens)	2	131	38	57	1217	2614	16.6	1533.8
<i>B. quadrimaculatum</i> (Linnaeus)	61	876	341	964	1011	1561	8.1	1533.8
<i>B. tetracolum</i> Say	0	0	0	0	0	2	18.8	934.3
<i>Bembidion</i> sp.	0	0	6	0	54	0	728.6	1227.4
<i>Bradycellus caucasicus</i> Chaudoir	0	1	0	0	0	4	45.7	1195.5
<i>B. harpalinus</i> (Audinet-Serville)	0	0	0	0	0	3	1169.7	1227.4
<i>Broscus cephalotes</i> (Linnaeus)	0	0	0	0	2	38	187.4	1147.9
<i>Calathus ambiguus</i> (Paykull)	0	0	0	0	1	309	271.8	1197.8
<i>C. erratus</i> (Sahlberg)	0	2	1	16	97	579	26	1227.4
<i>C. melanocephalus</i> (Linnaeus)	4	7	0	33	808	2017	26	1533.8
<i>C. micropterus</i> (Duftschmid)	0	0	0	0	4	0	443.7	715.4
<i>Carabus cancellatus</i> Illiger	355	270	0	0	0	0	20.2	876.9
<i>C. granulatus</i> Linnaeus	10	5	121	0	2	5	18.8	1106.9
<i>C. hortensis</i> Linnaeus	0	0	0	0	1	1	830.5	1007.3
<i>C. nemoralis</i> Müller	0	0	2	19	8	47	52.3	1362.4
<i>C. violaceus</i> Linnaeus	0	0	0	0	1	0	810.9	934.3
<i>Carabus</i> sp.	0	0	2	44	0	0	51	663.6
<i>Clivina fossor</i> (Linnaeus)	366	1073	202	2073	5819	3041	8.1	1533.8
<i>Cychrus caraboides</i> (Linnaeus)	0	0	0	0	1	2	248.9	1177.3
<i>Dicheirotichus rufithorax</i> (Sahlberg)	0	0	0	0	0	7	231.4	911.5
<i>Dromius sigma</i> (Rossi)	0	0	3	4	0	5	26	483.5
<i>Dyschirius globosus</i> (Herbst)	0	316	2	32	13	13	20.2	799.8
<i>D. politus</i> (Dejean)	0	0	0	0	0	3	134	483.5
<i>D. thoracicus</i> (Rossi)	0	7	0	0	0	0	83.9	400.7
<i>Dyschirius</i> sp.	0	0	41	0	0	0	18.8	1106.9
<i>Elaphrus riparius</i> (Linnaeus)	1	12	0	0	0	1	74.3	876.9
<i>Elaphrus</i> sp.	0	0	0	5	0	0	95.2	455.1
<i>Harpalus affinis</i> (Schränk)	8	36	102	219	253	522	29.4	1320.9
<i>H. latus</i> (Linnaeus)	0	5	68	57	4	10	18.8	1047.3
<i>H. luteicornis</i> (Duftschmid)	0	0	0	0	1	0	87.4	127.2
<i>H. quadripunctatus</i> Dejean	1	0	0	0	3	15	74.3	1195.5
<i>H. rufipes</i> (Degeer)	19	28	133	243	2245	1866	52.3	1533.8
<i>H. tardus</i> (Panzer)	0	0	0	0	0	6	66.7	586.5
<i>Harpalus</i> sp. + <i>Ophonus</i> sp.	0	0	2	28	2	0	187.4	716.3
<i>Lebia chlorocephala</i> (Hoffmannsegg)	0	1	0	1	0	0	273.2	523.8
<i>Leistus ferrugineus</i> (Linnaeus)	0	0	0	0	0	6	735.7	1227.4
<i>L. terminatus</i> (Hellwig)	0	1	5	0	16	27	145	1320.9
<i>Leistus</i> sp.	0	0	0	0	1	0	715.4	792.4
<i>Loricera pilicornis</i> (Fabricius)	71	125	136	74	210	224	16.6	1320.9
<i>Microlestes minutulus</i> (Goeze)	0	0	0	9	53	17	133.5	846.5
<i>Notiophilus aquaticus</i> (Linnaeus)	0	0	0	0	0	74	16.6	1301.2
<i>N. palustris</i> (Duftschmid)	0	0	0	4	0	1	231.5	1227.4
<i>Notiophilus</i> sp.	0	0	1	0	0	0	1 663.6	822.6
<i>Olisthopus rotundatus</i> (Paykull)	0	0	0	15	0	0	95.2	232

continued on the next page

AGRICULTURAL AND FOOD SCIENCE IN FINLAND

Appendix 1

continued from the preceding page

Species	Sii	Out	Jok	SW Fin	Viik I	Viik II	DD range:	
	74.3- 876.9	20.2- 580.6	18.8 -1106.9	81.9 510.9	40.7 1533.8	8.1 1362.4	min	max
<i>Oodes helopioides</i> (Fabricius)	0	1	0	0	0	0	250.6	335.2
<i>Ophonus nitidulus</i> Stephens	0	0	0	0	0	1	444.2	496.7
<i>O. puncticollis</i> (Paykull)	0	0	0	0	5	5	196.5	846.5
<i>O. rufibarbis</i> (Fabricius)	0	0	0	1	0	84	134	1169.7
<i>Patrobis assimilis</i> Chaudoir	0	0	0	0	1	0	135.3	180.6
<i>P. atrorufus</i> (Ström)	2230	376	124	1156	457	532	20.2	1502.7
<i>Platynus livens</i> (Gyllenhal)	0	0	0	0	1	0	538.7	566
<i>P. obscurus</i> (Herbst)	0	0	0	13	0	0	226.7	483.3
<i>Pterostichus crenatus</i> (Duftschmid)	96	27	0	19	12	3	52.3	1070.1
<i>P. cupreus</i> (Linnaeus)	758	739	2064	693	19	3	18.8	1533.8
<i>P. melanarius</i> (Illiger)	1650	761	1409	2042	6630	811	18.8	1533.8
<i>P. minor</i> (Gyllenhal)	0	0	96	0	0	0	18.8	1076.2
<i>P. niger</i> (Schaller)	1556	21	668	386	448	134	58.3	1320.9
<i>P. nigrita</i> (Paykull)	0	5	0	0	0	0	76.3	197.9
<i>P. oblongopunctatus</i> (Fabricius)	31	0	0	10	0	2	29.4	876.9
<i>P. strenuus</i> (Panzer)	44	59	219	90	3	31	16.6	1227.4
<i>Pterostichus sp.</i>	0	0	17	0	0	0	66.7	997.6
<i>Stomis pumicatus</i> (Panzer)	0	0	0	0	0	3	328.7	448.6
<i>Syntomus foveatus</i> (Geoffroy)	0	0	0	0	0	1	248.9	288.1
<i>S. truncatellus</i> (Linnaeus)	0	0	0	0	0	150	8.1	1147.9
<i>Synuchus vivalis</i> (Illiger)	123	5	4	81	989	183	74.3	1502.7
<i>Trechus discus</i> (Fabricius)	272	23	87	217	6292	171	74.3	1533.8
<i>T. micros</i> (Herbst)	0	0	27	75	809	199	40.7	1320.9
<i>T. quadristriatus</i> (Schranck)	36	3	592	124	1041	1004	18.8	1533.8
<i>T. rubens</i> (Fabricius)	1	0	0	0	7	0	74.3	1030
<i>T. secalis</i> (Paykull)	69	18	365	993	2814	2967	18.8	1533.8
<i>Trechus sp.</i>	0	0	2	0	3	1	305.3	1106.9
<i>Trichocellus placidus</i> (Gyllenhal)	2	0	0	0	0	1	16.6	876.9