The within-field spatial and temporal distribution of arthropods in winter wheat

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Abstract

The within-field spatial distribution of some common farmland arthropods from the Carabidae, Araneae and Collembola was assessed using two-dimensional grids of pitfall traps distributed across whole winter wheat fields. In the first year the extent to which arthropod capture was influenced by location within the field and sampling intensity was examined using three different sized grids (1.5m, 7.5m and 30m spacings). In the second year distributions within two different-sized winter wheat fields were compared. Spatial pattern and association between arthropods and weed cover were analysed using SADIE and trend surfaces were used to visualise distributions. Many of these arthropod groups exhibited aggregated distributions within the fields in clusters larger than 30m across therefore the numbers captured will vary depending on the location of sampling within a field. *Amara* species, *Bembidion lampros*, Carabidae and Lycosidae were predominantly found within 60m of the field edge. *Nebria brevicollis* and *Pterostichus madidus* were found within the field in patches of one and two hectares respectively. Linyphiidae were relatively homogeneously distributed across the fields. There was some evidence of clustering by Collembola. The spermophagous Carabidae and Lycosidae were positively associated with the degree of weed cover. SADIE analytical techniques were useful for identifying the importance and location of patches with higher and lower than average numbers, although a minimum of 36 sample points is recommended.

Key-words: SADIE, polyphagous predators, weeds, Carabidae, Araneae, Collembola, beneficial insects

Introduction

Much is now known of the ecology of arthropods within cereal crops. The most studied are the polyphagous and stenophagous predators, notably members of the Carabidae, Staphylinidae, Araneae and the parasitic Hymenoptera (reviews by Wratten & Powell, 1991; Lovei & Sunderland, 1996). However, many of these and other studies have revealed that there is considerable spatial heterogeneity in the distribution of arthropods within fields which has been linked to a number of environmental factors. These include physical factors such as soil type (Thiele, 1977), soil pH (Gruttke & Weigmann, 1990) and soil moisture (Hengeveld, 1979) and also characteristics such as vegetation cover provided by weeds (Speight & Lawton, 1976) or by differences in crop density (Honek, 1988), which can affect the microclimate. The type and quality of adjacent non-crop areas may also affect within-field distribution, through the provision of overwintering sites from which immigration occurs (Coombes & Sotherton, 1986; Jensen *et al*., 1989; Riedel, 1992; Holopainen, 1995). Prey distribution may also be important, since some species can locate areas of high prey density (Bryan & Wratten, 1984; Hance, 1987). Interactions between these environmental factors are likely and it is their combined effect, in conjunction with inter- and intra-species relationships, that determines a predator's distribution (Hemptinne *et al*., 1992).

Detailed descriptions of the spatial distribution of insect populations have only rarely been attempted, although if such data are combined with measurements of physical and environmental factors, this can reveal much about the environmental requirements and movement behaviour of individual species (Kennedy, 1972; Greig-Smith, 1979; Taylor, 1986). This approach may also aid the development of habitat manipulation strategies aimed at enhancing beneficial species (Powell *et al*., 1995) and assist in the design of sampling strategies (Parker & Turner, 1996; Winder *et al*., 1999). Insect spatial distributions also have important implications for the design of field studies (Perry, 1997), although this is either rarely addressed or it is assumed that a suitable experimental design (e.g. randomised block) will overcome any bias that results from spatial heterogeneity. The identification of intra- and inter-specific relationships may be aided by spatially-structured sampling.

Insect spatial pattern is rarely investigated, partly because of the intensive sampling effort required to gain such information but also because of previous limitations in statistical methodology. Traditional methods, for count data collected from a set of locations, examine numeric properties of the frequency distribution, such as the somewhat abstract relationship between the sample mean, m, and the sample variance, s^2 (Anscombe, 1949; Taylor, 1961; Lloyd, 1967; Iwao 1968). These methods make no use of information concerning the spatial location of the sample units, so their capacity to describe spatial pattern is limited and they can only infer non-randomness at some unknown spatial scale below that at which the data were collected. The methods of Bliss (1941) and Greig-Smith (1952) are better, but even these do not explicitly use the coordinates of the sample units, and require that sampling be done on a regular grid.

Recently however, a new class of techniques has been developed, termed SADIE (Spatial Analysis by Distance IndicEs), to detect and measure the degree of spatial pattern in spatially-referenced count data (Perry, 1998a & b; Perry *et al*., 1999). The methods make full use of the data concerning each count and the two-dimensional coordinates of the sample unit at which it was taken; there is no restriction on the location of the sample units. SADIE employs randomizations that condition on the observed counts and permute them amongst the sample units, so the analysis is complementary to those more traditional methods listed above, and independent of them. The randomizations conform to the null-hypothesis that the observed counts are arranged randomly amongst the sample units. By comparison of the observed arrangement with these randomizations, two indices of aggregation and corresponding tests of the null-hypothesis are derived. These relate to the overall degree of aggregation in the entire arrangement. Perry *et al*. (1999) have extended these methods to provide an index of clustering for each of the sample units, to measure the degree to which the observed count at each unit contributes to this overall aggregation. Furthermore, the clusters are identified separately, either as patches within which neighbouring units have counts relatively larger than the mean, or as gaps within which neighbouring units have relatively small counts. The SADIE class of techniques were also augmented by Perry (1998b) to provide indices and tests of spatial association for the case when two separate arrangements, perhaps different species, share the same sample units. The SADIE techniques were developed specifically for clustered ecological count data, in which patterns are dynamic and patchy, there are frequently a large proportion of zero counts, and abundance has a non-stationary covariance structure; such data is inappropriate for geostatistical analysis.

Before the spatial distribution of a species is evaluated it is essential that the appropriate scale be chosen to reflect the distribution pattern. Where arthropods have been sampled within cropping systems using a two-dimensional grid of pitfall traps, considerable spatial heterogeneity has been found (Hengeveld, 1979; Duffield & Aebischer, 1994; Holopainen, 1995; Thomas *et al*., 1998). In some cases the sampling scale for these grids had to be chosen to meet practical limitations. In other cases, the grid spacing was chosen based on the species' power of dispersal, in an attempt to ensure that each sampling location was independent.

Thus, very little is known of the spatial distribution of most farmland arthropod species within cereal ecosystems. In the first year of this study, the use of spatially structured sampling regimes was explored in conjunction with the use of SADIE. More specifically the effect of sampling location and grid spacing was examined for a range of different farmland arthropods. Assessments of cereal aphids were also made and are reported in Winder *et al*. (in press). Associations between predatory arthropods and the cereal aphids will be reported elsewhere. Because many of the predatory arthropods found within cereal fields invade the crop each year from the field boundary, in the second year the effect of field size was investigated.

Materials and methods

Sampling location and grid size

Arthropods were sampled intensively at three spatial scales in a 250m × 180m field of organic winter wheat, near Wimborne, Dorest, UK, on six occasions between 7 June and 12 July 1996. Four grids of pitfall traps (6cm diam.) with a single trap at each point were used: one 9× 7 grid with 30m spacing (large), which extended across the whole field; two 5 × 5 grids with 7.5m spacing with one located at the field edge and the other in the field centre (medium edge and medium inner) and one

6×5 grid with 1.5m spacing (small) located within the medium inner grid (Figure 1). The co-ordinates were based on an origin at the south-west corner of the sampling area. Pitfall traps, partly filled with water and detergent, were operated for two days then all arthropods were removed and stored in 70% alcohol. The majority of the catch comprised Carabidae and Staphylinidae, which were identified to species or genus, and Araneae, which were identified to family. Many of the identified taxa are known to feed upon cereal aphids and have been classified as beneficial. Percentage weed cover was assessed within a 0.25m^2 quadrat at each sample point on 28 June.

Effect of field size

Arthropods were sampled simultaneously in two winter wheat fields, of 4ha and 16ha, near Durdle Door, Dorset, UK, on five occasions at fortnightly intervals between May and July 1997. A grid of pitfall traps with approximately 30m spacing was used within each field with a single trap at each sampling point. In the larger field, the grid was 8 units wide and between 8 to 11 units long, with 75 traps in all. In the smaller field it was 6×4 units with 5 extra traps, making 29 in all. The pitfall traps, partly filled with water and detergent, were operated for two days then all arthropods were removed and stored in 70% alcohol. All arthropods were identified as in 1996. Percentage weed cover was assessed within a 0.25m^2 quadrat at each sample point on 12 June. The location of each pitfall trap was surveyed and located using the national grid reference.

Data Analysis

In both years, seasonal activity periods caused considerable between species variation in capture rates on particular dates. Furthermore, numbers of individual species were often too small at each sample unit for informative analyses on specific dates. Therefore, to obtain a measure of activity within a locality totals of counts over all sampling dates for each year were analysed.

(i) Comparison of sampling location and scale, 1996

To study the numeric properties of the data, sample means and variances were computed for each scale. To test for differences in abundance between the four scales, total counts, c, transformed to $\log_{10}(c+1)$, were compared using analyses of variance for each taxa. Spatial pattern was studied by computation of the overall SADIE indices I_a and J_a based on distances to regularity and crowding (Perry, 1998b), respectively, together with their associated probabilities P_a and Q_a, for each scale separately. Where necessary, this was supplemented by a description of the degree of clustering in the counts in the form of 'patches' of large counts, using overall index $\bar{\mathrm{v}}_i$ and associated probability P_i, or of 'gaps' of small counts, using overall index $\bar{\mathrm{v}}_i$ and associated probability P_I (Perry *et al.*, 1999). For a particular set, if all of these indices have values around unity, this indicates that the data conform to the null hypothesis of spatial randomness; a value of at least one index well above unity indicates spatial non-randomness of some form. Where a clustering probability is quoted without a subscript it refers to both the patch and gap probabilities. A cluster is defined as a set of neighbouring units, for which the absolute value of the unit clustering index, v_i, is greater than 1.5 for all units in the set (Perry *et al.*, 1999). Clusters should be assumed to be roughly circular unless specified otherwise.

(ii) Comparison of field sizes, 1997

Identical methods were used to those above, except that no analyses of variance were done to compare abundances.

(iii) Spatial association

The spatial association between the arthropods and weed cover, was measured, for each scale and field separately, by computation of the SADIE index I_t and associated probability P_t (Perry, 1998b). The null hypothesis tested by P_t is that the two spatial patterns are located randomly with respect to one another; alternatively, species may be positively associated with or negatively dissociated from one another.

Distribution data is presented as two-dimensional contour maps from counts, drawn using the package SURFER.

Results

General results from 1996

During 1996, the effect of spatial location and grid size was investigated. There was a considerable degree of temporal variation in the capture of predatory arthropods. Only one carabid species, *Nebria brevicollis* Fabricius (Coleoptera: Carabidae), was captured in sufficient numbers for analysis. This was most abundant on the first sample date but their captures declined to about one fifth of this on all subsequent dates (Fig. 2). The numbers captured on each date, with the exception of the first sample, were too low for SADIE analysis, however, when examined the location of the arthropods was consistent through time and therefore totals across all dates indicated where the arthropods were predominantly present. The total number of Carabidae were most abundant on the first sample date, declined until mid-June and then started to increase predominantly because *Pterostichus melanarius* Illiger (Coleoptera: Carabidae) started to emerge. Lycosidae (Araneae) and Collembola showed a gradual decline whereas Linyphiidae (Araneae) increased over the sampling period.

There were significant differences in the means for all the taxa analysed (*F*-tests, Table 1). This would be expected for where a taxa exhibits a heterogeneous distribution because each grid was sampling a different location. However, for Collembola, Linyphiidae, Lycosidae and weed cover, the mean was smallest for the small scale, and often much greater for the large scale, whilst *N. brevicollis* showed no distinct trend. Such significant differences in density between the scales imply the existence of spatial pattern; this implication is valid even if subsequent within-scale analyses all show that the counts were distributed at random within each of the separate grids. Furthermore, because the grids have relatively few sample units in common, it cannot be expected that density differences between scales, will result in detectable within-scale pattern at the larger scale. For example, the Collembola count within the medium-inner grid was only about one third of that within the large-scale grid (Table 1), although the four counts (Figs. 3 & 4) in the units that contributed to both grids: 24, 11, 37 ,7, were typical at the large scale and did not indicate a region of low density at the large scale (Fig. 3). Indeed, there was little indication of spatial pattern at the larger scale ($I_a = 1.07$, $P_a = 0.29$, Table 1), and only weak clustering ($P > 0.25$).

Comparison between the grids in 1996

During 1996 there were some indications of spatial pattern. *N. brevicollis* showed a large and significant value of I_a confirming strong aggregation within the large grid (Table 1), and the v_i indices confirmed that this was due to a single dominant cluster of approximately 1ha, located in the left area of the grid (Fig. 3). For the medium-edge grid ($\bar{v}_i = 1.33$, $P_i < 0.05$), patchiness occurred in the top left corner (Fig. 5). Total Carabidae were significantly aggregated within the large grid with areas of low counts ($\bar{v}_j = -1.53$, $P_i < 0.01$) and some patches ($\bar{v}_i = 1.30$, $P_i = 0.05$) mainly within 60m of the field edge.

Clustering by the Linyphiidae during 1996 never achieved significance ($P > 0.1$) at any scale, and the large counts of this taxa appeared to be randomly distributed. By contrast, the Lycosidae were highly aggregated at the large scale. Here, the pattern was manifest as a single large gap ($\bar{v}_j = 1.61$, $P_j < 0.01$) extending 180m down almost the entire left side of the large grid, and three small patches ($\bar{v}_i = 1.64$, $P_i < 0.01$) comprising ten sample units, spread along the right-hand edge and foot of the grid. A similar degree of aggregation was found at the medium-edge scale, especially at the foot of this grid, coincident with the edge of the field. No significant pattern or clustering ($P > 0.1$) was found further into the field, within the medium-inner (Fig. 4) and small grid (Fig. 6), where abundance was notably less.

Counts for Collembola were much larger than for most other taxa, and were very variable at the large scale, ranging from 3 to 110. Caution is required when interpreting contour maps for such large counts, because they often suggest aggregation where there is little or no evidence of anything but a random arrangement of variable counts. Indeed, at the large and medium-edge scales (Figs. 3,5) the indices I_a and J_a showed no evidence of aggregation and clustering was no greater than expected by chance ($P > 0.25$). However, at the medium-inner ($\bar{v}_i = 1.25$, $P_i = 0.07$; $\bar{v}_j = 1.13$, $P_j = 0.19$) and small ($\bar{v}_i = 1.23$, $P_i = 0.09$; $\bar{v}_j = 1.23$, $P_j = 0.1$) scales (Figs. 4,6) there was moderate clustering into both patches and gaps.

Weed cover and associations

Weed cover in 1996 only exhibited slight aggregation within the medium-inner grid where there was greater cover along the right-hand edge (Fig. 4). The near significance of the aggregation at the small scale was characterized by significant clustering into two small patches ($\bar{v}_i = 1.32$, $P_i < 0.05$) of 1.5m diameter, and a slightly larger gap ($\bar{v}_j = 1.22$, $P_j < 0.05$).

There were significant associations ($P_t < 0.1$) with weed cover for Lycosidae within the large and small grids (Table 2). No other arthropods were associated with weed cover. Within the large grid weed cover was greatest around the edges as were the numbers of Lycosidae, thus the significant association may have been coincidental both predominating at the field edge. It is, however, likely that the Lycosidae were responding to weed cover because they were also associated with weed cover in the small grid.

General results from 1997

The distribution of arthropods and weeds was examined in a large (16ha) and a small field (4ha) using a grid of pitfall traps with approximately 30m spacing. Numbers and diversity of taxa were greater than in 1996 allowing analysis for some species. As found in 1996 there was considerable degree of temporal variation in the capture of predatory arthropods. Of the Carabidae the capture of *Amara* species (Coleoptera: Carabidae) did not vary much over the sampling period while that of *Bembidion lampros* Herbst (Coleoptera: Carabidae) declined. *Pterostichus madidus* Fabricius (Coleoptera: Carabidae) counts were highest on the last sample date when they formed 70% of the total Carabidae captured. The Linyphiidae counts were also highest on the last sample date, while activity of Lycosidae declined over the sampling period. Collembola exhibited a peak on 29 May, otherwise capture was relatively consistent. As found in the previous year some arthropod groups exhibited distinct spatial pattern, although often this was only within the larger field (Table 3).

Comparison of field sizes in 1997

Predatory groups

The *Amara* species showed moderate aggregation (Table 3) in the large field, manifest mainly as a large area of several gaps on the left side of the field. Of the eight counts of 5 or more, six occurred on the field edge (Fig. 8). In the small field there was strong and significant aggregation and clustering; the large gap (Fig. 9) comprised ten units, but there was also a patch of about 50m radius. In both fields counts were predominantly highest near the field edges. The pattern for *B. lampros* in the large field featured a large and significant gap ($\bar{v}_j = 1.32$, $P_j = 0.05$) extending over 2ha in the middle of the field (Fig. 8) and strong patchiness ($\bar{v}_i = 1.28$, $P_i = 0.06$) along the top edge of the large field. Three small patches ($\bar{v}_i = 1.40$, $P_i < 0.05$) caused significant clustering in the *B. lampros* population on the left side of the small field (Fig. 9). Although *B. lampros* was captured across the whole of the large and small fields, when data for individual sample dates were examined, the highest counts were predominantly confined to the field edges in the large field, with some up to 60m into the field. Similarly, in the small field some higher counts were recorded at 60m from the field edge which was almost the field centre. *Pterostichus madidus s*howed strong aggregation within the large field, clustered into two patches of approximately 4ha each ($\bar{v}_i = 1.42$, $P_i < 0.05$), one extending over 200m along the left-hand edge and another equally long near the right-hand edge. There were also two gaps ($I_j = 1.41$, $P_j < 0.05$), the larger covering about 1ha (Fig. 8). By contrast, in the small field (Fig. 9) there was little clustering. This species had relatively high counts even in the field centres.

During 1997, Linyphiidae did not such evidence of clustering into patches or presence of gaps. In the large field although showing a preference for the field edge with noticeable gaps in the centre of both fields, there was only weak statistical evidence to confirm this (Table 3).

Collembola were clustered within the large field with significant patches and gaps, but in the small field there was only significant evidence for patches ($\bar{v}_i = 1.34$, $P_i = 0.05$).

Weed distribution and associations

Weed cover only exhibited aggregation in the small field, where there were some high counts in the left corners with the remainder of the field being relatively bare (Fig. 9).

Amara species are predominantly phytophagous carabids explaining why they occurred in areas with more weed cover, as evidenced by the relatively large value of the spatial association index I_t for both fields (Table 4). Collembola were associated with weed cover in the large field, notably in the upper and lower right areas of the field (Fig. 8).

Discussion

The temporal variation in arthropod activity was expected given that counts were from broad taxonomic groups within which there would be species with differing phenologies and consequently their activity periods will vary, as found by Booij *et al.* (1995). Despite this there was considerable stability in the arthropod distributions between dates within each field, although this data was not presented. Totals for all sampling dates were used but nevertheless provide an indication of where activity was most concentrated during the assessment period. Arthropods are often assumed to be evenly distributed within arable fields (Wallin, 1986), although most of the arthropods examined in this study, in both years, exhibited some spatial pattern, with defined areas of high and low activity. This is in agreement with other research on polyphagous arthropods (Hengeveld, 1979; Duffield & Aebischer, 1994; Holopainen, 1995; Thomas *et al*., 1998). For most taxa examined here, the 30m sampling grid used in 1996 was of sufficient resolution to detect clusters, which often extended over areas larger than 1ha. There was a tendency for aggregation indices to be greater at this large scale, although this may be because the number of sample units was greatest for the large grid, so the power to detect spatial pattern was enhanced. In particular, clusters tend not to be detected by the SADIE methods unless more than about six neighbouring sample units all have above or below average counts. Hence, the smaller grids at the medium and small scales would have less chance of detecting clusters. However, aggregation was sometimes detected within the medium-sized grids (7.5m), but usually when this scale of pattern was itself nested hierarchically within patterns of greater size extending over distances greater than 30m. The small grid was inappropriate for most taxa because the mean was often lower than for the other scales; significant aggregation was never detected at this scale, although there was moderate clustering of Collembola and strong clustering of weed cover. During 1997, the significant ($P_a < 0.05$) aggregation within the large field shown by *B. lampros, P. madidus*, Carabidae and Collembola. By contrast, within the small field the sampling grid was usually too small to detect more than one cluster. Ideally grid size should be chosen according to the species under investigation, although some compromise is usually needed in multi-species evaluations. The SADIE indices provided a suitable means of assessing the size and significance of clusters which was not always apparent from their visual appearance when plotted, provided sufficent sampling points were used. These and other data have indicated that a minimum of 25 units is needed and preferably at least 36. Thus, sampling scale may have to be adjusted to ensure sufficient sampling points can be accommodated within the area under investigation.

There was considerable difference in the distributions detected between the medium-edge and medium-inner scales because some taxa, such as Lycosidae, predominantly inhabited the field edges. This highlights the importance of sample position and trap layout within a field and may explain why there are often considerable differences in arthropod capture between fields in large-scale studies (Holland *et al*., 1998). Unless sampling is very intensive, then the coincidence or otherwise of a sampling grid with clusters of relatively large population density is fortuitous. Much random error may be introduced by chance impositions of sampling areas onto unrepresentative areas of fields. Thus, studies within fields that use the replicated plot designs recommended for agrochemical assessments, may uncover considerable variation between plots prior to the imposition of treatments. Perry (1997) suggested that such assessments should always use these initial abundances as covariates.

Numbers of individual species collected over the duration of each experiment were sometimes insufficient for analysis. Capture rates could have been improved by using more traps at each sampling point, or by leaving them open for longer. However, in 1996 traps within the small scale were only 1.5m apart; more intensive trapping risked over-sampling, and subsequent population reduction. Mark-release-recapture techniques overcome this problem, but are suitable only for larger species and require a much greater sampling effort. At the 30m scale, more pitfall traps per sampling site would have been beneficial. The relatively small invertebrate capture rates within the organic winter wheat field in 1996 were unexpected. Suction samples from a 0.5m^2 area were also taken at each sampling location but with the exception of Collembola no other taxa were captured in sufficient numbers for analysis.

Some of the Carabidae sampled were predominantly found around the field edges, for example: *Amara* species and *B. lampros*. This would be expected for *Amara* species since they are spermophagous and weed cover was greatest at the field edges. *Amara* species were also found to consume arthropods including cereal aphids (Sunderland, 1975; Sunderland & Vickerman, 1987). The middle of arable fields is unlikely to provide sufficient seed resources for spermophagous species, except within the weedier areas, as demonstrated here by their spatial association with weed cover. *B. lampros* over-winter both within the field (Riedel, 1995) and the margins (Sotherton, 1984) and have been shown to disperse into the field during the summer (Coombes & Sotherton, 1986), returning to the field edges late in the season prior to hibernation (Wallin, 1987). These samples were collected during the summer, so *B. lampros* would be expected to be found distributed across the whole field, but in this study they were predominantly captured within 60m of the field edge.

The preference for the field edges also made it difficult to identify the size of clusters. In 1996 there were some isolated clusters of up to 90m width for *N. brevicollis*, however in 1997 within the large field clusters of carabid species extended over greater distances either linearly along field edges or across several hectares. Brust (1990) suggested that carabids establish burrows and foraging areas and remain within these unless the food supply diminishes. Larger species are able to forage over larger distances and they would be expected to occupy a greater area. Den Boer (1990) supports this view using the term metapopulation to describe these groups of local populations. Baars & Van Dijk (1984) estimated that individuals of *Pterostichus versicolor* Sturm (size 9-12mm) were moving around within an area of about 12.5ha. The smaller *Calathus melanocephalus* Linnaeus (6-9mm) was estimated to move around an area of 2ha. Because non-adjacent, individual fields were sampled in this study it was not possible to verify the presence of any metapopulations, although within fields clusters were smaller than those found above. An extensive study by Thomas *et al*. (1998) using mark-recapture demonstrated limited dispersal; the majority of *P. melanarius* were captured within 55m of their release site after 30 days. Areas of high activity-density were also detected, often only $10m^2$ even though they are capable of moving greater distances (Wallin & Ekbom, 1994).

Relatively little is known of the abiotic and biotic factors governing spatial distributions for individual species, especially within agroecosystems. Furthermore, these factors may or may not interact, so it is difficult to identify whether one or more factors govern the distribution of a species (Thiele, 1977). Many experiments have examined individual components of the likely environmental requirements. These were reviewed by Thiele (1977) and included climatic factors such as temperature and humidity; chemical factors, the most applicable to agroecosystems being soil pH and calcium content; and environmental structure such as the substrate. In the latter, aspects of soil type are likely to be important, but also surface composition and its penetrability. Some species showed a preference for leaf litter whilst others preferred open areas (Thiele, 1977). Similarly, in crops the density of weeds will determine the degree of cover and possibly of food abundance, and may also influence the microclimate. In this study it was only the spermophagous species that were associated with the weedier areas. These factors may also interact; for example, soil type may influence the moisture content and thereby the microclimate. Soil type also effects the substrate and suitability for burrowing, oviposition and over-winter survival.

The environmental requirements of the Araneae described here are less well known. Here, the Lycosidae favoured field edges. However, some variation between species in this family must be expected because their humidity requirements differ considerably between species (Pulz, 1987), as do their hunting strategies (Bristowe, 1971). In contrast, the Linyphiidae were relatively evenly distributed across all the fields and this would be expected given their powers of dispersal by ballooning (Meijer, 1977) and walking (Sunderland, 1987), as demonstrated by the rapidity with which they reinvade insecticide treated fields (Thomas *et al*., 1990).

These experiments were designed to explore the extent of arthropod spatial pattern within farmland and to test the potential of these novel statistical techniques. They revealed that there was considerable spatial heterogeneity for a range of arthropod taxa which warrants more detailed investigation and especially to identify the importance of abiotic and biotic factors in regulating their distributions. These will help determine whether habitat manipulation is possible and aid in the design of management practices to encourage polyphagous predators, as part of an integrated approach to crop protection. Spatial sampling can help this process because measurements are made using naturally-occurring distributions. The SADIE techniques were valuable in identifying when spatial pattern was present and v_i and v_j indices located these areas which was not possible with previous statistical methods.

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Table 1. Summary statistics comparing the effect of sample grid size in 1996. F values are from analysis of variance comparing grids. Indices I_a and its associated probability P_a indicate overall degree of clustering; values of I_a=1 indicate randomly arranged counts, while I_a>1 indicate aggregation of counts into clusters. $\bar{v}_j$ is the average over all inflows indicating presence of clustering into gaps with its associated probability of departure from randomness P_j. $\bar{v}_i$ is the average over all outflows indicating patchiness with its associated probability of departure from randomness P_i.

Scale	Mean	I_a	P_a	$\bar{v}_j$	P_j	$\bar{v}_i$	P_i
Nebria brevicollis (F=2.9*)							
Large	4.1	1.73	0.005	-1.67	0.001	1.74	0.001
Medium edge	2.2	1.19	0.12	-1.09	0.23	1.33	0.03
Medium inner	3.5	0.78	0.95	-0.79	0.94	0.87	0.80
Small	3.7	0.84	0.86	-0.79	0.96	0.84	0.88
Carabidae (F=21.5***)							
Large	14.9	1.49	0.01	-1.53	0.008	1.30	0.05
Medium edge	15.0	1.19	0.14	-1.34	0.04	1.15	0.16
Medium inner	7.0	0.82	0.88	-0.71	0.80	0.80	0.94
Small	7.3	0.85	0.76	-0.92	0.66	0.93	0.63
Linyphiidae (F=8.6***)							
Large	74.7	1.21	0.11	-1.14	0.18	1.11	0.20
Medium edge	85.2	1.10	0.23	-1.15	0.13	1.14	0.16
Medium inner	79.6	1.11	0.25	-1.21	0.09	1.15	0.15
Small	55.6	1.02	0.40	-1.03	0.33	1.04	0.33
Lycosidae (F=20.2***)							
Large	15.2	1.63	0.003	-1.61	0.004	1.64	0.002
Medium edge	14.0	1.59	0.005	-1.45	0.004	1.27	0.06
Medium inner	4.8	1.02	0.38	-1.11	0.23	1.04	0.33
Small	3.3	1.24	0.08	-1.20	0.10	1.11	0.19
Collembola (F=65.6***)							
Large	46.6	1.07	0.29	-0.97	0.51	1.10	0.24
Medium edge	29.8	1.03	0.41	-1.05	0.30	0.92	0.67
Medium inner	16.8	1.28	0.07	-1.13	0.19	1.25	0.07
Small	2.87	1.24	0.08	-1.23	0.09	1.23	0.09
Weed cover							
Large	15.9	1.17	0.13	-1.13	0.18	1.05	0.31
Medium edge	11.0	0.86	0.77	-1.05	0.30	0.92	0.67
Medium inner	10.2	1.77	0.005	-1.61	0.001	2.00	0.001
Small	2.6	1.14	0.18	-1.23	0.09	1.23	0.09

Table 2. Association statistics comparing arthropod and weed distributions in the different grids during 1996. Data sets are associated if $I_t>1$ and dissociated if $I_t<1$. Values P_t indicate the significance of associations for I_t.

	r	I_t	P_t
Nebria brevicollis			
Large	0.14	0.90	0.71
Medium edge	0.16	1.0	0.49
Medium inner	-0.04	1.0	0.53
Small			
Carabidae			
Large	-0.08	0.99	0.52
Medium edge	0.44	1.13	0.15
Medium inner	-0.11	0.94	0.81
Small	-0.01	1.03	0.32
Linyphiidae			
Large	0.25	1.10	0.12
Medium edge	-0.03	0.99	0.70
Medium inner	0.03	1.0	0.54
Small	0.07	1.04	0.13
Lycosidae			
Large	0.33	1.24	0.05
Medium edge	0.16	1.11	0.13
Medium inner	0.15	1.04	0.40
Small	0.12	1.21	0.09
Collembola			
Large	-0.28	1.0	0.48
Medium edge	0.17	0.99	0.53
Medium inner	-0.49	0.75	0.86
Small	0.06	0.88	0.74

Table 3. Summary statistics comparing the effect of field size in 1997. Indices I_a and its associated probability P_a indicate overall degree of clustering; values of I_a=1 indicate randomly arranged counts, while I_a>1 indicate aggregation of counts into clusters. $\bar{v}_j$ is the average over all inflows indicating presence of clustering into gaps with its associated probability of departure from randomness P_j. $\bar{v}_i$ is the average over all outflows indicating patchiness with its associated probability of departure from randomness P_i.

Field size	Mean	I_a	P_a	$\bar{v}_j$	P_j	$\bar{v}_i$	P_I
Pitfall sampling							
Amara spp.							
Large	1.8	1.24	0.09	-1.20	0.12	1.07	0.26
Small	3.3	1.55	0.005	-1.54	0.01	1.76	0.002
Bembidion lampros							
Large	7.7	1.39	0.03	-1.32	0.05	1.28	0.05
Small	6.4	1.22	0.13	-1.10	0.23	1.40	0.03
Pterostichus madidus							
Large	13.2	1.65	0.003	-1.41	0.02	1.42	0.02
Small	9.9	1.02	0.38	-1.08	0.28	0.88	0.70
Carabidae							
Large	38.8	2.0	0.005	-1.86	0.001	2.06	0.001
Small	33.6	1.57	0.008	-1.49	0.02	1.33	0.04
Linyphiidae							
Large	28.8	1.25	0.08	-1.21	0.10	1.21	0.10
Small	28.1	1.04	0.35	-1.03	0.36	1.04	0.35
Lycosidae							
Large	6.4	1.10	0.25	-1.09	0.24	1.17	0.14
Small	6.5	0.99	0.42	-0.93	0.59	1.0	0.41
Collembola							
Large	22.0	1.47	0.01	-1.26	0.04	1.35	0.03
Small	25.9	1.14	0.20	-1.04	0.34	1.34	0.05
Weed cover							
Large	4.09	1.02	0.40	-1.51	0.01	1.51	0.01
Small	17.3	1.89	0.003	-1.83	0.001	1.27	0.08

Table 4. Association statistics for arthropods with weed cover in 1997. Data sets are associated if $I_t > 1$ and dissociated if $I_t < 1$. Values P_t indicate the significance of associations for I_t.

	Large field			Small field		
	r	I_t	P_t	r	I_t	P_t
Amara spp.	0.23	1.14	0.07	0.27	1.44	0.19
B. lampros	-0.09	1.04	0.33	-0.14	1.03	0.44
P. madidus	0.03	0.93	0.70	-0.16	1.12	0.18
Carabidae	0.24	1.13	0.37	-0.03	1.17	0.33
Linyphiidae	0.18	1.09	0.21	0.14	1.08	0.15
Lycosidae	0.15	1.12	0.15	-0.14	1.08	0.26
Collembola	0.26	1.27	0.02	0.14	1.15	0.26

Figure 1. Location of pitfall traps within a winter wheat field in 1996. For the large grid the pitfall traps are arranged in an approximately 30m spacing. For the medium edge (ME) and medium inner grids (MI) the traps are at 7.5m spacing, with the small grid using 1.5m spacing positioned within one corner of the medium inner grid.

Figure 2. Temporal variation in the capture of arthropods in the pitfall traps. Values presented for arthropods from the pitfall traps are total counts per sample date from the four grids located in a winter wheat field during 1996.

Figure 3. Arthropod counts and percentage weed cover sampled on an approximately rectangular 30m grid in a winter wheat field during 1996, categorised by interpolated contouring into equally spaced shaded density classes. Above-average clustering at each sample unit into patches of greater than average neighbouring counts is measured by the clustering index, v_i. Below-average clustering creating gaps of less than average neighbouring counts is measured by the clustering index, v_j. Strong clustering into patches is indicated by units surrounded by circles with $1.5< v_i$. Strong evidence of gaps is indicated by units surrounded by squares with $1.5< v_j$. In each case, the average value of the patch clustering for the entire sample, $\bar{\bar{v}}_i$, is shown above the map, together with its statistical significance on the null hypothesis that the observed counts were arranged randomly amongst the sample units.

Figure 4. Arthropod counts and percentage weed cover sampled on a 7.5m grid located at the edge of a winter wheat field during 1996, categorised by interpolated contouring into equally spaced shaded density classes. Notation, methodology and symbols are the same as in figure 2.

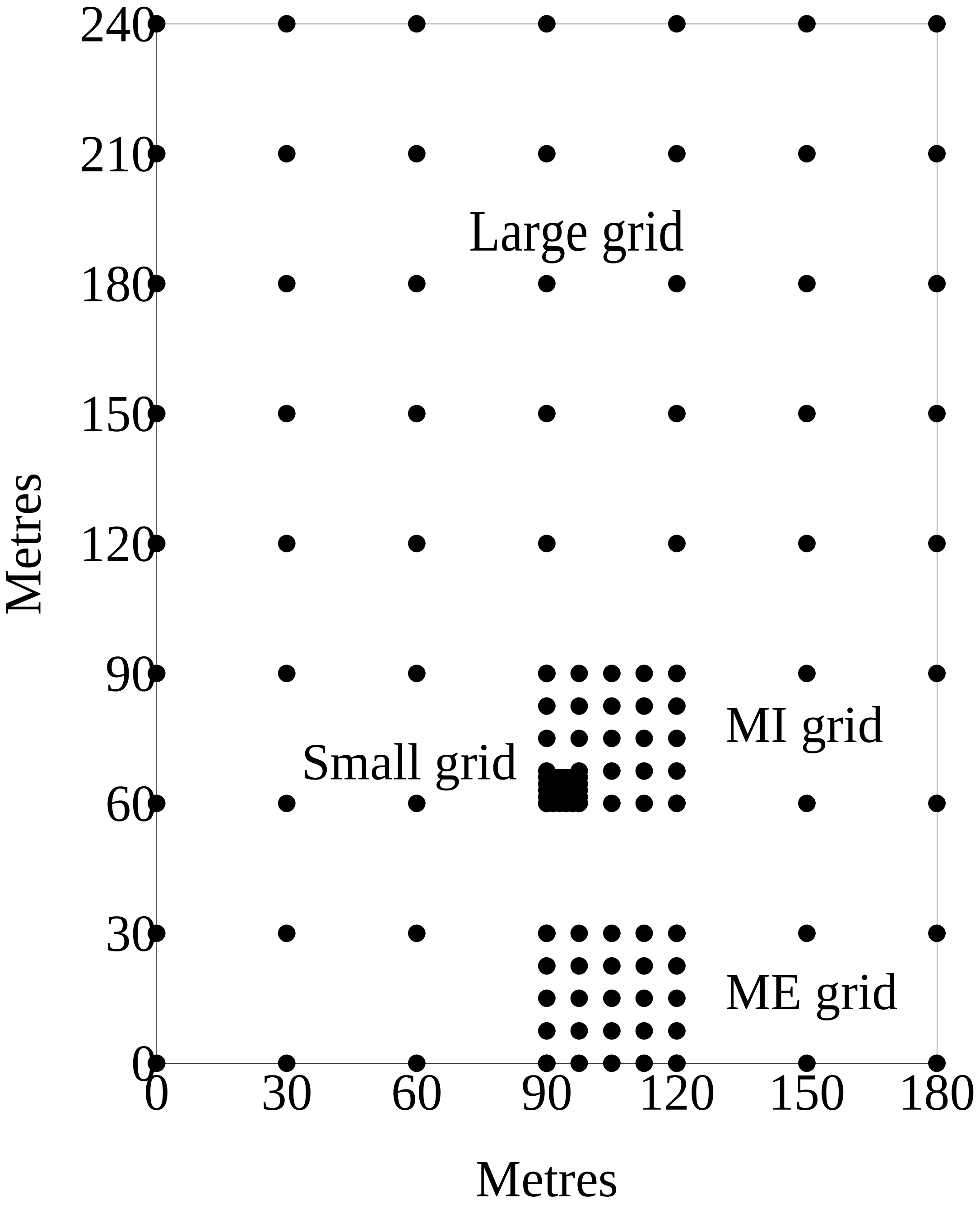
Figure 5. Arthropod counts and percentage weed cover sampled on a 7.5m grid located within the centre of a winter wheat field during 1996, categorised by interpolated contouring into equally spaced shaded density classes. Notation, methodology and symbols are the same as in figure 2.

Figure 6. Arthropod counts and percentage weed cover sampled on a 1.5m grid, positioned within one corner of the 7.5m grid located in the centre of a winter wheat field during 1996. Counts were categorised by interpolated contouring into equally spaced shaded density classes. Notation, methodology and symbols are the same as in figure 2.

Figure 7. Temporal variation in the capture of arthropods in the pitfall traps. Values presented for arthropods from the pitfall traps are total counts per sample date from the large field and small winter wheat fields during 1997.

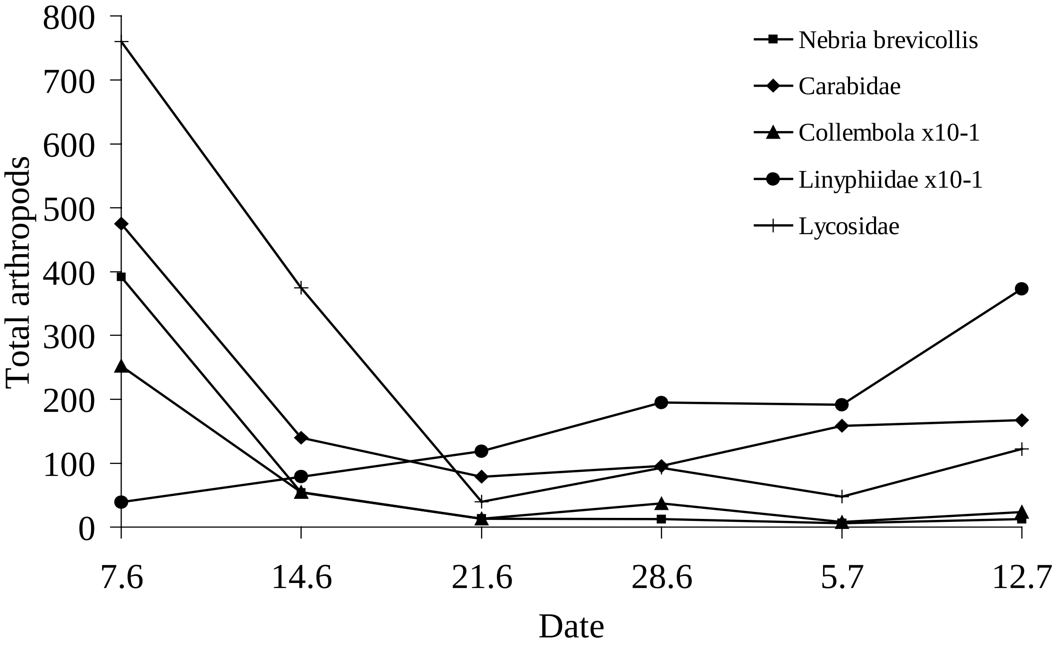
Figure 8. Arthropod counts and percentage weed cover sampled on an approximately 30m grid across the whole of a large (16ha) winter wheat field during 1997, categorised by interpolated contouring into equally spaced shaded density classes. Notation, methodology and symbols are the same as in figure 2.

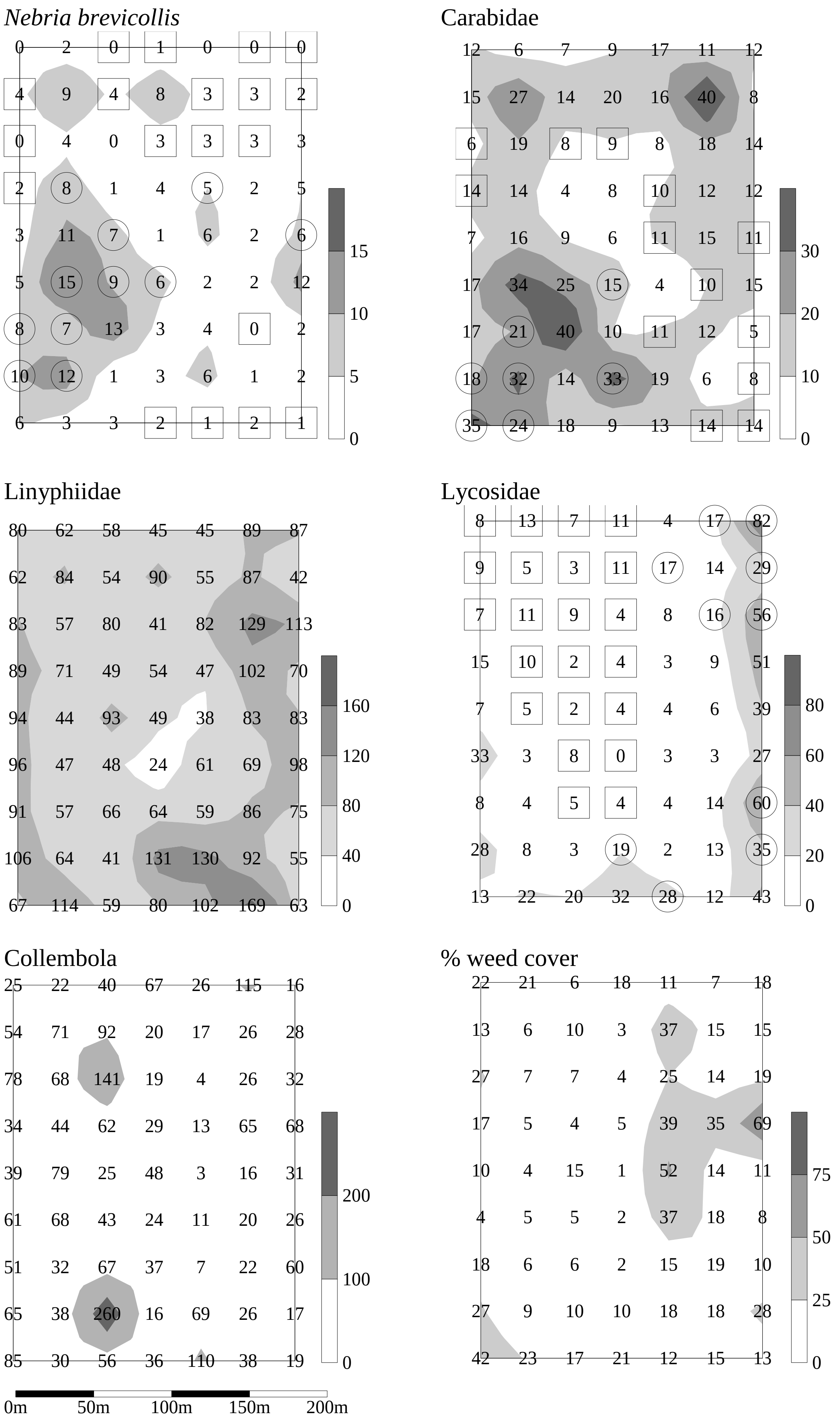
Figure 9. Arthropod counts and percentage weed cover sampled on an approximately 30m grid across the whole of a small (4ha) winter wheat field during 1997, categorised by interpolated contouring into equally spaced shaded density classes. Notation, methodology and symbols are the same as in figure 2.



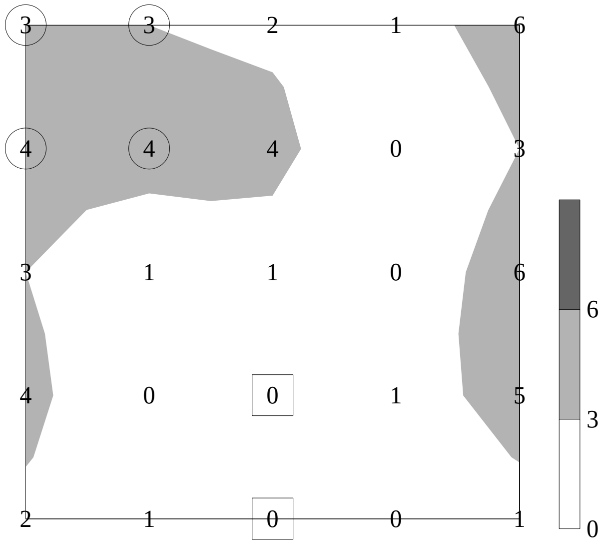
240
210
180
150
120
90
60
30
0
Metres
Large grid
MI grid
Small grid
ME grid
0
30
60
90
120
150
180
Metres

Fig. 2

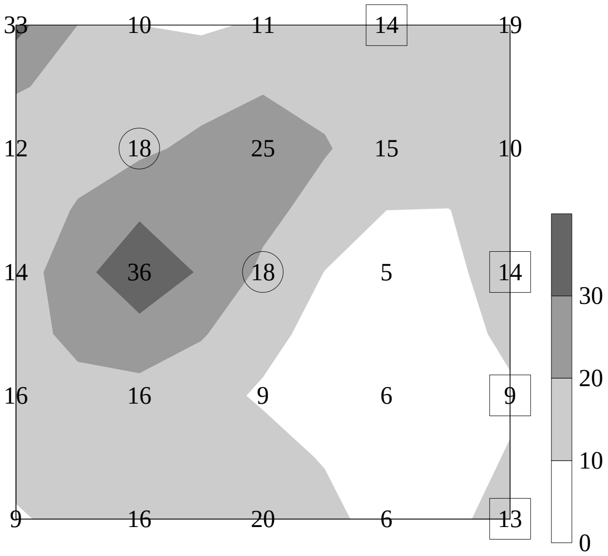

800
700
600
500
400
300
200
100
0
Total arthropods
7.6
14.6
21.6
28.6
5.7
12.7
Date
Nebria brevicollis
Carabidae
Collembola x10-1
Linyphiidae x10-1
Lycosidae


Nebria brevicollis
0 2 0 1 0 0 0
4 9 4 8 3 3 2
0 4 0 3 3 3 3
2 8 1 4 5 2 5
3 11 7 1 6 2 6
5 15 9 6 2 2 12
8 7 13 3 4 0 2
10 12 1 3 6 1 2
6 3 3 2 1 2 1
15
10
5
0
Carabidae
12 6 7 9 17 11 12
15 27 14 20 16 40 8
6 19 8 9 8 18 14
14 14 4 8 10 12 12
7 16 9 6 11 15 11
17 34 25 15 4 10 15
17 21 40 10 11 12 5
18 32 14 33 19 6 8
35 24 18 9 13 14 14
30
20
10
0
Linyphiidae
80 62 58 45 45 89 87
62 84 54 90 55 87 42
83 57 80 41 82 129 113
89 71 49 54 47 102 70
94 44 93 49 38 83 83
96 47 48 24 61 69 98
91 57 66 64 59 86 75
106 64 41 131 130 92 55
67 114 59 80 102 169 63
160
120
80
40
0
Lycosidae
8 13 7 11 4 17 82
9 5 3 11 17 14 29
7 11 9 4 8 16 56
15 10 2 4 3 9 51
7 5 2 4 4 6 39
33 3 8 0 3 3 27
8 4 5 4 4 14 60
28 8 3 19 2 13 35
13 22 20 32 28 12 43
80
60
40
20
0
Collembola
25 22 40 67 26 115 16
54 71 92 20 17 26 28
78 68 141 19 4 26 32
34 44 62 29 13 65 68
39 79 25 48 3 16 31
61 68 43 24 11 20 26
51 32 67 37 7 22 60
65 38 260 16 69 26 17
85 30 56 36 110 38 19
200
100
0
% weed cover
22 21 6 18 11 7 18
13 6 10 3 37 15 15
27 7 7 4 25 14 19
17 5 4 5 39 35 69
10 4 15 1 52 14 11
4 5 5 2 37 18 8
18 6 6 2 15 19 10
27 9 10 10 18 18 28
42 23 17 21 12 15 13
75
50
25
0
0m
50m
100m
150m
200m

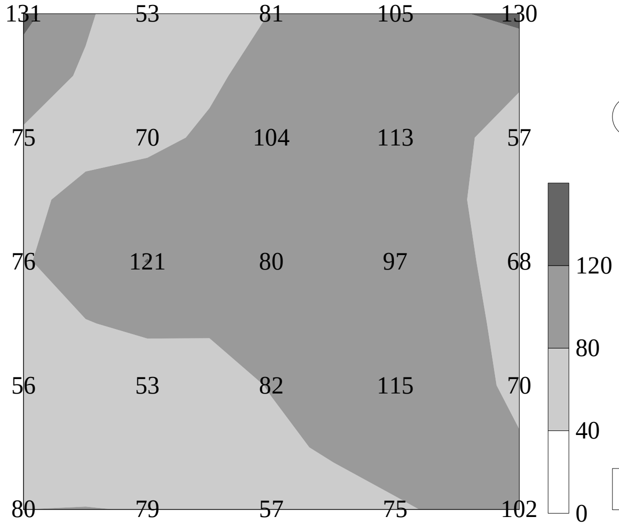
Nebria brevicollis



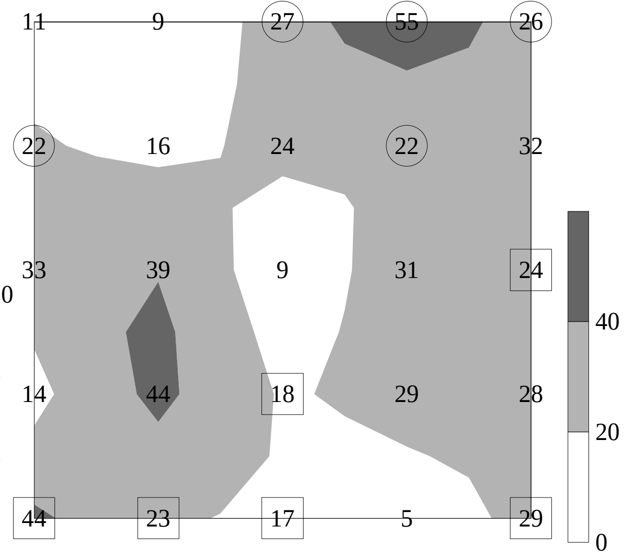
Carabidae



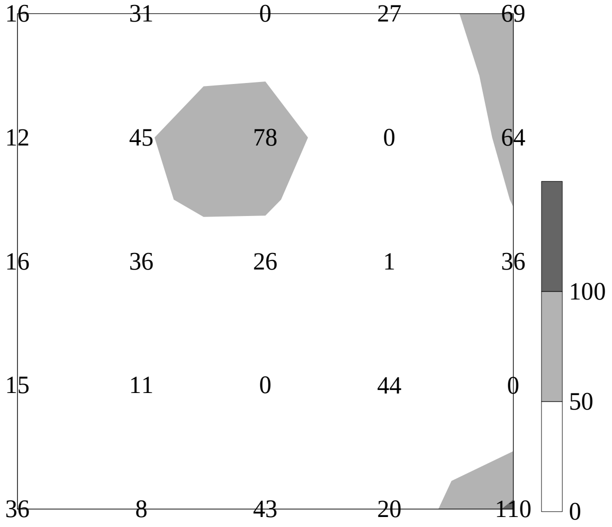
Linyphiidae



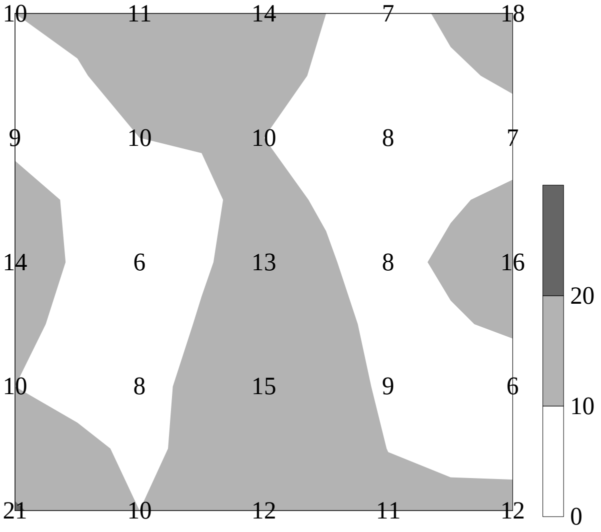
Lycosidae



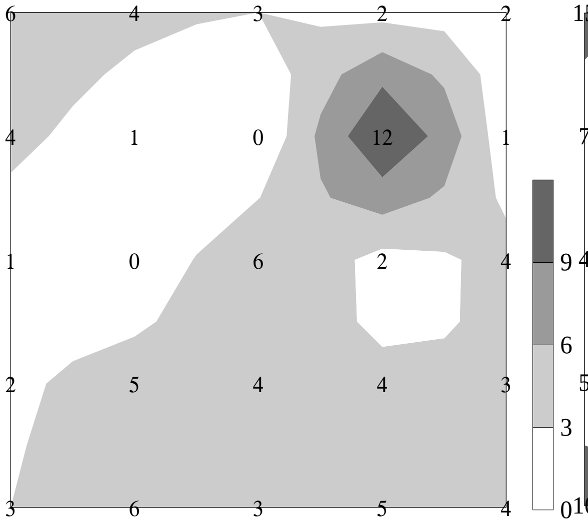
Collembola



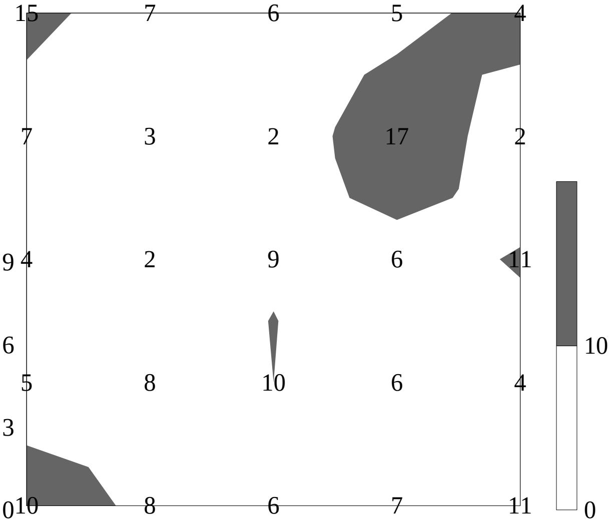
% weed cover



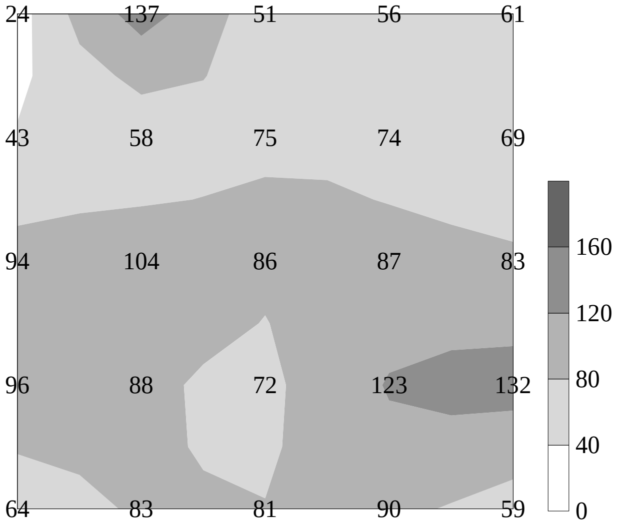
Nebria brevicollis



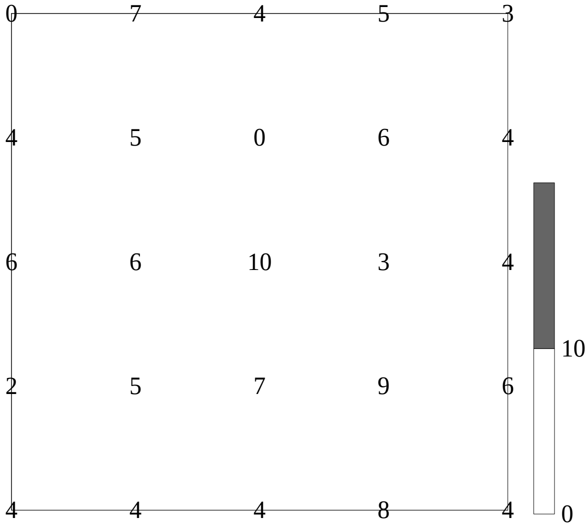
Carabidae



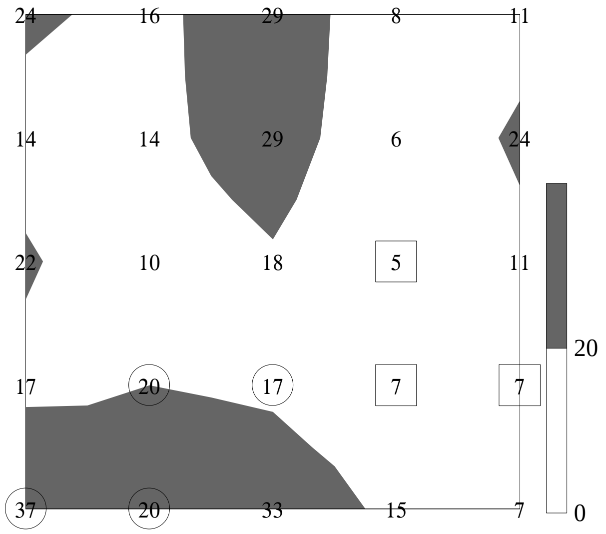
Linyphiidae



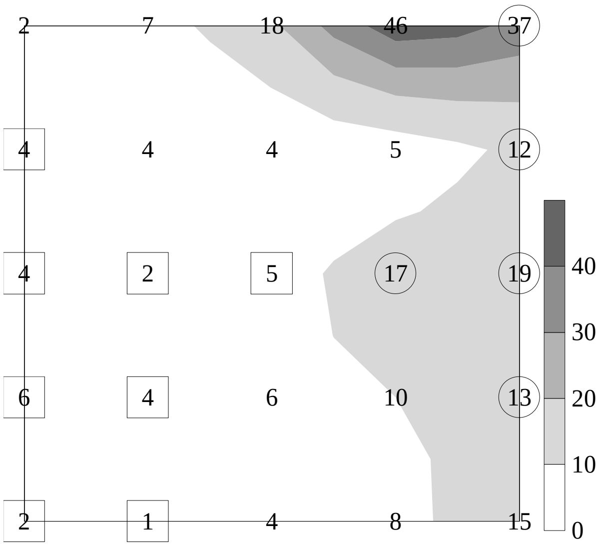
Lycosidae



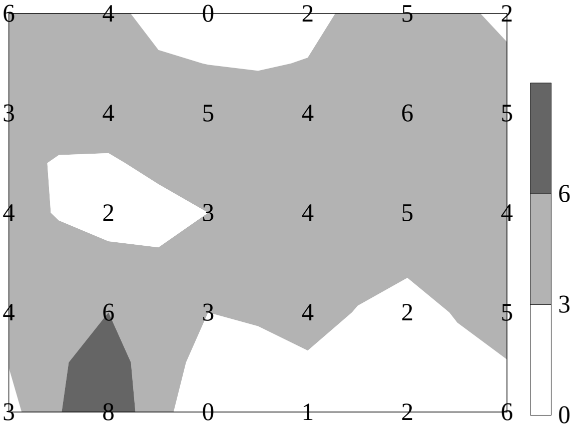
Collembola



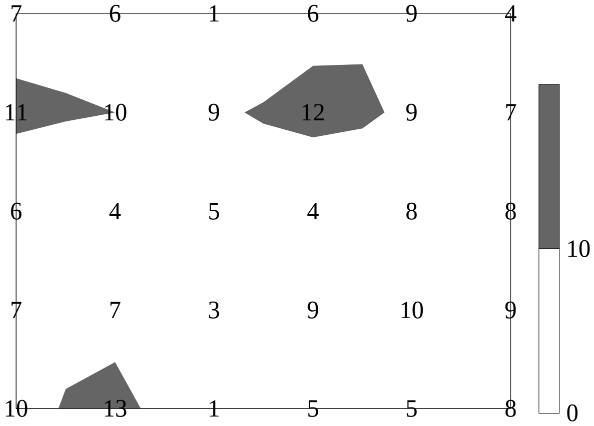
% weed cover



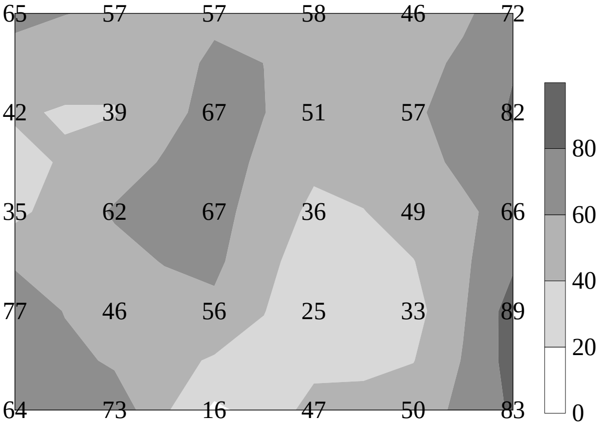
Nebria brevicollis



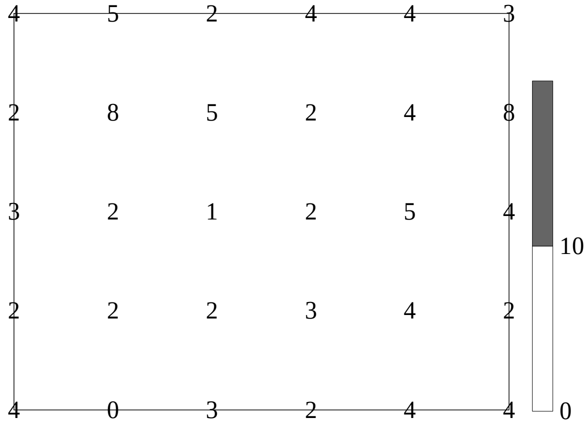
Carabidae



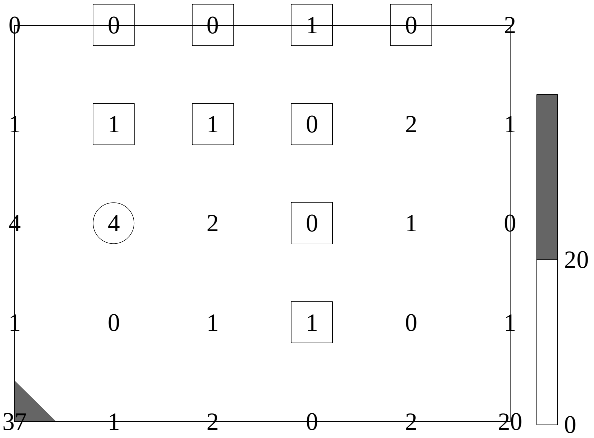
Linyphiidae



Lycosidae



Collembola



% weed cover

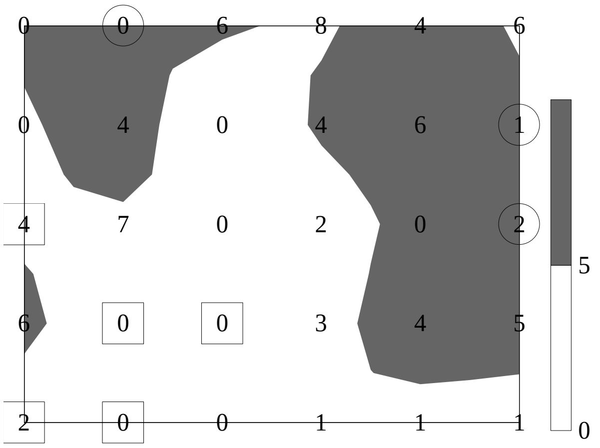
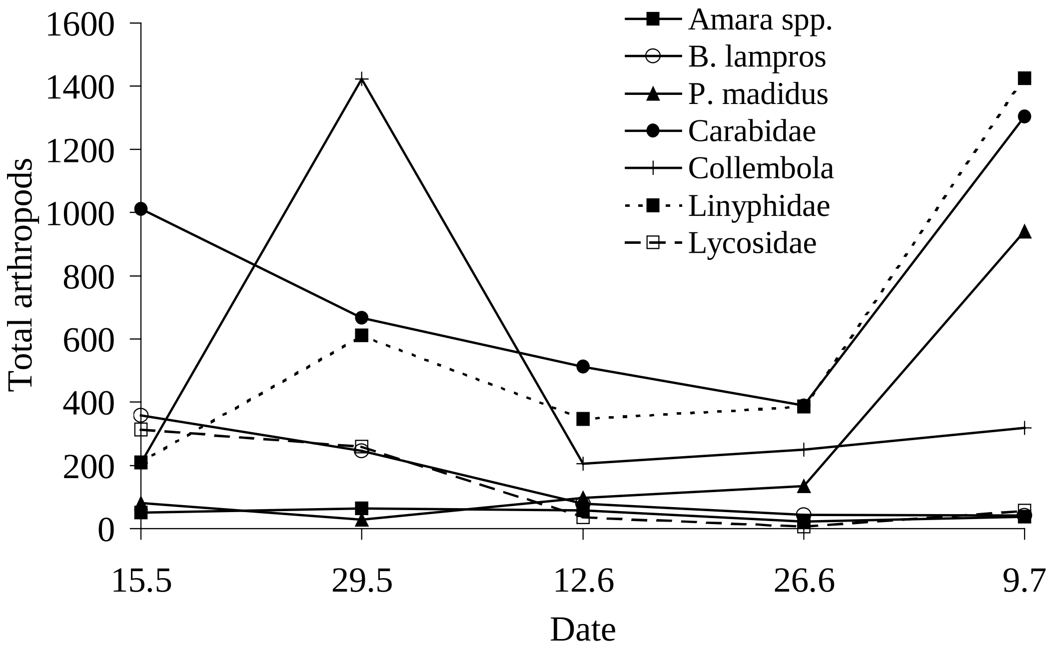
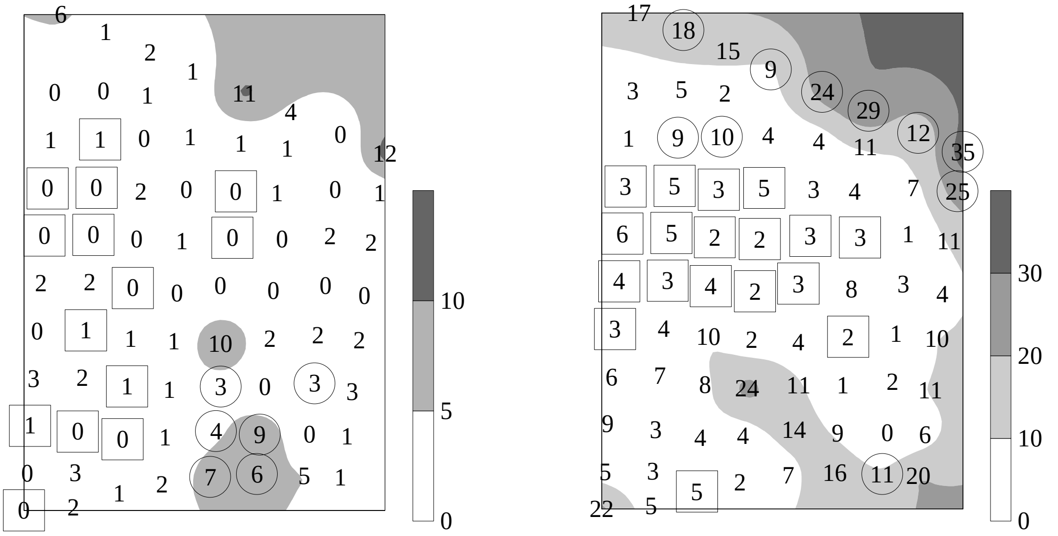


Fig. 7



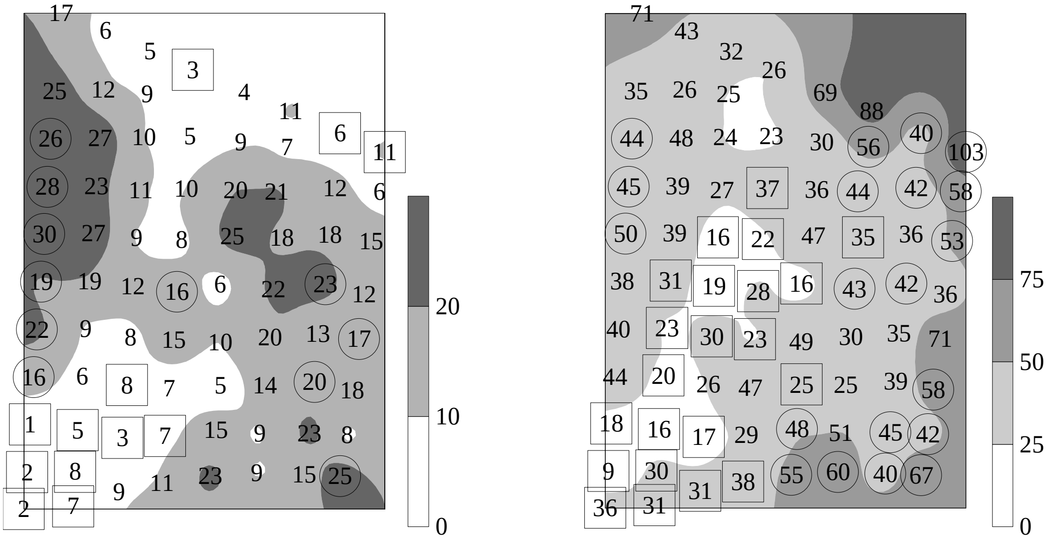
Amara spp.
B. lampros
P. madidus
Carabidae
Collembola
Linyphidae
Lycosidae
Total arthropods
1600
1400
1200
1000
800
600
400
200
0
15.5
29.5
12.6
26.6
9.7
Date

Figure 8 (eight parts over two pages)



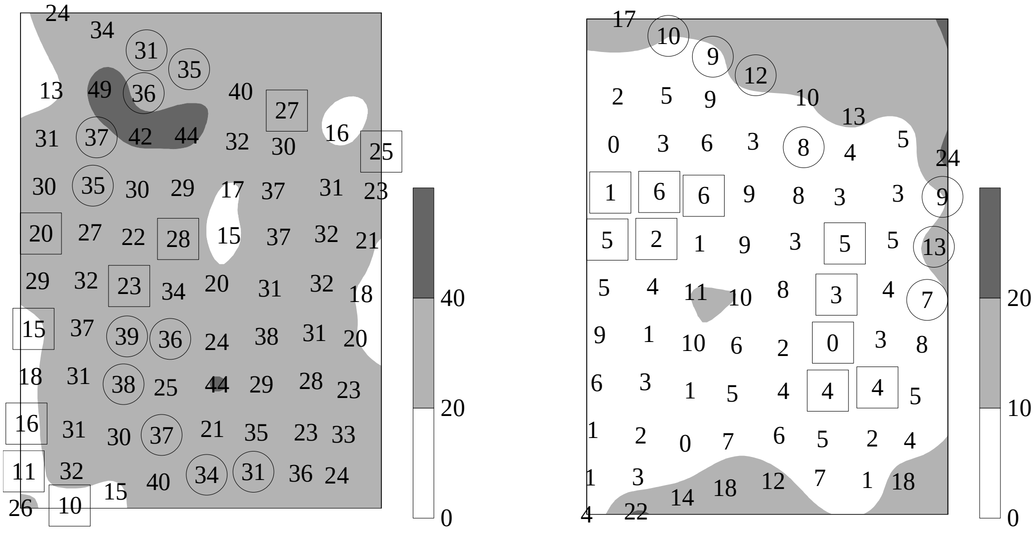
Amara spp. (Coleoptera: Carabidae)

Bembidion lampros (Coleoptera: Carabidae)



Pterostichus madidus (Coleoptera: Carabidae)

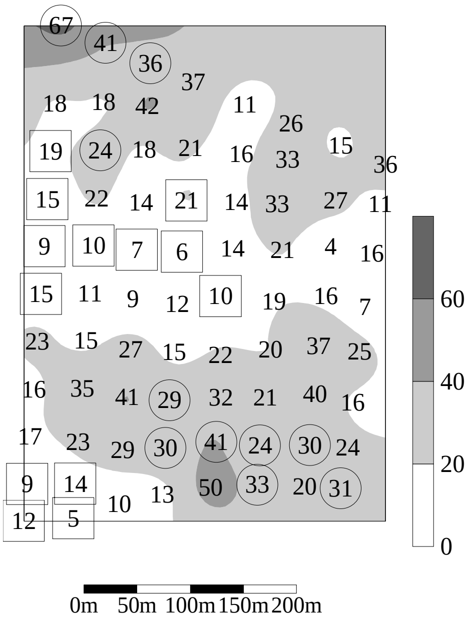
Carabidae



Linyphiidae

Lycosidae

Collembola



% weed cover

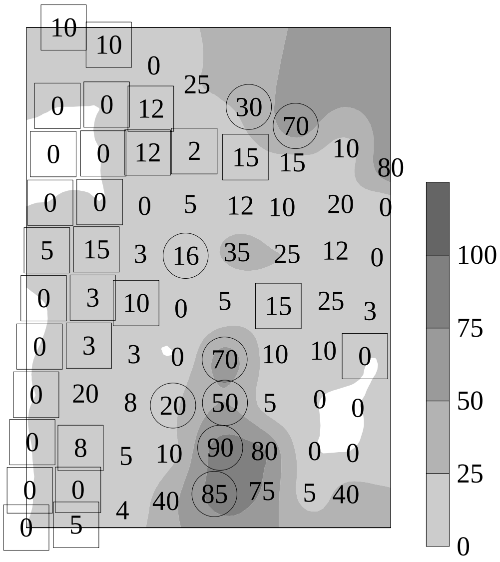
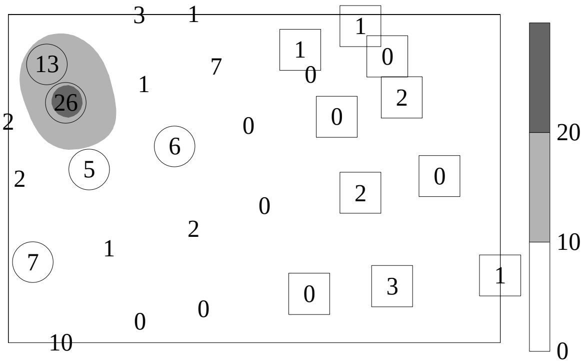
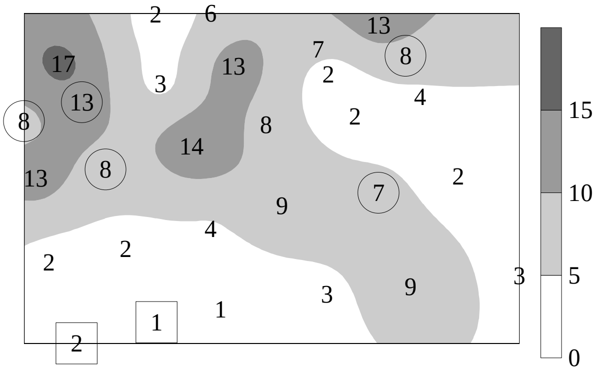


Figure 9

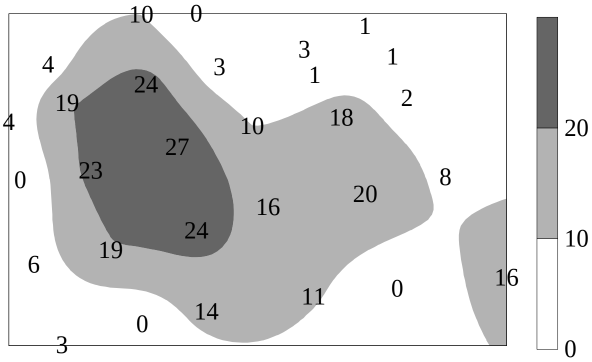
Amara spp. (Coleoptera: Carabidae)



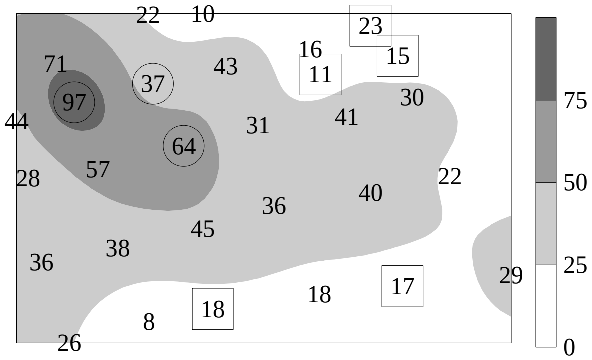
Bembidion lampros (Coleoptera: Carabidae)



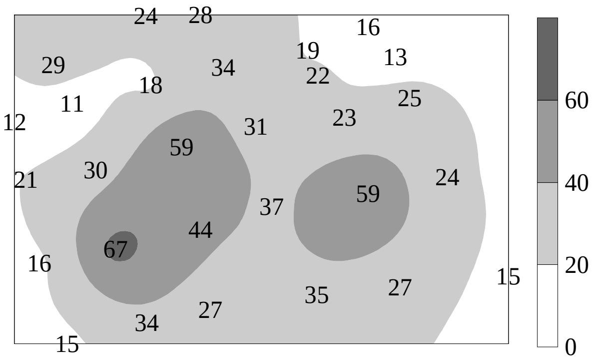
Pterostichus madidus (Coleoptera: Carabidae)



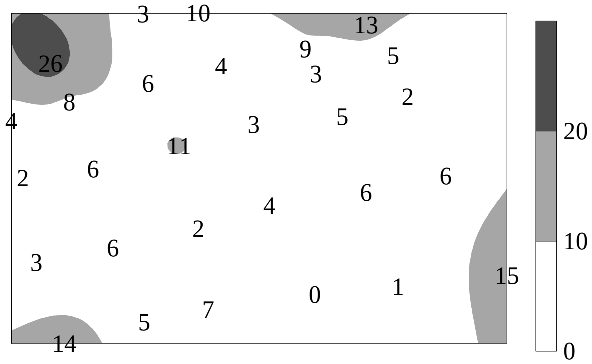
Carabidae



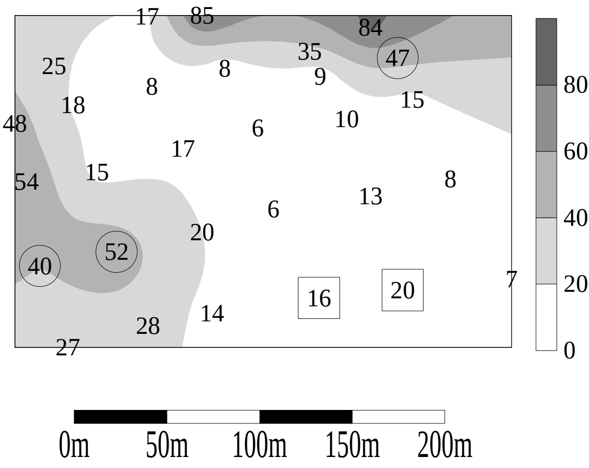
Linyphiidae



Lycosidae



Collembola



% weed cover