

Do predators aggregate in response to pest density in agroecosystems? Assessing within-field spatial patterns

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Summary

1. The spatial heterogeneity of predator populations is an important component of ecological theories pertaining to predator–prey dynamics. Most studies within agricultural fields show spatial correlation (positive or negative) between mean predator numbers and prey abundance across a whole field over time but generally ignore the within-field spatial dimension. We used explicit spatial mapping to determine if generalist predators aggregated within a soybean field, the size of these aggregations and if predator aggregation was associated with pest aggregation, plant damage and predation rate.

2. The study was conducted at Gatton in the Lockyer Valley, 90 km west of Brisbane, Australia. Intensive sampling grids were used to investigate within-field spatial patterns. The first row of each grid was located in a lucerne field (10 m from interface) and the remaining rows were in an adjacent soybean field. At each point on the grid the abundance of foliage-dwelling and ground-dwelling pests and predators was measured, predation rates [using sentinel *Helicoverpa armigera* (Hübner) egg cards] and plant damage were estimated. Eight grids were sampled across two summer cropping seasons (2000/01, 2001/02).

3. Predators exhibited strong spatial patterning with regions of high and low abundance and activity within what are considered to be uniform soybean fields. Ground-dwelling and foliage-dwelling predators were often aggregated in patches approximately 40 m across.

4. Lycosidae (wolf spiders) displayed aggregation and were consistently more abundant within the lucerne, with a decreasing trap catch with distance from the lucerne/soybean interface. This trend was consistent between subsequent grids in a single field and between fields.

5. The large amount of spatial variability in within-field arthropod abundance (pests and predators) and activity (egg predation and plant damage) indicates that whole field averages were misleading. This result has serious implications for sampling of arthropod abundance and pest management decision-making based on scouting data.

6. There was a great deal of temporal change in the significant spatial patterns observed within a field at each sampling time point during a single season. Predator and pest aggregations observed in these fields were generally not stable for the entire season.

7. Predator aggregation did not correlate consistently with pest aggregation, plant damage or predation rate. Spatial patterns in predator abundance were not associated consistently with any single parameter measured. The most consistent positive association was between foliage-dwelling predators and pests (significant in four of seven grids). Inferring associations between predators and prey based on an intensive one-off sampling grid is difficult, due to the temporal variability in the abundance of each group.

8. *Synthesis and applications.* This study demonstrated that generalist predator populations are rarely distributed randomly and field edges and adjacent crops can have an influence on within-field predator abundance. This must be considered when estimating arthropod (pest and predator) abundance from a set of samples taken at random locations within a field.

Introduction

A growing awareness of the negative impacts of widespread synthetic insecticide use has led to the greater adoption of integrated pest management programmes (IPM). These rely on a sound knowledge of the ecology and population biology of both pest and beneficial species within agricultural systems. In particular, sampling schemes designed for scouting of pest and beneficial natural enemy abundance (prior to insecticide application) often assume that the population is distributed randomly across the field (tested by Dillon & Fitt 1990; Dillon 1992). However, evidence from a growing number of studies (Holland *et al.* 1999; Ferguson *et al.* 2000, 2003; Thomas *et al.* 2001) suggests that this assumption is unjustified. The within-field abundance and activity of arthropods is often patchy (Hughes 1996), in common with dispersion patterns found in biological communities (Bishop 1981; Legendre & Fortin 1989; Southwood & Henderson 2000). The recent interest in precision farming stems from the realization that it is impractical to view a field as homogeneous in terms of yield potential, crop, soil and growth characteristics (Blackmore 1994; Sylvester-Bradley *et al.* 1999). It is expected that fields of the size utilized in some intensive agricultural regions (100 ha or greater) will show some degree of heterogeneity in both crop characteristics and arthropod distribution (Schotzko & Quisenberry 1999). A greater knowledge of the spatial pattern of pest populations can be used to design more targeted insecticide applications (termed Precision Integrated Pest Management) and so contribute to site-specific resistance management programmes (Blom & Fleischer 2001; Blom *et al.* 2002). Furthermore, spatial data on predator populations can be combined with physical and environmental measurements to reveal a great deal about their ecological requirements.

The spatial heterogeneity of predator populations is an important component of the ecological theories pertaining to predator–prey dynamics (Kareiva 1990). The aggregation of predators around areas of high prey abundance contributes to the numerical response of the predator. The numerical and functional responses influence the impact of predators on prey populations (Hassell & May 1986; Kareiva 1987). Despite its importance little field research has been conducted on patterns of predator abundance within fields. Bishop (1981) found that three spider species were equally distributed in the outer, middle and inner portions of a cotton field throughout most of the season and corre-

sponded well with the location of their prey. Holland *et al.* (1999) used a grid of pitfall traps to investigate arthropod spatial abundance patterns in wheat. Linyphiidae were relatively homogeneous across the fields but Collembola displayed evidence of clustering. Thomas *et al.* (2001) found that carabid species in a barley field were aggregated most of the time and each taxa preferred different areas of the field and field margin habitats. *Helicoverpa* spp. egg cards have been used to investigate spatial and temporal variation in egg predation and parasitism in sweetcorn fields (Scholz 2000). *Trichogramma* parasitoids foraged over the entire field throughout the vegetative stage of the crop but the action of Formicidae was restricted to the crop edges.

An intensive spatially explicit sampling scheme is required to answer questions about the spatial patterns of arthropod abundance within fields. Spatially explicit sampling, while being labour-intensive, can provide valuable information about pest and beneficial dynamics within the crop, which may lead to better management decisions (Hughes 1996). A characteristic of a successful biological control agent is their ability to locate and extinguish patches of high prey abundance, termed ‘spatially density-dependent mortality’ (Walde & Murdoch 1988; Kareiva 1990). Kareiva (1990) suggests that the rate of aggregation is an important factor in prey suppression. If a predator’s rate of aggregation is slow they may be overwhelmed by local reproduction of the prey. Examples of field studies that investigate spatially density-dependent mortality are rare. Most studies demonstrate spatial correlation (positive or negative) between predators and prey across a whole field over time but ignore the within-field spatial dimension. Even more unusual are studies that include the temporal dimension. Recently, some studies have begun to use intensive within field sampling combined with spatial pattern analysis to investigate the spatial distribution of predators and prey. Winder *et al.* (2001) investigated spatio-temporal dynamics of two aphid species and a predatory carabid at the field scale. There was transient spatial structure for individual species abundance and spatially coupled dynamics between species. Warner *et al.* (2003) found that two carabid species were spatially associated with the larvae of *Psylliodes chrysocephala* (L.) (Coleoptera: Chrysomelidae), a pest of oilseed rape. Polyphagous predators (carabids and staphylinids) have been shown to aggregate to patches of high aphid density in a wheat field (Bryan & Wratten 1984). Despite these studies there is little direct field evidence that generalist predators

aggregate to locally high pest densities as theory predicts (Murdoch *et al.* 1998).

A key problem associated with estimating predator–prey interactions using intensive sampling schemes is that the spatial patterns observed are often difficult to interpret. If two populations are sampled at a single point in time the spatial pattern observed will be influenced by the temporal pattern in predator–prey population interaction and growth. Despite difficulties with interpretation, spatially explicit, large-scale field studies are necessary for understanding fundamental predator–prey dynamics (Winder *et al.* 2001) as well as for many applied aspects of pest management sampling schemes. We used spatially explicit sampling and mapping techniques to investigate the within-field spatial patterns of predator abundance, pest abundance, estimates of predator impact on prey using *Helicoverpa armigera* (Hübner) egg cards and plant damage. An intensive grid sampling scheme across the interface between soybean and adjacent lucerne fields was used to answer the following questions: (i) do generalist predators aggregate in patches within a soybean field; (ii) what is the size of these aggregations; and (iii) does predator aggregation correlate with pest aggregation, plant damage or predation rate?

Materials and methods

Within-field spatial patterns were investigated using 42 sampling sites 20 m from each other in a 100 × 120 m grid. The X and Y co-ordinates of each sampling site were recorded. This large sampling grid was found to be best suited for detecting aggregation in the predator taxa sampled during preliminary experiments (Pearce 2004). The first row of the grid was located within the lucerne field (10 m from the interface) and the remaining rows in the adjacent soybean field (first row 10 m from the interface). In total, eight such grids were sampled across two summer cropping seasons (2000/01 and 2001/02).

SAMPLING SITES

The experimental fields were located at the Gatton campus (27°34' S, 152°20' E) of the University of Queensland in the Lockyer Valley, Queensland. A wide variety of crops are grown in the region, including irrigated and non-irrigated grain crops, forage crops and horticultural crops. In summer temperature ranges from a maximum of 35 °C to a minimum of 15 °C. The study coincided with a severe drought in the region with lower than average rainfall recorded in both summer seasons.

In the first season (2000/01) three grids in two fields (Mendel 3.2 ha and Horti 4.4 ha) were sampled. In Horti one grid was sampled at the beginning (13 February 2001) of the growing season, and in Mendel two grids were sampled at the beginning (3 March 2001) and middle (1 April 2001) of the growing season. In both

fields soybean (cv. Cawana) was planted in rows (75 cm row spacing) during the last week of December 2000. The adjacent lucerne fields (Mendel, cv. Sceptere and Horti, cv. Sequel/L69) were planted 2 years previously. Horti field was different to the other sites in that there was a grass road (5 m in width) separating the soybean from adjacent lucerne. This site had previously been a horticultural cropping area so the grid was divided up into smaller plots by grassy roads (but all 42 sampling sites were located in the soybean).

In the second season (2001/02) five grids in two fields (Gilbert A 5.5 ha and Gilbert C 8.8 ha) were sampled. In Gilbert A two grids were sampled per season, once at the beginning (14 January 2002) and once in the middle (15 March 2002) of the soybean growing season. In Gilbert C three grids were sampled at the beginning (14 January 2002), middle (27 February 2002) and end (3 April 2002) of the growing season. The grid in Gilbert A was extended to include the weedy margin on the other side of the soybean (51 sampling sites in the grid). In both fields soybean (cv. Warrigal) was planted in rows (75 cm row spacing) in the first week of December 2001. The adjacent lucerne (cv. Hallmark/Sequel HR) was planted early in the same year. In both seasons the soybean was cultivated inter-row to reduce weeds, irrigated when necessary, but no insecticides were applied.

SAMPLING TECHNIQUES

The lucerne was cut and bailed approximately every 4 weeks during the summer months. Grid sampling lasted for 5 days (the length of time pitfall traps were open) and commenced 1 week after the adjacent lucerne field had been cut, which allowed time for the lucerne to be dried and bailed. Day-active, plant-dwelling arthropods were collected using a vacuum sampler (Echo PB-2105) with a 12 cm diameter plastic tube attached over the intake fan. A collection bag (0.5 mm mesh, 20 cm diameter opening and 40 cm in length) was placed in the nozzle of the tube to trap arthropods and secured with a rubber band. Sampling commenced as soon as the dew dried off the plants in the morning and was completed within 3 hours. In order to reduce the time taken to sample the whole grid, each row of six sites was sampled sequentially from the top to the bottom of the grid. In the soybean a 25 cm row of plants (in the lucerne a 25 cm² area) were sampled by running the nozzle of the vacuum sampler up the stems of each plant and through the foliage. Collection bags were removed from the nozzle while the vacuum was still running, sealed and kept chilled until they were returned to the laboratory. The arthropods were killed by placing the collection bags in a freezer overnight. Arthropods were sorted, identified to family level and stored in 80% ethanol.

Pitfall traps were used to collect ground-dwelling arthropods over a 5-day period. The traps consisted of a 7 cm diameter plastic sleeve buried flush with the ground surface, into which a plastic disposable drinking

cup (200 mL) was inserted and three-quarters filled with 50% ethanol and a small amount of detergent. A lid made from a plastic plate was placed 3 cm above the trap for protection. A single trap was located at each of the 42 sampling sites within a grid and left open for 5 days and nights. After 3–4 days all traps were checked and ethanol added if necessary. Traps were emptied and sieved (0.5 mm mesh) in the field to remove any dirt or debris that had fallen into the trap. Collection vials were returned to the laboratory, sorted and identified to family level under a dissecting microscope.

All arthropods collected were grouped into categories (pests, predators, wasps and others) for data analysis based on known feeding strategies (see Johnson *et al.* 2000 and Pearce 2004 for species list). Particular arthropod orders and/or families (e.g. Formicidae, Araneidae) that were present in high numbers across grids and considered potential predators of *Helicoverpa* spp. (Lepidoptera: Noctuidae) were also separated for the analysis.

PREDATION AND PLANT DAMAGE

Predation was assessed using a single *H. armigera* egg card attached to the upper side of a leaf in the top third of a plant at each grid sampling point. Adult male and female moths were placed into an oviposition cage in the laboratory immediately after eclosing from their pupal case. The walls of the cage were lined with a paper towel and fresh honey solution was supplied every second day. The female moths laid eggs onto the paper towel. Pupae were supplied weekly from a culture at the Queensland Department of Primary Industries, Toowoomba (see Scholz 2000). A paper towel with 20 eggs was stapled to a 6 cm by 2 cm rectangle of white cardboard. All eggs were less than 48 h old when introduced into the field. Cards were placed in the field at 4:00 p.m., collected at 10:00 a.m. the next day (exposed for 18 h), placed into separate zip-lock bags and transported to the laboratory. Eggs were examined under a dissecting microscope and egg mortality based on characteristic damage (Scholz *et al.* 2000) was attributed to: sucking predators, chewing predators, missing (also counted as chewing predators, but may be due to abiotic mortality factors) and remaining (not consumed). The egg cards were stored in a temperature cabinet (14:10 light:dark; 24:20 °C; 65% relative humidity) until the remaining eggs hatched or parasitism was observed. Egg mortality (chewed, sucked and missing) per card, whether or not the card was found by predators (defined as greater than 10% egg mortality per card) and numbers of eggs parasitized were used in data analysis.

Leaf area loss (percentage), pod damage (number of seeds per pod damaged), plant height (cm) and weed density (rank abundance category) were measured at each grid site. Leaf damage was calculated in the field by selecting 10 leaves per sampling site haphazardly and estimating percentage leaf area loss (Colton *et al.* 1995).

DATA ANALYSIS

Spatial patterns in the grid data were examined using Spatial Analysis by Distance Indices (SADIE), which has been developed for the spatial analysis of ecological data in the form of spatially referenced counts. SADIE measures the minimum effort that individuals in the population need to expend to move to a completely regular or uniform arrangement (Perry *et al.* 1999). A complete description of this methodology is available in Perry (1998), Perry *et al.* (1999) and at <http://www.rothamsted.bbsrc.ac.uk/pie/sadie>.

A number of indices are produced which quantify the degree of non-randomness within a set of data. The null-hypothesis tested is that the counts within the grid are arranged randomly with respect to each other. An index of aggregation (I_a) equals 1 when the counts are arranged randomly in the grid, but if I_a is greater than 1 the counts are aggregated into clusters. I_a and its associated probability (P_a) indicate the overall degree of clustering (P_a is the probability that the observed counts are arranged randomly among the given sample units and was considered significant when < 0.05).

Clusters can be in the form of patches or gaps. Patches are defined as neighbourhoods of units with counts that are larger than the overall grid mean. The index V_i and its associated probability P_i indicate the degree of patchiness. If the index V_i is greater than 1 then the units belong to a patch. Gaps are defined as neighbourhoods of units with counts smaller than the overall grid mean. The index V_j and its associated probability P_j indicate the presence of gaps. If V_j is equal to negative 1 (-1) then there is a random arrangement of counts, but if V_j is less than negative 1 (< -1) then gaps are present.

At each X, Y coordinate a clustering index was calculated for each data set (for example, foliage-dwelling predators and foliage-dwelling pests). The overall spatial association between two data sets was assessed by examining correlation between the clustering indices of each set. The QUICK ASSOCIATION ANALYSIS SHELL (version 1.5.2) program was used to assess the degree of association between any two variables measured at the same X, Y locations within the grid (see Winder *et al.* 2001). The method depends upon calculating the similarity in the clustering indices of two sets of data produced by the initial SADIE test for spatial pattern. A SADIE measure of local spatial association (χ_p) is calculated between the first set of cluster indices and the second set of cluster indices at one X, Y point. If χ_p is negative (e.g. $\chi_p = -3.0$) there is a strong negative association (dissociation) between the two data sets at this X, Y point. If χ_p is positive (e.g. $\chi_p = 4.2$) there is a strong positive association between the two data sets at this X, Y point. This measure of local association, χ_p , may be mapped and contoured to graphically display patterns in association.

An overall measure of the spatial association (c) between the two sets of cluster indices is obtained by

Table 1. Summary of SADIE analysis results for data collected in soybean fields adjacent to lucerne (2000/01 season). The Index of aggregation (I_a) indicates the overall degree of clustering in the grid, V_j indicates the presence of gaps (neighbourhoods of units with counts smaller than the overall grid mean), V_i indicates the presence of patches of high abundance (neighbourhoods of units with counts larger than the overall grid mean)

Variable	Horti.	Grid 1		Mendel	Grid 1		Mendel	Grid 2	
	I_a	Mean V_j	Mean V_i	I_a	Mean V_j	Mean V_i	I_a	Mean V_j	Mean V_i
% Eggs predated	0.97	-0.95	0.97	1.58	-1.64**	1.67**	0.98	-1.01	1.04
Egg cards found	0.94	-0.88	0.95	1.24	-1.24	1.15	1.01	-1.01	1.01
No. eggs parasitized	-	-	-	1.08	-1.07	1.17	-	-	-
% Leaf area loss	1.38	-1.37**	1.44**	1.71	-1.61**	1.62**	1.96	-1.69**	1.94**
Vacuum samples									
Total arthropods	0.77	-0.76	0.79	0.88	-0.83	0.92	1.24	-1.25	1.35*
Pests	0.79	-0.76	0.91	0.82	-0.76	0.87	1.15	-1.16	1.13
Other	-	-	-	0.90	-0.91	0.93	-	-	-
Predators	0.77	-0.77	0.89	1.31	-1.24	1.20	1.72	-1.60**	1.43**
Predatory Hemiptera	-	-	-	1.31	-1.31*	1.26	1.52	-1.45**	1.49**
Syrphidae	-	-	-	1.34	-1.29	1.26	-	-	-
Araneae	0.86	-0.87	0.87	0.93	-0.93	0.92	1.39	-1.33*	1.16
Pitfall traps									
Total arthropods	1.30	-1.26	1.18	0.81	-0.87	0.89	1.21	-1.19	1.30
Pests	1.74	-1.57**	1.41**	0.97	-0.93	1.05	0.87	-0.97	0.83
Wasps	1.21	-1.26	0.91	1.36	-1.35**	1.42**	1.19	-1.18	1.16
Other	1.03	-0.96	0.92	1.05	-1.02	1.08	1.51	-1.45**	1.36**
Predators	1.46	-1.37**	1.36**	1.08	-1.04	1.17	1.18	-1.15	0.96
Araneae	0.98	-1.00	0.89	1.91	-1.94**	1.62**	1.20	-1.12	1.22
Lycosidae	1.04	-1.01	1.05	1.48	-1.52**	1.39**	0.99	-1.01	1.04
Dermaptera	2.10	-1.89**	1.81**	1.39	-1.39**	1.38**	1.16	-1.17	1.16
Predatory Coleoptera	1.53	-1.46**	1.55**	-	-	-	-	-	-
Carabidae	1.33	-1.34*	1.12	-	-	-	-	-	-
Predatory Formicidae	1.37	-1.29	1.33*	1.18	-1.13	1.21	1.17	-1.16	0.95

Bold values ($P_a < 0.05$) suggest that there is significant spatial pattern (i.e. the counts are not arranged randomly). **Values are not distributed randomly within the sample grid (i.e. there are significant patches and gaps in the distribution). *Values are distributed into gaps or patches only. Dash indicates parameter not collected or not analysed due to low numbers.

averaging all the χ_p -values across the grid. An assessment is made of the significance of χ by testing against values χ_{rand} using a randomization test. Allowance is made for small-scale autocorrelation in both sets of clustering indices, which reduces the effective sample size using the method of Dutilleul (Dutilleul *et al.* 1993). The effective size of the combined data sets is computed and degrees of freedom adjusted. Critical limits are inflated by a scale factor, and the significance of the randomization test adjusted. If $P < 0.025$ there is a significant positive association, and if $P > 0.975$ there is a significant negative association between the two variables.

Only variables within a sampling grid were compared (i.e. not between subsequent grids collected within a season in a single field). Predominantly those variables that had shown significant spatial clustering in the first analysis were used in the association analysis. Contour maps of the abundance data were produced in the ArcGIS program package using ArcView. The program produces a contour map by interpolating between two data points within a grid. For the edge traps in which there was no adjacent data point this could not be completed.

Results

WITHIN-FIELD SPATIAL PATTERNS

The variables that showed significant amounts of spatial aggregation varied between each field and each grid (Tables 1 and 2). All predatory taxa exhibited strong spatial aggregation (i.e. clusters of high abundance) in a number of grids. Ground-dwelling predators showed significant spatial aggregation in two of seven grids (Horti grid 1, Table 1; Gilbert C grid 1, Table 2) and the foliage-dwelling predators in four of seven grids (Mendel grids 1 and 2, Table 1; Gilbert A grid 1 and Gilbert C grid 2, Table 2). In Gilbert A grid 1 the ground-dwelling Araneae were most abundant in lucerne, with decreasing numbers in the adjacent soybean (Fig. 1). Foliage-dwelling Araneae were more abundant at the other end of the field adjacent to the weedy edge. Ground-dwelling Araneae are aggregated significantly in four of seven grids (Mendel grid 1, Table 1; Gilbert A grid 1, Table 2, Fig. 1; Gilbert C grids 1 and 2, Table 2). Lycosidae spiders may have heavily influenced this pattern as they displayed aggregation in four of the seven grids (Tables 1 and 2) and were consistently most abundant within the

Table 2. Summary of SADIE analysis results for data collected in soybean field adjacent to lucerne (2001/02 season). The index of aggregation (I_a) indicates the overall degree of clustering in the grid, V_j indicates the presence of gaps (neighbourhoods of units with counts smaller than the overall grid mean), V_i indicates the presence of patches of high abundance (neighbourhoods of units with counts larger than the overall grid mean)

Variables	Gilbert A						Gilbert C								
	Grid 1			Grid 2			Grid 1			Grid 2			Grid 3		
	I_a	Mean V_j	Mean V_i	I_a	Mean V_j	Mean V_i	I_a	Mean V_j	Mean V_i	I_a	Mean V_j	Mean V_i	I_a	Mean V_j	Mean V_i
% Eggs predated	1.06	-1.02	1.13	1.03	-1.02	1.02	1.22	-1.30*	1.25	0.92	-0.92	0.90	1.03	-1.03	1.01
Egg cards found	0.94	-0.94	0.95	1.01	-1.11	1.10	0.83	-0.84	0.83	0.86	-0.86	0.86	1.21	-1.20	1.21
% Leaf area loss	1.68	-1.53**	1.49**	1.30	-1.58**	1.35**	1.43	-1.40*	1.22	1.84	-1.54**	1.89**	1.67	-1.45**	1.63**
Plant height (cm)	–	–	–	–	–	–	1.48	-1.54*	1.22	1.14	-1.22	1.23	1.24	-1.26	1.26
Vacuum samples															
Total arthropods	2.09	-1.92**	1.92**	2.47	-2.20**	2.09**	1.17	-1.09	1.25	0.85	-0.87	0.80	–	–	–
Pests	2.02	-1.75**	1.78**	2.50	-2.33**	2.40**	1.15	-1.13	1.38	0.87	-0.88	0.89	–	–	–
Other	–	–	–	1.29	-1.23	1.28*	1.61	-1.61**	1.64**	1.28	-1.25	1.31*	–	–	–
Predators	2.07	-2.04**	2.12**	0.92	-0.90	0.82	0.79	-0.78	0.86	1.51	-1.39*	1.27	–	–	–
Predatory Hemiptera	1.57	-1.47**	1.42**	0.80	-0.80	0.82	–	–	–	1.20	-1.16	1.02	–	–	–
Araneae	1.59	-1.60**	1.35**	1.33	-1.24	1.14	0.90	-0.91	0.99	1.24	-1.23	1.37*	–	–	–
Pitfall traps															
Total arthropods	0.94	-0.93	0.90	1.22	-1.11	1.05	1.98	-1.90**	1.98**	0.84	-0.87	0.99	–	–	–
Pests	0.90	-0.95	0.93	1.42	-1.46*	1.20	1.44	-1.33**	1.37**	1.33	-1.28	1.26	–	–	–
Wasps	0.98	-0.95	1.14	0.94	-0.98	0.94	0.73	-0.75	0.83	1.68	-1.66**	1.63**	–	–	–
Other	0.89	-0.98	0.91	1.15	-1.10	0.98	1.76	-1.69**	1.81**	2.14	-1.94**	2.00**	–	–	–
Predators	1.11	-1.09	0.90	1.30	-1.21	1.30*	1.61	-1.56**	1.74**	0.94	-0.93	0.95	–	–	–
Araneae	2.07	-1.91**	1.45**	1.07	-0.93	1.04	2.02	-1.83**	1.69**	1.93	-1.95**	1.55**	–	–	–
Lycosidae	2.23	-2.14**	1.87**	1.23	-1.17	1.19	1.67	-1.62**	1.41**	2.13	-2.21**	1.76**	–	–	–
Dermaptera	1.08	-1.08	1.02	1.49	-1.44*	1.26	1.60	-1.61**	1.74**	1.78	-1.59**	1.59**	–	–	–
Predatory Formicidae	1.35	-1.28	1.06	1.29	-1.23	1.28	1.24	-1.23	1.23	1.14	-1.17	0.98	–	–	–
Predatory Staphylinidae	1.79	-1.79**	1.76**	–	–	–	–	–	–	1.51	-1.48**	1.52**	–	–	–
Carabidae	1.26	-1.24	1.32*	–	–	–	1.92	-2.07**	1.78**	0.97	-0.94	1.01	–	–	–

Bold values ($P_a < 0.05$) suggest that there is significant spatial pattern (i.e. the counts are not arranged randomly). **Values are not distributed randomly within the sample grid (i.e. there are significant patches and gaps in the distribution). *Values are distributed into gaps or patches only. Dash indicates parameter not collected or not analysed due to low numbers.

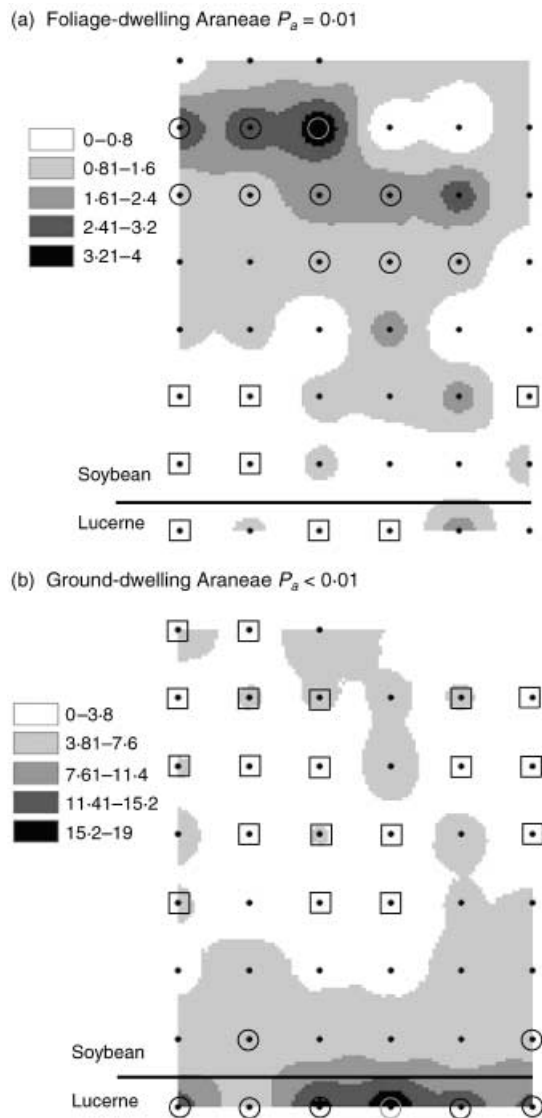


Fig. 1. Spatial distribution pattern of two variables measured in Gilbert A grid 1. (a) Abundance of Araneae collected by vacuum sampler at each grid point and (b) abundance of Araneae captured in pitfall traps open for 5 days. Squares around grid sample sites indicate $V_j < -1.5$ (the presence of gaps), circles around grid sample sites indicate $V_i > 1.5$ (the presence of patches). The solid line shows the edge of the soybean and adjacent lucerne field. The distance between each grid point is 20 m.

lucerne with decreasing trap catch with distance from lucerne (Fig. 2). Foliage-dwelling Araneae were significantly aggregated in three of seven grids (Mendel grid 2, Table 1; Gilbert A grids 1 and 2, Table 2).

Predatory Formicidae were abundant in pitfall traps during the first season (minimum ± 1 SE; Horti grid 1, mean = 84.4 ± 9.1 per pitfall trap; maximum Mendel grid 1, 89.0 ± 5.7) but in the second season their numbers were much lower (minimum Gilbert C grid 1, 8.3 ± 2.9 ; maximum Gilbert A grid 2, 38.6 ± 12.9). Formicidae displayed significant spatial aggregation in two of seven grids (Horti grid 1, Table 1; Gilbert A grid 1, Table 2) and were generally more abundant around the edges of the grids. Dermaptera reached high numbers in Horti

grid 1 (29.1 ± 2.6) and were highly aggregated (Table 1, $P_a < 0.01$) in a single patch. Foliage-dwelling predatory Hemiptera were aggregated significantly in three of seven grids (Mendel grids 1 and 2, Table 1; Gilbert A grid 1, Table 2).

Spatial aggregation of pests was observed in a number of grids. Ground-dwelling pests were aggregated in four of seven grids (Horti grid 1, Table 1; Gilbert A grid 2 and Gilbert C grids 1 and 2, Table 2) and the foliage-dwelling pests aggregated in two of seven grids (Gilbert A grids 1 and 2, Table 2). The greatest average egg predation on cards ($56\% \pm 6.5$) was recorded in Gilbert A grid 2 and the lowest ($16\% \pm 4.9$) in Mendel grid 1. Predation of *H. armigera* eggs was significantly aggregated in two of eight grids (Mendel grid 1, Table 1; Gilbert C grid 2 m Table 2) and was strongly aggregated in a further two (Gilbert C grids 1 and 2, Table 2). In some grids egg predation appeared to be higher in lucerne and decreased with distance from the interface (e.g. Gilbert C grid 1, $P_a = 0.09$, Table 2). Some egg parasitism was recorded in Mendel grid 1, but the rate was very low (mean 1.52 ± 0.65 parasitized eggs per card) and was not significantly aggregated ($P_a = 0.26$, Table 1).

Despite the lack of insecticide application, plant damage in terms of leaf area loss and pod damage was very low. The highest mean leaf area loss was only $6\% \pm 0.33$. Pod damage was so low in the first season that it could not be analysed. Leaf area loss was significantly aggregated in most grids (five of eight grids) due probably to overall low levels of leaf damage. In both seasons pest damage to plants would not have affected yield.

TEMPORAL PATTERNS

The aggregations observed within a grid were not always stable across the season. In Mendel field (Table 1), foliage-dwelling total predators, Araneae and predatory Hemiptera were aggregated significantly in both the first and second grids. Ground-dwelling Araneae, Lycosidae and Dermaptera were aggregated highly at the start of the season but displayed a random spatial pattern by the second grid. In Gilbert A field (Table 2) all the foliage-dwelling arthropods taxa were aggregated significantly at the start of the season but only pests and Araneae remained so later. Ground-dwelling Araneae (and Lycosidae) were aggregated significantly in the first grid but only ground-dwelling pests and Dermaptera displayed significant aggregation in the second grid. In Gilbert C field (Table 2) foliage-dwelling predators were aggregated only in the second grid. Most ground-dwelling taxa displayed significant aggregation in both the first and second grids (exception being the total predators and Carabidae that showed a random pattern in the second grid).

Egg predation increased as the season progressed in Mendel and Gilbert A fields. For Mendel field (Table 1) egg predation was strongly aggregated in the first grid only, and for Gilbert A (Table 2) there was no evidence

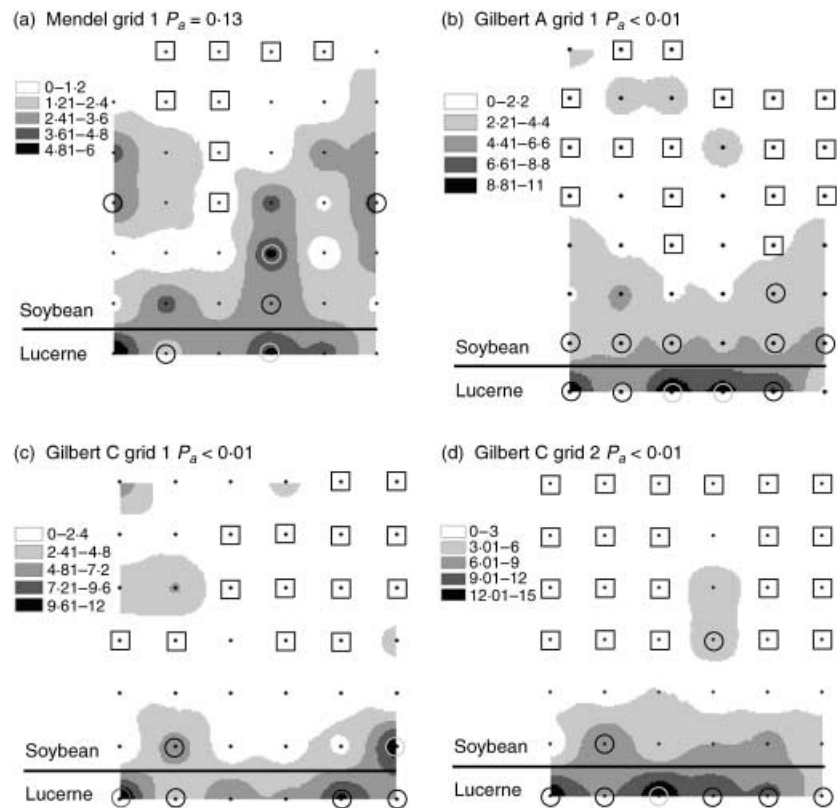


Fig. 2. Spatial pattern of Lycosidae abundance in pitfall traps in four sampling grids. (a) Strong spatial aggregation, (b–d) significant spatial aggregation. Squares around grid sample sites indicate $V_j < -1.5$ (the presence of gaps), circles around grid sample sites indicate $V_j > 1.5$ (the presence of patches). The solid line shows the edge of the soybean and adjacent lucerne fields. Scale indicates numbers captured per pitfall trap open for 5 days. The distance between each grid point is 20 m.

of aggregation in either grid. In Gilbert C field (Table 2) egg predation was strong aggregated across the whole season (but only significant in grid 2).

WITHIN-FIELD SPATIAL ASSOCIATIONS

Spatial association analysis for each grid was restricted to combinations of comparisons of interest to this study. Variables that showed significant spatial association differed between each grid (Table 3). While there were areas of positive and negative association within each grid, across a whole grid the significant relationships were mostly positive.

In the first season, in Horti grid 1 there was a significant positive association between foliage-dwelling pests and predators ($P < 0.01$). Similarly, predators and pests collected in pitfall traps showed some positive association ($P = 0.07$, Fig. 3). In Mendel grid 1 there was a significant positive association between egg predation and ground-dwelling Araneae (Araneae $P < 0.01$, and Lycosidae $P = 0.01$, Table 3). Egg predation ($P = 0.02$), ground-dwelling Araneae ($P < 0.01$) and Lycosidae ($P < 0.01$) were also associated significantly (positively) with leaf area loss. A strong positive association was observed between ground-dwelling pests and Araneae ($P = 0.04$) and Lycosidae ($P = 0.04$) that was not significant (at the $P < 0.025$ level, Table 3). Mendel grid 1 and grid 2 showed a strong positive rela-

tionship between foliage-dwelling predators and pests (grid 1 $P = 0.02$, grid 2 $P = 0.01$, Fig. 3). In Mendel grid 2 there was a strong disassociation between egg predation and leaf area loss ($P = 0.97$, Table 3).

In the second season leaf area loss was associated significantly with foliage-dwelling pests ($P < 0.01$), predators ($P = 0.01$) and Araneae ($P < 0.01$) in Gilbert A grid 1 (Table 3). Foliage-dwelling pests and predators were associated positively ($P < 0.01$, Fig. 3) but ground-dwelling pests and Lycosidae were associated negatively ($P = 0.99$). Egg predation was associated negatively with leaf area loss ($P = 0.91$) and foliage-dwelling predators ($P = 0.95$), but the relationship was not significant. There was a minor positive association between the ground-dwelling predators and pests ($P = 0.06$) in Gilbert A grid 2 and foliage-dwelling pests and Araneae were significantly negatively associated ($P = 0.98$). In Gilbert C grid 1 egg predation was associated positively with pitfall-trapped Carabidae beetles ($P = 0.03$). In Gilbert C grids 1 and 2 plant height displayed significant associations between a number of foliage-dwelling arthropod groups and some ground-dwelling arthropods (predators $P < 0.01$, Araneae $P = 0.02$, other $P = 0.02$) and egg predation ($P = 0.03$). While in Gilbert C grid 1 plant height and Lycosidae were associated positively ($P = 0.01$), in the following grid (grid 2) they were associated negatively ($P > 0.975$). The opposite pattern was seen for leaf area loss and

Table 3. Summary of results from SADIE spatial association analysis between data collected from sampling grids positioned across the interface between a soybean and adjacent lucerne field. The overall measure of association (χ) for the two data sets were obtained by measuring the similarity between two sets of SADIE clustering indices for each variable

Season		Horti	Mendel	Mendel	Gilbert A	Gilbert C	Gilbert C	Gilbert C	Gilbert C
Variable 1	Variable 2	grid 1 2000/01	grid 1 2000/01	grid 2 2000/01	grid 1 2001/02	grid 2 2001/02	grid 1 2001/02	grid 2 2001/02	grid 3 2001/02
% Egg predated	% Leaf area loss	0.13	0.33	-0.30	-0.33	0.12	-0.06	-0.26	-0.25
% Egg predated	PT predator	-0.20	-0.14	0.23	0.19	-0.22	0.26	-0.16	-
% Egg predated	PT Carabidae	-	-	-	-	-	0.33	-	-
% Egg predated	PT Araneae	-	0.50	-	0.27	-	-	-0.20	-
% Egg predated	PT Lycosidae	-	0.38	-	0.07	-	0.09	-0.20	-
% Egg predated	V predator	0.12	-0.23	-0.02	-0.28	-0.11	0.11	0.29	-
% Egg predated	V Araneae	-	-	-	-0.12	-	-	-	-
% Egg predated	Plant height	-	-	-	-	-	0.45	0.30	-0.02
V pest	V predator	0.71	0.36	0.34	0.59	-0.13	-0.03	-0.25	-
V pest	V Araneae	-	-	-	-	-0.32	-	-	-
V other	V predator	-	0.35	-	-	-	-	-	-
V pest	PT pest	-	-	-	-	-0.06	-	-	-
V pest	PT Lycosidae	-	-0.03	-	-0.36	-	0.38	0.13	-
PT pest	PT predator	0.24	-0.15	-0.04	0.44	0.25	0.42	0.16	-
PT pest	PT Dermaptera	-	-	-	-	-0.14	-	-	-
PT pest	PT Carabidae	-	-	-	-	-	0.38	-	-
PT pest	PT Araneae	-	0.29	-	-0.17	0.24	0.29	-0.11	-
PT pest	PT Lycosidae	-	0.29	-	0.03	-	0.35	-	-
PT pest	PT other	-	-	-	-	-	0.41	-	-
V pest	Plant height	-	-	-	-	-	0.48	-	-
V predator	Plant height	-	-	-	-	-	-0.06	0.51	-
PT predator	Plant height	-	-	-	-	-	0.55	-0.33	-
PT Araneae	Plant height	-	-	-	-	-	0.54	-	-
PT Lycosidae	Plant height	-	-	-	-	-	0.42	-0.71	-
V Araneae	Plant height	-	-	-	-	-	-	0.33	-
V Other	Plant height	-	-	-	-	-	-	0.35	-
% Leaf area loss	V Predator	-	-	0.44	0.40	-	-	-	-
% Leaf area loss	V Araneae	-	-	0.41	-	-	-	-	-
% Leaf area loss	PT Araneae	-	0.51	-	-	-	-	-	-
% Leaf area loss	PT Lycosidae	-	0.46	-	-0.26	-	-0.47	0.27	-
% Leaf area loss	PT pest	-0.14	-	0.24	-	0.00	-0.07	-0.06	-
% Leaf area loss	V pest	-0.05	0.12	0.10	0.41	-0.15	-0.43	-0.25	-

Bold values ($P < 0.025$ for a positive association, or $P > 0.975$ for a negative association) are significant. V: vacuum sample (foliage-dwelling taxa). PT: pitfall trap (ground-dwelling taxa). Dash indicates variable not analysed.

Lycosidae (grid 1 $P > 0.975$, grid 2 $P = 0.05$). The results suggest that there may be biological factors associated with plant height (such as plant complexity or increasing leaf surface area) that may have an impact on arthropod populations. Gilbert C grid 3, with a reduced data set, showed no significant associations but there was a strong negative association between egg predation and leaf area loss ($P = 0.92$).

Discussion

WITHIN-FIELD SPATIAL PATTERNS

Predators were not distributed evenly within what are considered to be uniform soybean fields, but rather exhibited strong spatial patterning with regions of high and low abundance and activity. A similar result was found by Ferguson *et al.* (2003) for various pests of oilseed rape (*Bassica napus* L.) and by Holland *et al.* (1999) for predators in wheat fields. Ground-dwelling and foliage-dwelling predators were often aggregated

in patches of approximately 40 m across. A variety of grid sizes have been used (Perry *et al.* 1999, 30 m spacing, 63 sites; Holland *et al.* 1999, 30 m spacing, 63 sites; Winder *et al.* 2001, 12 m spacing, 256 sites; Thomas *et al.* 2001, 10 m spacing, 156 sites; Ferguson *et al.* 2003, 43.5 m spacing, 36 sites, Holland *et al.* 2005, 40 m spacing along rows, 20 m spacing between rows, 973 sites) to examine spatial pattern in various arthropods. Smaller-scale grids (7.5 m spacing, 25 sites and 1.5 m spacing, 30 sites) have less chance of detecting clusters (Holland *et al.* 1999; Pearce 2004) and a minimum of 36 sample sites per grid is recommended. The grid size chosen will depend on the taxa under investigation (Holland *et al.* 1999, 2005), but when investigating a variety of taxa, such as in this study, a grid size of at least 20 m spacing appears to be the most useful.

The ground-dwelling and foliage-dwelling predators showed very different within-field spatial patterns (for example Fig. 1). While many predator groups showed irregular patterns of aggregation within a grid and between grids, a few demonstrated a consistent pattern

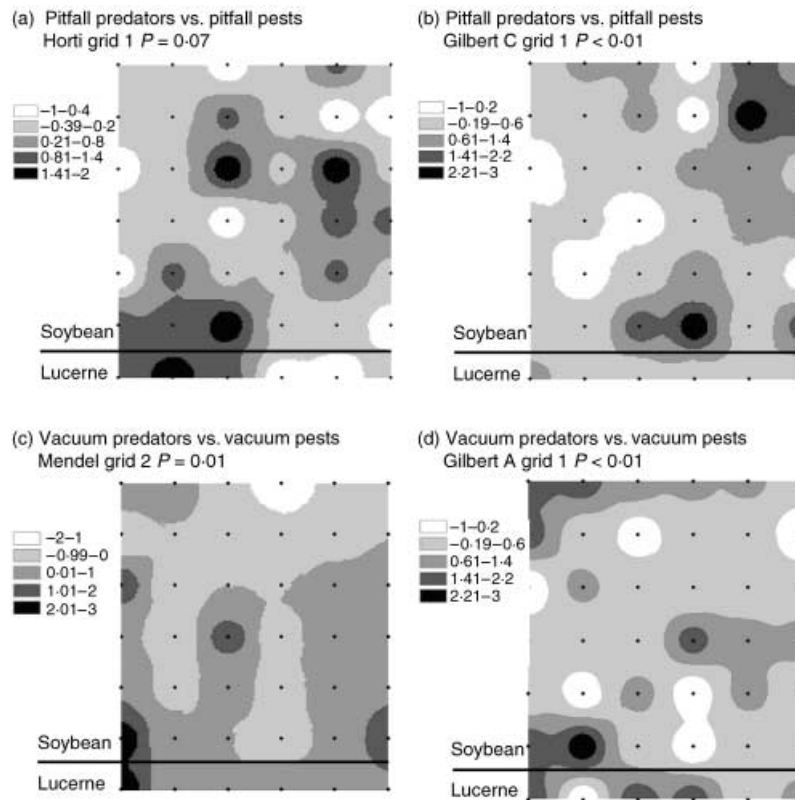


Fig. 3. Spatial association maps for predators and pests collected in pitfall traps (PT) and vacuum samples (V) in four grids. At each grid point the SADIE measure of spatial association (χ_p) between predators and the pests has been mapped and contoured. negative values (white areas) show a strong disassociation between the two groups and positive values (black areas) show a strong association. The solid black line indicates the interface between the lucerne and soybean fields. The distance between each grid point is 20 m.

across grids (and across fields). Lycosidae were generally more abundant in lucerne, with decreasing abundance into the soybean with distance from the interface (Fig. 2). Similarly, Holland *et al.* (1999) found that Lycosidae were more abundant near wheat field edges. Mark-recapture experiments have demonstrated that Lycosidae are capable of crossing the soybean/lucerne interface and are highly mobile (travelling greater than 5 m per day) (Hallander 1967; Pearce & Zalucki 2002; Pearce 2004). Previous studies have shown that Lycosidae are successful in highly disturbed systems with regular periods of barren ground (Marshall & Rypstra 1999; Martin & Major 2001; Marshall *et al.* 2002). Martin & Major (2001) found that there was a clear difference in the lycosid assemblage across a woodland/grazing paddock interface (New South Wales wheat belt, Australia), but this change was due to differences in abundance of individual species rather than a change in species composition, implying that species found in the woodland are not restricted to that habitat and do move up to 20 m into the adjacent disturbed paddock. Lycosid species in soybean fields differ in behavioural responses that may influence spatial patterns in abundance (Buddle & Rypstra 2003). Emigration of one lycosid species was influenced by habitat quality (no-till, conventional tilled and mulched soybean), but another species was unaffected (also see Thorbek & Bilde 2004).

A finer level of taxonomic resolution and further information on life histories of lycosid species in Australian agroecosystems is required for a greater understanding of the spatial patterns observed.

Whole-field averages of arthropod abundance (pests and predators) and activity (egg predation and plant damage) can be misleading if there is a great deal of spatial variability within a field. This is best illustrated in Gilbert C field, which showed similar levels of average egg predation in both grids (32% in grid 1 and 40% in grid 2), but very different spatial patterns of egg predation. Scholz (2000) found a similar result for egg predation and parasitism. These results have serious implications for the sampling of arthropod abundance between-fields and the reliability of sampling within-fields. For pest species a management strategy that involves insecticide applications in response to scouting data is more cost-effective than the routine prophylactic use of insecticides or no action at all (Lamp *et al.* 1991). However, the use of scouting data for management decisions relies on the fact that the estimate of arthropod abundance calculated from a set of samples collected within a field is an accurate reflection of true abundance. The influence of underlying population spatial pattern on the accuracy of scouting data is unknown, and given the small sample numbers used in most scouting programmes it may have an impact on

management decisions. The recent incorporation of predator abundance data into management tools (e.g. the predator to pest ratio used in cotton, Mensah 2002a,b) means that the value of spatial information on arthropod abundance, predatory activity and damage will increase (Hughes 1996).

There was a great deal of temporal change in the spatial patterns observed within a field. Generally the significant spatial patterns for particular taxa were not maintained from one sampling date to the next, with the exception of egg predation in Gilbert C field (Table 2), which was aggregated strongly across all three sampling grids. It appears that the sampling interval utilized in this study was not sufficient to resolve changes in spatial distribution patterns across time (and for this reason association analysis was not performed on subsequent grids within a single field). From these results we can conclude that the aggregations observed in these fields are generally not stable for the entire season. Thomas *et al.* (2001) also found that aggregations of carabid species within fields were associated positively between consecutive samples (less than 1 week) and maintained over longer time-scales (5–6 weeks) but not across the whole season.

WITHIN-FIELD SPATIAL ASSOCIATIONS

Predator aggregation did not consistently correlate with pest aggregation, plant damage or predation rate. The most consistent positive association was between foliage-dwelling predators and pests (significant in four of seven grids, Table 3). Often the spatial pattern in predator abundance was the same as for all arthropod groups sampled and associated more clearly with an underlying parameter such as plant height (e.g. Gilbert C grids 1 and 2, Table 3). Ferguson *et al.* (2003) found a similar result, with the spatial variation in oilseed rape plant growth stage influencing the distribution of pest species. Much clearer spatial association results have been obtained in studies of pest species with low mobility (e.g. aphids in wheat fields, Winder *et al.* 2001).

The predominance of positive associations between most of the pairs of data sets examined may be a result of the taxonomic resolution employed. Predator and pest assemblages may display a different temporal abundance pattern and association pattern to individual predator and pest species. Bryan & Wratten (1984) found that of all the predators caught in pitfall traps only carabids and staphylinids aggregated to artificially created patches of aphids. The ability to detect significant associations may have been limited by the coarse taxonomic groupings selected.

Changes in the temporal patterns of spatial associations (within a field sampled multiple times during the season) become important when trying to interpret the associations within a wider context of seasonal patterns in pest and predator populations. We would expect all types of associations (positive, negative and none) depending on what point in time sampling was con-

ducted (Winder *et al.* 2001). For example, if we were to sample a field intensively at a single point in time, to determine if predators aggregate in response to high prey density, a number of patterns may arise. If the populations were measured when predators locate relatively abundant prey patches, a positive spatial association may occur. Some time later the predators may have extinguished or reduced this prey patch and a negative spatial association is more likely. Alternatively, the two populations may show no correlation in space (no association). As Stanley (1997) notes, the absence of significant correlations does not automatically suggest no predatory impacts or interactions between the two populations. The combination of unsynchronized, positive and negative associations between guilds of predators and their prey may result in the appearance of no correlation at all. Previous studies have focused on sampling a single field frequently throughout a season (Thomas *et al.* 2001; Winder *et al.* 2001; Warner *et al.* 2003); however, few conclusions can be drawn on how representative the patch locations are for other fields in the study region.

A limited selection of variables that may be related to predator abundance were sampled in this study. Environmental conditions (temperature, humidity), soil conditions (organic matter and pH), plant nutrition (Denno *et al.* 2002), dispersal ability and the location of external overwintering sites were not measured, but may influence the distribution of some predator groups. It is clear that predators are rarely distributed randomly within a field, and field edges and adjacent crops can have an influence on predator abundance of some taxa (also see Holland *et al.* 2005). The same can be said for pest arthropods. This should be kept in mind when estimating arthropod (pest and predator) abundance from a set of samples taken at random locations within a field.

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