

# The role of large-scale spatially explicit and small-scale localized processes on the population dynamics of cereal aphids

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## Abstract

A field-scale study of the spatially explicit interaction between the carabid *Poecilus cupreus* Linnaeus, and two common aphid species (*Sitobion avenae* (Fabricius) and *Metopolophium dirhodum* (Walker)) in winter wheat was conducted. All three species showed considerable spatial pattern at the field scale. Activity-density of *P. cupreus* was an order of magnitude higher in the central part of the field compared to its periphery. Where *P. cupreus* activity-density was highest, *S. avenae* and *M. dirhodum* population peaks were delayed. Additionally, in the case of *M. dirhodum*, lower maximum counts were evident where *P. cupreus* activity-density was highest. An analysis of the movement of individual *P. cupreus* using release–recapture indicated that those beetles within the centre of the field exhibited reduced displacement, which may have caused the generation or maintenance of spatial pattern. Crop density was also measured throughout the field. Although crop density had no large-scale spatial pattern, its variability at the small-scale was consistent with an influence on aphid population dynamics. This study demonstrates empirically that both large-scale spatially explicit and small-scale localized processes influenced aphid population dynamics simultaneously.

**Keywords:** spatial, cereal aphids, SADIE, spatially explicit

## Introduction

It is widely accepted that processes mediating population dynamics can only be fully understood within a spatial context. The inclusion of spatially explicit information may enhance our ability to detect important ecological processes, such as density dependence (Veldtman & McGeoch, 2004). However, the lack of large-scale field studies that retain the spatial component intrinsic within these data is a major

obstacle to our development of an understanding of ecological processes (Steinberg & Kareiva, 1997; Schindler, 1998). There is also recognition that an understanding of the spatial distribution and temporal dynamics of insect populations can facilitate the development of conservation biological control strategies (Brenner *et al.*, 1998; Thomas *et al.*, 2001; Symondson *et al.*, 2002; Kean *et al.*, 2003; Holland *et al.*, 2005) as well as the promotion of biodiversity-based agri-environment schemes (Kleijn & Sutherland, 2003).

Aphids are a common pest in cereal crops, which may cause economic damage, and it is known that a multitude of natural enemies contribute to suppression of their populations. Carabid beetles are important beneficial organisms in

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agricultural systems (Kromp, 1999; Menalled *et al.*, 1999; Sunderland, 2002) and aphid predation by these polyphagous predators has been shown to positively affect yield in cereals (Ostman *et al.*, 2003). Generalist predators are considered important in limiting exponential increases in their prey populations (Chiverton, 1986; Settle *et al.*, 1996; Riechert *et al.*, 1999). Due to the relatively long life-history (~1 year) of carabids relative to their aphid prey, within-season control can only be mediated by spatio-temporal processes in predatory activity of an existing population (Southwood & Comins, 1976). Additionally, other factors such as crop density or quality may also influence aphid population dynamics (Honek, 1985, 1987, 1991) or the movement of predators (Honek, 1988) but little is known regarding their spatially explicit effect.

The goal in this study was to develop an understanding of the spatially explicit interaction between aphid prey and a generalist natural enemy (a ground beetle), in a single cereal field during crop development. In the context of conservation biological control, the short-term response of a 'resident' generalist predator population is considered to be a key component in pest population suppression (Symondson *et al.*, 2002). It is possible to hypothesize a number of ways in which predators and prey may interact, dependent on their spatial distributions. For example, areas within a field where sedentary predators are relatively abundant may exhibit pest populations that are relatively low. Conversely, predators may actively respond to prey patches by movement causing a dynamic interaction in space and time (Winder *et al.*, 2001a) with pest suppression occurring both locally and ephemerally. Alternately, little or no spatial interaction may be present if the natural enemy is ineffective; other biotic or abiotic factors may exert a much greater influence on distribution of predators and prey. Hence, we determined firstly whether there is evidence of spatial pattern in pest and predator populations and secondly whether there are any observable spatial associations between predators and prey which support such hypotheses.

We studied the spatially explicit interaction between the carabid *Poecilus cupreus* Linnaeus, two common aphid species (*Sitobion avenae* Fabricius and *Metopolophium dirhodum* (Walker)) and an easily measured indicator of crop growth, crop density. *Poecilus cupreus* is abundant and active in cereal fields between May and September, overwintering predominately as adults in margins and fields and breeding in spring (Holland & Luff, 2000). We have adopted an individual-based and spatially explicit approach, using a combination of capture-recapture and spatial analysis by distance indices (SADIE) methodology. SADIE was developed specifically for ecological data in the form of counts (Perry *et al.*, 1999). These methods identify areas of clustering (as 'patches' and 'gaps') of individuals within a population and allows the association or dissociation between spatial patterns to be determined (Winder *et al.*, 2001a; Perry & Dixon, 2002).

## Materials and methods

### Field studies

The study was conducted during 2003 within a 3.75 ha field of conventionally managed winter wheat surrounded by hedged banks at Coffinswell, Devon, UK. No insecticides were applied to the crop during the study period.

A sampling grid, with 12 m spacing was arranged within, and fully covered, the field. Each of the 204 sampling locations were marked with a numbered flag and flexicane.

Sampling was conducted on nine occasions at weekly intervals between 19 May and 18 July. Decimal crop growth stage (Zadoks *et al.*, 1974) was recorded on each sampling occasion. Visual counts of *S. avenae* and *M. dirhodum* were taken on each sampling date, at each of the 204 sampling locations by recording the number of individuals present on 24 randomly selected tillers. After the crop had ripened, crop density was assessed at each location by counting the number of tillers within a 0.1 m<sup>2</sup> quadrat.

*Poecilus cupreus* activity-density was measured at each location using barrier-connected pitfall trapping (Winder *et al.*, 2001b) with a capture-recapture protocol. At each location, five dry pitfall traps were arranged in a cross formation 0.5 m apart, connected by plastic-sheet barriers dug into the ground. Traps were opened for 24 h during each of the nine consecutive sampling weeks. On each trapping occasion, cohorts of beetles were collected from each location and retained within plastic boxes (with air holes) containing moist crumpled paper towels and food (moist dog food pellets). Beetles were fed *ad libitum* to reduce the degree of stress undergone during the marking process and to ensure that 'hungry' individuals likely to be highly motivated to immediately disperse were not released. The number of beetles was recorded at each location. All unmarked individuals were uniquely marked with a three-digit code using a field-based laser marking procedure (Griffiths *et al.*, 2005) and their sex recorded. Any recaptured marked individuals were retained in the same manner and their individual code recorded. All beetles were returned to their point of capture and released within 48 h. The maximum possible recorded displacement for an individual, equal to the maximum distance between locations in the field, was 300 m.

### Spatial and statistical analysis

Spatial pattern was measured and tested by the SADIE red-blue method, which identifies areas in which observed counts are either arranged effectively at random or form clusters of units in local neighbourhoods with consistently large or small counts (Perry *et al.*, 1999). A cluster of relatively high density counts nearby to each other is termed a patch; a similar cluster of relatively small or possibly zero counts is termed a gap. In SADIE, spatial pattern is measured locally, at each sampled unit, through an index of clustering which may be contoured by interpolation and mapped. Units with counts greater than the overall mean are assigned a patch cluster index ( $v_i$ ), which by convention is positive; units with counts less than the mean are assigned a gap cluster index, by convention negative ( $v_j$ ). For random arrangements of the observed counts, expected values of  $v_i$  and  $v_j$  are +1 and -1, respectively. Typically, patches are represented on maps by contoured areas shaded red, where all neighbouring sample units have cluster indices,  $v_i > 1.5$ ; gap contour areas where all units have indices,  $v_j < -1.5$  are shaded blue. Unshaded areas represent locations where counts are arranged effectively at random. Hence, patch (red), gap (blue) and random (unshaded) 'neighbourhoods' may, or may not, be detected within the sampled area. Using this technique, red-blue analyses were conducted for aphid counts, *P. cupreus* activity-density and crop density.

Two populations may be spatially associated, dissociated, or occur at random with respect to one another (Perry & Dixon, 2002). Local spatial association was measured using the index  $\chi_k$ , based on similarity between the clustering index of the two populations measured at the  $k$ th unit. If the  $n$  indices of set one are denoted  $z_{k1}$ , with mean  $q_1$  and those of set two  $z_{k2}$ , with mean  $q_2$ , then  $\chi_k = n(z_{k1} - q_1)(z_{k2} - q_2) / [\sum_k (z_{k1} - q_1)^2 \sum_k (z_{k2} - q_2)^2]^{1/2}$ . Positive values of  $\chi_k$  arise from coincidences of patches or of gaps in both populations; negative values from opposite cluster types. Overall spatial association,  $X$  was calculated as the mean of local values,  $X = \sum_k \chi_k / n$ , equivalent to the simple correlation coefficient between  $z_{k1}$  and  $z_{k2}$ . Significance of  $X$  was tested by randomizations, with values of  $z_k$  reassigned amongst the units, after allowance for small-scale spatial autocorrelation in either set of  $z_k$  (Dutilleul, 1993). Association may be calculated either between two different taxa on the same occasion, or, pairwise, between the same taxa sampled on successive occasions; the latter is a measure of change of spatial pattern, with positive values indicating stability.

At each location, summary population parameters, namely maximum count and the week in which this occurred were determined for both *S. avenae* and *M. dirhodum*. For *P. cupreus*, total activity-density, calculated by summing the counts over all sampling occasions was calculated at each location. Capture-recapture data were analysed to provide information on the displacement of individual beetles during the study. For each capture-recapture event, the distance between the origin and destination trap was measured using Pythagoras' theorem. At each location, average displacement of all beetles recaptured on the next trapping occasion was calculated. Using these data we determined, using regression analysis,

whether displacement at each location could be related to either aphid abundance or beetle activity-density respectively.

## Results

### Spatial pattern of aphids, beetles and crop density

Both *S. avenae* (fig. 1a) and *M. dirhodum* (fig. 1b) infested the study field. As an average, *S. avenae* and *M. dirhodum* populations peaked during week 4 (reaching approximately 13 and 6 aphids location<sup>-1</sup> respectively), the week prior to crop flowering. Hence, the average peak total aphid population was approximately 0.8 aphid shoot<sup>-1</sup>. *Sitobion avenae* persisted strongly for most of the study period, declining substantially only towards the end of the season, whilst *M. dirhodum* declined consistently from week 5 onwards. Both species exhibited considerable large-scale spatial pattern (fig. 1d, e; fig. 2). *Sitobion avenae* patch clusters were largely absent during weeks 1–2, developing and progressing across the field from week 3 (ear emergence) onwards. *Metopolophium dirhodum* showed large-scale spatial pattern between weeks 1–4 (with distinct patches and a gap area spanning the centre of the field), a collapse in spatial pattern in weeks 5–6 followed by the reemergence of some spatial pattern in weeks 7–9 (although the number of *M. dirhodum* within the field during this period was low).

Spatial analysis demonstrated considerable large-scale spatial pattern in the week at which aphid populations peaked (fig. 3a,b; table 1). For both species, distinct 'neighbourhoods' were evident, where aphids predominantly peaked 'early' (weeks 1–4) or 'late' (weeks 5–9) in the season. No spatial pattern in maximum counts was

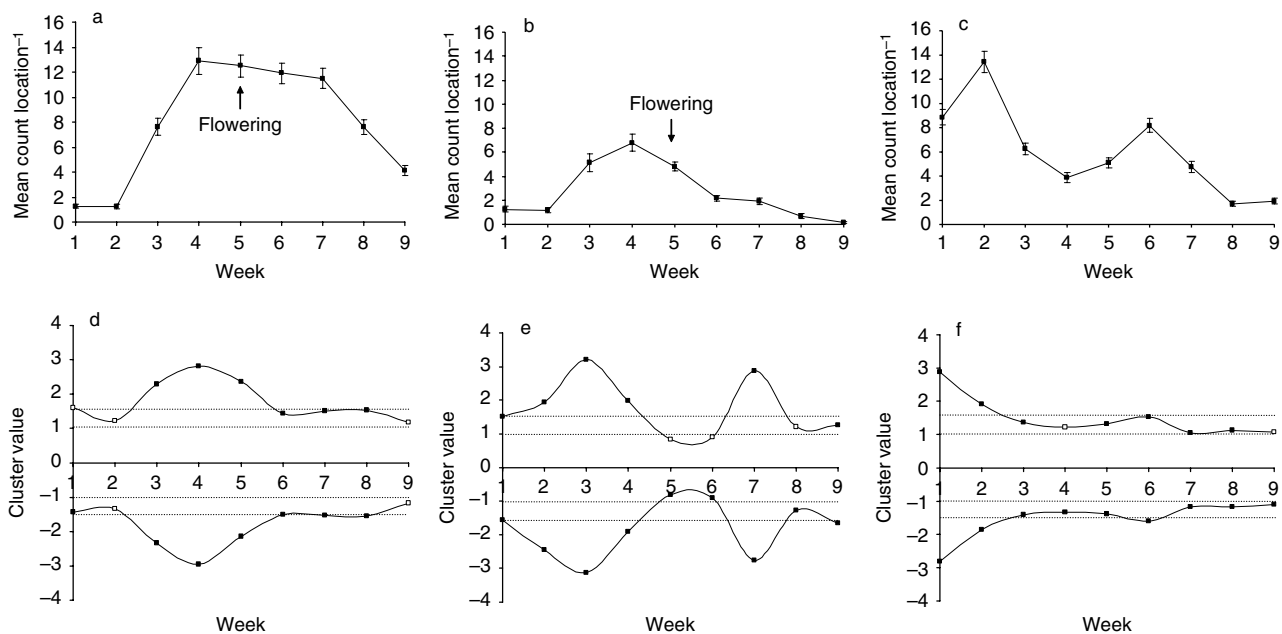


Fig. 1. Mean counts (a–c, number location<sup>-1</sup> ± s.e.) and spatial analysis by distance indices (SADIE) patch ( $v_i$ ) and gap ( $v_j$ ) cluster indices (d–f, with significant values denoted by filled markers) for *Sitobion avenae* (a and d), *Metopolophium dirhodum* (b and e) and *Poecilus cupreus* (c and f). Curves above and below x-axes denote patch and gap cluster values respectively. Dotted lines show expected values for random arrangements (+1, -1) and clustering 1.5 times expectation (+1.5, -1.5). Significant values indicate a departure from a random distribution.

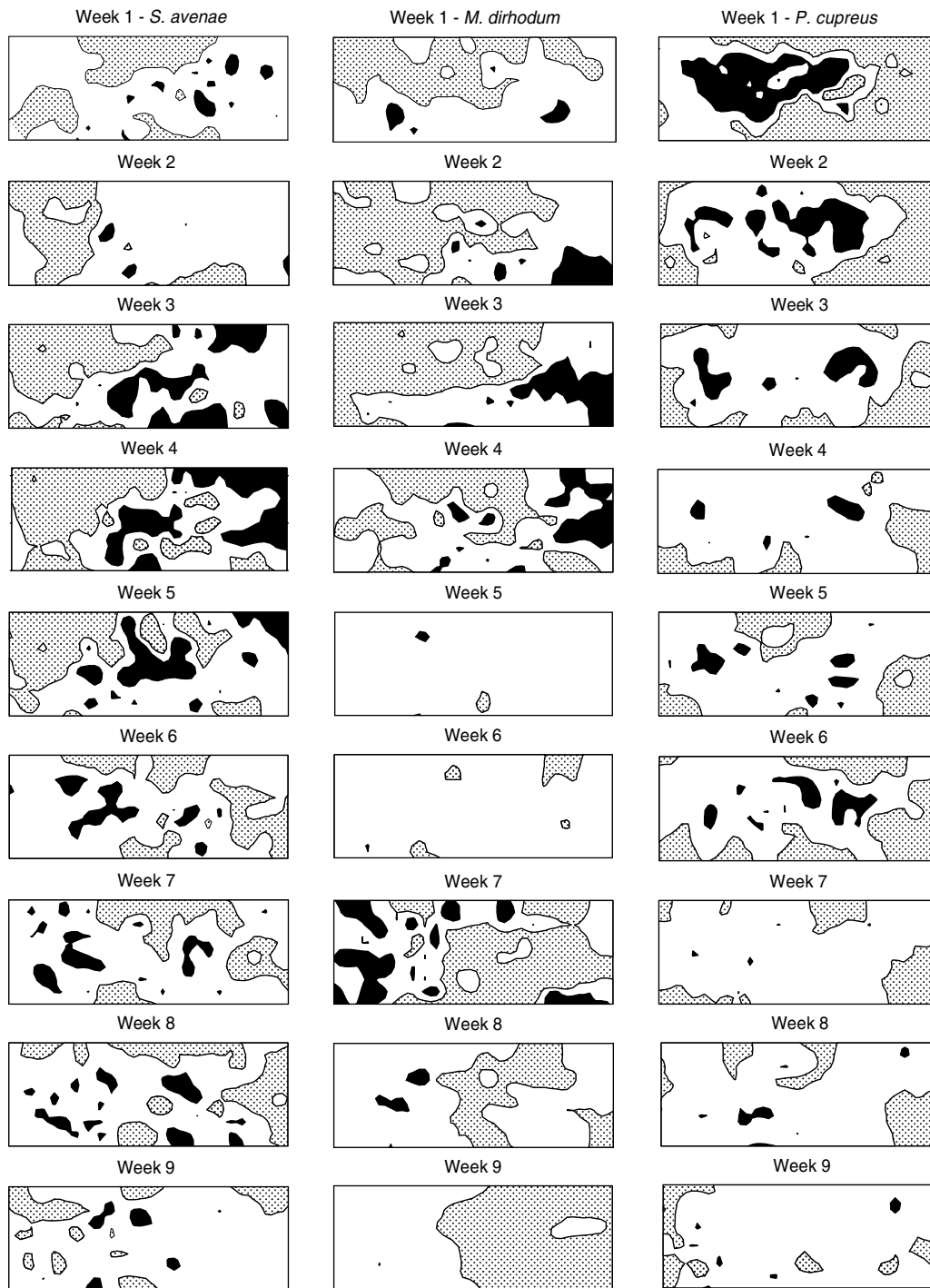


Fig. 2. Sequences of 'red-blue' plots for *Sitobion avenae*, *Metopolophium dirhodum* and *Poecilus cupreus* for a nine-week sampling period. Darker shading ('red') indicates patch clusters within which interpolated values of  $v_1 > 1.5$ ; lighter shading ('blue') indicates gap clusters within which interpolated values of  $v_1 < -1.5$ ; within white areas counts are arranged effectively at random.

evident for *S. avenae*, which occurred randomly within the field (table 1). Spatial pattern in maximum counts, however, was evident for *M. dirhodum*, with a gap area of low counts within the central part and a single edge of the field (table 1).

*Poecilus cupreus* activity-density was highest in weeks 1 and 2 of the study, followed by a general decline (fig. 1c). Considerable spatial pattern was evident throughout the study, although the strength of clustering declined as the season progressed (fig. 1f). This spatial pattern was

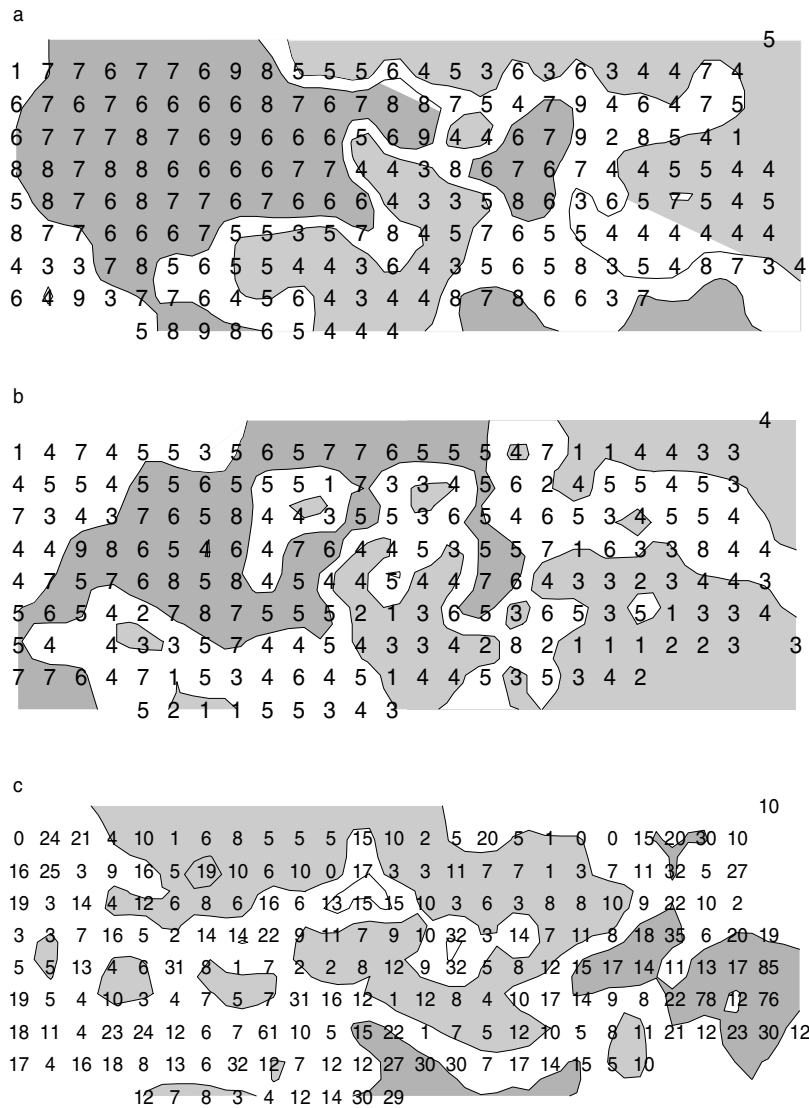


Fig. 3. 'Red-blue' plots of summary population parameters a) and b) peak week for *Sitobion avenae* and *Metopolophium dirhodum* respectively and c) maximum count for *M. dirhodum*. Integers indicate observed data. Darker shading ('red') indicates patch clusters within which interpolated values of  $v_i > 1.5$ ; lighter shading ('blue') indicates gap clusters within which interpolated values of  $v_i < -1.5$ ; within white areas counts are arranged effectively at random.

consistent throughout most of the season with distinct zones of high (in the centre of the field) and low (within the periphery of the field) activity-density respectively (fig. 2). Total activity-density, was up to an order of magnitude higher within the centre of the field compared to its periphery (fig. 4; table 1).

Some variation in the displacement of beetles was observed during the sampling period. During the early part of the study (weeks 1-3), average displacement of individuals varied between 25 m and 40 m. There was then a large apparent increase in displacement, to a mean distance of about 65 m between weeks 4-5, followed by a gradual decline in displacement until the end of the sampling period. Of the 2273 recaptures, 53.1% were female. No differences in

displacement between male and female beetles were evident. Regression of average weekly displacement of *P. cupreus* (D) on total activity-density caught at each location (B) was negative ( $\sqrt{D} = -0.08 \text{Log}_{10}(B+1) + 7.2$ ,  $t = 16.5$ ,  $r = -0.3$ ,  $P < 0.001$ ). No relationship between aphid abundance and displacement was evident. Hence, in spatially explicit terms, the central region of the field where activity-density was highest had *P. cupreus* individuals that tended to exhibit relatively low displacement rates.

No large-scale spatial pattern was evident for crop density (table 1). Mean ( $\pm 1$  s.e.), minimum and maximum crop densities were  $428 \pm 6$ , 220 and 660 shoots  $\text{m}^{-2}$  respectively. Hence, there was considerable local variation in crop density which occurred randomly within the field.

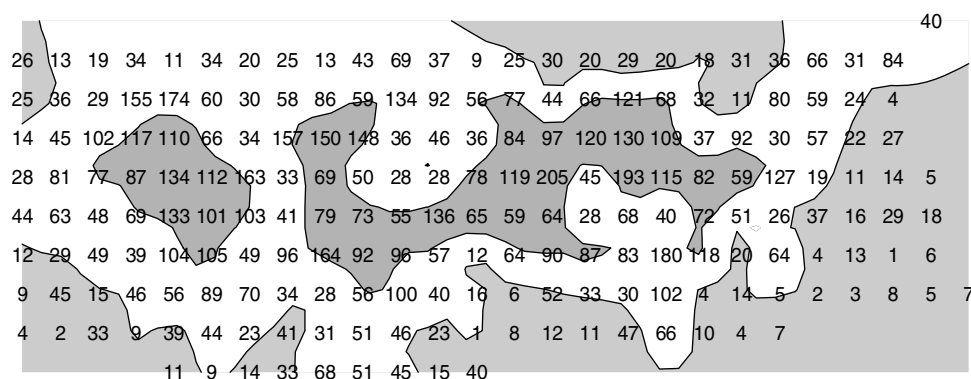


Fig. 4. 'Red-blue' plot of total *Poecilus cupreus* activity-density. For explanation, see fig. 3.

#### Spatial relationships between aphids, beetles and crop density

We investigated whether there was evidence that *P. cupreus* activity-density or crop density influenced aphid population parameters. For *M. dirhodum* there was a negative regression relationship between maximum aphid count (M) on total *P. cupreus* activity-density (B);  $\text{Log}_{10}(M+1) = -0.15\text{Log}_{10}(B+1) + 1.2$ ,  $r = -0.17$ ,  $t = -2.4$ ,  $P = 0.018$ . This was reflected in spatially explicit terms by a strong spatial dissociation ( $X = -0.2732$ ,  $P = 0.0009$ ). Where *P. cupreus* activity-density was concentrated within the centre of the field, *M. dirhodum* counts were generally correspondingly low. Additionally, there was a positive regression relationship between total *P. cupreus* activity-density and the week (W) in which the aphid population peaked ( $\text{Log}_{10}(W+1) = 1.17\text{Log}_{10}(B+1) + 3.2$ ,  $r = 0.25$ ,  $t = 3.6$ ,  $P < 0.001$ ) with strong association in spatially explicit terms ( $X = 0.3028$ ,  $P = 0.001$ ). Hence, at the field scale, locations with high *P. cupreus* activity-density had later-peaking aphid populations.

For *S. avenae*, no relationship between maximum aphid count and *P. cupreus* activity-density was evident, although a positive regression relationship between total *P. cupreus* activity-density and the week in which the aphid population peaked ( $\text{Log}_{10}(W+1) = 0.64\text{Log}_{10}(B+1) + 5.1$ ,  $r = 0.14$ ,  $t = 2.0$ ,  $P = 0.046$ ) occurred with strong positive association in spatially explicit terms ( $X = 0.2746$ ,  $P = 0.0017$ ). Hence, at the field scale, locations with high *P. cupreus* activity-density had late-peaking *S. avenae* populations.

Table 1. Spatial analysis by distance indices (SADIE) gap ( $\nu_j$ ) and patch ( $\nu_i$ ) indices, with associated probabilities, for summary population parameters of *Sitobion avenae*, *Metopolophium dirhodum* and *Poecilus cupreus*.

	Gap index		Patch index	
	$\nu_j$	$P_j$	$\nu_i$	$P_i$
<i>S. avenae</i>				
Peak week	-3.0	<0.001	3.3	<0.001
Maximum count	-0.8	0.79	0.8	0.83
<i>M. dirhodum</i>				
Peak week	-2.6	<0.001	2.6	<0.001
Maximum count	-2.1	<0.001	1.9	<0.001
<i>P. cupreus</i>				
Beetle count	-2.6	<0.001	2.6	<0.001
Crop density	-1.1	0.23	1.1	0.22

For *S. avenae*, maximum count was negatively related to crop density (D);  $\text{Log}_{10}(M+1) = -0.00056\text{Log}_{10}(D+1) + 1.59$ ,  $r = -0.16$ ,  $P = 0.006$ . No such relationship was apparent for *M. dirhodum*. Conversely, regression of crop density on peak aphid week was non-significant for *S. avenae* but a significant negative relationship was evident for *M. dirhodum* ( $W = -0.0031D + 5.76$ ,  $r = -0.13$ ,  $P = 0.05$ ). Hence, although crop density had no large-scale spatial pattern, its variability at the small-scale was consistent with an influence on aphid population dynamics.

#### Discussion

In this study, it has been shown that considerable spatial pattern was evident at the field-scale in populations of both pest (aphid) and beneficial (beetles) insects. As in previous studies, their spatial dynamics are shown to be ephemeral in space and time (Schotzko & O'Keefe, 1989; Schotzko & Quisenberry, 1999; Winder *et al.*, 1999; 2001a; Holland *et al.*, 2004a), particularly for aphids. The reasons for the presence of such spatial pattern remain unclear but it has been demonstrated that at least two factors contribute.

In regions of high *P. cupreus* activity-density, aphid population peak was either delayed or reduced. Whilst it is impossible to completely eliminate an unmeasured confounding variable as the reason for this effect, it is likely that *P. cupreus* was the cause of the observed suppression of aphid population development. It is important to note that the conclusions drawn from the observed regression relationships are corroborated by the expected spatially explicit SADIE associations or dissociations between aphids and *P. cupreus*. *Poecilus cupreus* is a known aphid predator and its observed distribution resulted in order of magnitude differences in activity-density between 'gap' and 'patch' neighbourhoods. The most convincing evidence of a controlling effect was observed for *M. dirhodum*, a species feeding primarily on the lower leaves. *Poecilus cupreus* exhibits efficient systematic sampling, foraging for aphids near the base of cereal plants (Wallin & Ekblom, 1994) and shows some preference for this species (Kielty *et al.*, 1999; Mundy *et al.*, 2000). *Metopolophium dirhodum* is probably more apparent to this ground active predator than the ear-infesting *S. avenae* which may be residing in 'enemy free space' (Jeffries & Lawton, 1984; Hopkins and Dixon, 1997) and therefore less affected by predatory activity-density.

It is also possible to conclude that *P. cupreus* only contributed to pest suppression within a system with a multitude of natural enemies, given that the correlation coefficients of the regression relationships were low. There is little evidence that this species is a primary biological control agent in this system. Indeed, this is what would be expected when a single generalist predator is studied in a highly complex natural enemy system. It would be useful to conduct further studies at the field scale where the spatial pattern of a range of natural enemies (e.g. generalist predators, coccinellids, syrphids, parasitoids, etc.) are recorded simultaneously in relation to those of a pest species to determine whether an additive suppressive (or otherwise) effect could be detected. However, the logistic and resource implications of this approach are very difficult. It would also be informative to conduct a study in fields where higher aphid populations were evident in order to determine whether a similar response was observed.

Repetition in other fields and crops would also be useful to corroborate these conclusions, although similar findings were observed in cereal aphid-*Pterostichus melanarius* (Illiger) (Winder *et al.*, 2001a, 2005) and aphid-carabid larvae (Holland *et al.*, 2004a) studies. Exclusion studies have also shown experimentally that reduced densities of polyphagous predators have shown marked increases in aphid population growth (Edwards *et al.*, 1979; Chiverton, 1986; Schmidt *et al.*, 2003), treatments analogous to the patches and gaps of *P. cupreus* in our unmanipulated field study.

It was also demonstrated that a plant growth parameter, crop density had a 'local' effect. No large-scale spatial pattern was evident for crop density, but it was linked to aphid population parameters at the local scale. A range of other crop quality parameters could be measured (e.g. nutritional status) although it is extremely difficult to do this in relation to the experience of the pest. Honek (1985, 1987) investigated the effects of crop density on the dynamics of *M. dirhodum* and *S. avenae* and concluded that for *M. dirhodum* population growth was advanced and rate of increase was elevated in dense stands and attributed this to microclimate effects. We found that where crop density was highest locally, *M. dirhodum* populations peaked earlier which support this observation. For *S. avenae*, Honek (1985, 1987) concluded that populations increased simultaneously with little measurable crop density effect. In the present study, we found that high crop density areas had lower peak *S. avenae* populations, which may be due to the dispersal of the aphid population between more numerous shoots.

*Poecilus cupreus* showed considerable spatial stability, which was particularly evident early in the season. Other studies of individual carabid species' spatio-temporal distribution have also shown stable patch dynamics within years (Thomas *et al.*, 1998, 2001; Fernandez-Garcia *et al.*, 2000; Holland *et al.*, 2004b, 2005). It is evident, therefore, that there is large-scale spatial self-organization for this species although the cue for this is unclear (i.e. physical environmental, prey availability, reflection from field boundary, etc.). Mathematical models of small-scale ecological interactions predict the self-organization of large-scale spatial patterns (Hassell *et al.*, 1994) although few empirical studies have corroborated their existence (Rohani *et al.*, 1997). Displacement was lower in areas of the field where the highest beetle activity-density was recorded; this suggests firstly that intraspecific competition may be limited and secondly that stable patches within the field were due to

reduced activity (measured as displacement). The reason for the apparent preference for the centre of this field is unknown. One possibility is the presence of sufficient total prey to elicit differential walking behaviour (Wallin & Ekbohm, 1994). It is known that area-restricted search may yield predator aggregation (Kareiva & Odell, 1987) even when an individual's response to prey density may be weak (Ives *et al.*, 1993). However, in a meta-analysis, Langellotto & Denno (2004) were unable to confirm that predator aggregation was attributable to prey availability. Additionally, other abiotic (e.g. soil moisture) or biotic factors may be responsible (reviewed by Thomas *et al.*, 2002). Monsrud & Toft (1999) showed that artificial honeydew caused an aggregative numerical response by aphid natural enemies. It is therefore possible that some other underlying correlated factor might be the causative factor.

The importance of spatial structure (i.e. non-random distributions) in the dynamics of interacting populations, particularly in theoretical studies (Sapoukhina *et al.*, 2003) and the complexity of multi-species systems (Cardinale *et al.*, 2003), is well recognized. The results from the present study suggest that predictive models for use in integrated pest management should include both local and large-scale spatial processes to describe the system. Additionally, precision spraying of insecticides would require detailed knowledge of aphid spatial pattern at the time of application if it was to be applied to target patches of aphids. Further studies would help our understanding of these complex systems to support optimal pest management strategies.

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