

Modelling the dynamic spatio-temporal response of predators to transient prey patches in the field

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Running title: Spatio-temporal response of predators to prey

Type of article: REPORT

Number of words in abstract: 143

Numbers of words in manuscript: 4635 (including references and figure legends)

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Biosketch. Linton Winder's research interests relate to the population dynamics of generalist predators and their prey, and in particular how spatio-temporal pattern mediates such interactions.

Summary

The spatio-temporal dynamics of two aphid species (*Metopolophium dirhodum* and *Sitobion avenae*) and a generalist predator (*Pterostichus melanarius*) were observed in a field-scale study using a grid of 256 sampling locations with a 12m spacing. Using Spatial Analysis by Distance Indices we demonstrate that populations show ephemeral spatial pattern at the field-scale. We observed a positive, lagged beetle response to this aphid pattern; conversely, the aphids displayed a negative, lagged response to beetle spatial pattern. Examination of the local structure of the spatio-temporal dynamics revealed a strong response by the beetle population to aphid patches. The temporal structure of spatial associations between the species show a strong correspondence with those from a conceptual model of predator-prey spatial interaction. The spatially coupled dynamics were sufficiently strong for the predator to have a negative effect on the intrinsic rate of increase of their prey.

Introduction

A major ecological question is the degree to which spatial pattern predicted by theoretical models of predator-prey dynamics (Hassell *et al.* 1991; Comins & Hassell 1996) are observable in the field. Laboratory or microcosm experiments may produce repeatable findings but often relate to much too small a scale (Schindler 1998). The lack of spatially explicit, large-scale field studies is identified as a major obstacle to the understanding of fundamental ecological processes (Steinberg & Kareiva 1997). Most of the data used thus far to study spatio-temporal dynamics have come from large-scale, long-term systems, spanning many generations.

We show that transient spatio-temporal pattern is critical in understanding predator-prey dynamics by surveying an unmanipulated predator-prey system of two aphids (*Sitobion avenae* F. and *Metopolophium dirhodum* Walker) and a generalist predator (*Pterostichus melanarius* Illiger), within a 4ha. field. We show that the spatial distributions of predator and prey are dynamically coupled, and that the effect of this generalist predator is sufficient to suppress prey populations that are considered to be pests.

To support our analysis, we extend the Spatial Analysis by Distance Indices (SADIE) methodology, developed explicitly for the spatial analysis of ecological data in the form of spatially referenced counts (Perry, *et al.* 1999). The technique seeks to identify areas of clustering into patches (neighbourhoods of relatively high density), or into gaps (neighbourhoods of relatively low density) by ascribing an index that quantifies the degree to which the sampled count (at that location) contributes towards clustering. Randomization tests condition explicitly on the observed counts and allow for local

population density, so inferences relate solely to the spatial arrangement of the counts relative to one another. In particular, the magnitude of the patch (or gap) index at a specific location is completely independent of the count there. This approach allows hypothesis testing for the presence of spatial pattern in the form of clustering, both into patches and into gaps, and facilitates the quantification of the size, location and shape of identifiable clusters. The SADIE approach contrasts with geostatistics and allied traditional approaches that utilize correlograms. Firstly, it is designed for situations where species are distributed patchily into discrete aggregations with relatively well-defined boundaries, rather than those where densities may be mapped as relatively smoothly-varying surfaces underpinned by a stationary process. The former cases, where individuals are studied, correspond to Pickett *et al*'s (1994) 'thing ecology' operated on by Stern's (1998) 'Lagrangian' methods - the latter cases to 'stuff ecology' operated on by 'Eulerian' methods. Secondly, SADIE is more concerned with the measurement and testing of spatial pattern, rather than the geostatistical goal of estimation of density in unsampled areas.

Our approach to the study of spatio-temporal dynamics also differs from traditional techniques that use an individual time series as the unit of study. Traditional techniques introduce a spatial component by comparing several such series using cross-correlation or statistics relating to the geographical locations from which the series were derived. Instead, we focus on the spatial structure, and establish the temporal component by studying the evolution of this structure over time. This is achieved by quantifying the similarity between two patterns from different occasions, through the degree of spatial association between them. A new measure of local spatial association, X , is defined, that is a natural extension of the SADIE technique outlined above. Again, this

technique differs from traditional techniques that assess similarity on the basis of correlation between the densities of the two populations in the form of logarithmically transformed counts. By contrast, the new SADIE method assesses similarity on the basis of the clustering indices; this approach therefore intrinsically allows for the spatial pattern in each component population. It deliberately downweights those isolated large- and small- density values with small cluster indices that are locally spatially-random, so X , the new measure of local association, is not greatly affected by noise of this form. We demonstrate that, for the data considered here, this technique has greater power to detect significant association when it is present.

Materials and methods

We monitored the distribution of the aphids *S. avenae* and *M. dirhodum* and the predatory carabid beetle *P. melanarius* in a conventionally managed winter wheat field. Generalist predators are important in limiting exponential increases in their prey (Riechert *et al.* 1999) and a scale intermediate to meters and kilometers is appropriate for the study of *P. melanarius* (Firle *et al.* 1998) which disperses almost entirely by walking. Hence, a 16 by 16 grid, with 12m spacing was used to record field-scale spatial pattern. This yielded $n = 256$ sample units at different locations. For each sampling location counts of aphids were done by the visual inspection of 25 shoots. Activity-density measurements of *P. melanarius* using 24 hour barrier-connected pitfall trapping (Winder *et al.* 2001) were recorded on five sampling occasions at two-weekly intervals.

Perry *et al.* (1999) defined two forms of clusters. A unit, i , within a patch cluster, is one of a neighbourhood of units (sampled locations) each with a count, c_i , that is larger than the sample mean, m ; a unit, j , within a gap cluster is one of several nearby units, each with count, c_j , less than m . An index of clustering is ascribed to each unit; either v_i , for units with $c_i > m$, or v_j , for units with $c_j < m$. For a random arrangement of the counts, v_i has an expectation of 1 and a unit that belongs to a patch is indicated by a value of $v_i > 1$. For a random arrangement of the counts, v_j (which is negative by convention) has an expectation of -1 and a unit that belongs to a gap is indicated by a value of $v_j < -1$. Tests of non-randomness are available, based on randomizations of the arrangement of the observed counts amongst the sample units. In these tests, the mean value of the clustering index over the patch units, \bar{v}_i , is usually compared with its expectation of 1 and, separately, the mean value over the gap units, \bar{v}_j , is compared with its expectation of -1 . Also, critical values U_i and L_j are available for individual values of v_i and v_j , respectively. Following their calculation, the values of the clustering indices may be mapped, interpolated and contoured. We usually define clusters as areas enclosed by contour levels of $+1.5$ or -1.5 ; these indicate clustering ($v_i > 1.5$ or $v_j < -1.5$) half as great again as expected by chance. Whilst arbitrary, the average magnitude of the indices within contours bounded by these ± 1.5 levels have been found to approximate well to values of U_i and L_j corresponding to 95th centiles of their respective randomization distributions. Once identified, clusters may be measured for size, shape, location and proximity to other clusters.

The above analysis was done for each of the five sample occasions for the aphids *S. avenae*, *M. dirhodum*, and the beetle *P. melanarius*, but results are not presented for occasions one and five for the aphid *M. dirhodum*, for which densities were small. The location and size of a cluster is identified by the centroid and the area, respectively, of the region enclosed by the appropriate contour level and these parameters were calculated for the aphids, which may represent local populations within identifiable areas (Hanski & Gilpin 1997) where distinct predator-prey dynamics might develop.

Two populations may be spatially positively associated, negatively dissociated, or occur at random with respect to one another (Perry 1998). Local spatial association was measured using a new index χ_k , based on the similarity between the clustering indices of the two populations, measured locally at the k th sample unit. Suppose the patch and gap indices of population one are denoted z_{k1} , where $k = 1, \dots, n$. Further, suppose they have a mean denoted by q_1 . Similarly, let the n cluster indices of population two be denoted z_{k2} , with mean q_2 . The definition of χ_k is given by:

$$\chi_k = n(z_{k1}-q_1)(z_{k2}-q_2)/[\sum_k(z_{k1}-q_1)^2\sum_k(z_{k2}-q_2)^2]^{1/2}$$

Thus, positive values of χ_k arise from coincidences of patches or of gaps in both populations; negative values from opposite cluster types. Overall spatial association, X , is calculated as the mean of local values, $X = \sum_k \chi_k / n$, and this is in fact equivalent to the simple correlation coefficient between the cluster indices, z_{k1} and z_{k2} , of the two populations, measured over the $k = 1, \dots, n$ values. Significance of X was tested by randomizations, with values of z_k reassigned amongst the units, after allowance for small-scale spatial autocorrelation in z_k from either population (Dutilleul 1993). Local

association was calculated for each of the 25 possible combinations over the five lagged sample occasions, for each of the two predator-prey species pairs, *P. melanarius*-*S. avenae* and *P. melanarius*-*M. dirhodum*. Results are not presented for *M. dirhodum* on the first and last sample occasion, for which too few individuals were recorded. These results were compared with those obtained by calculation of simple correlation coefficients between logarithmically transformed counts, tested for significance after transformation to a Fisher z -score.

In theoretical studies, predator-prey population dynamics are examined using phase-plane analysis in order to investigate relative population change (Crawley 1992). The spatially explicit component of our data allowed us to examine the phase-plane trajectories by vectors calculated locally. Vertical and horizontal components of each vector are the change in standardized *P. melanarius* and *M. dirhodum* density, respectively, between dates. The count c_{kpq} for sample unit k , species p , on date q was standardized to: $d_{kpq} = (c_{kpq} - \bar{c}_{pq}) / s_{pq}$, where \bar{c} and s represent, respectively, the mean and standard deviation of c_k over the values of k . The population vector at unit k was the resultant of the component $(d_{kbq+1} - d_{kbq})$ measured in the y -direction for the beetle and the component $(d_{kaq+1} - d_{kaq})$ measured in the x -direction for the aphid. After a search for the most appropriate scale for analysis, values were calculated using 2×2 blocks of sample units, yielding an 8×8 grid; this helped to overcome the effects of excessive variability and missing values.

Using the same 8×8 grid, the standard measure of logarithmic population growth rate, r_q , was calculated for the change in beetle population between successive dates in each sample unit, $\ln(c_{kbq+1}) - \ln(c_{kbq})$. This was regressed on v_{kaq} , the strength of aphid

clustering on date q , at explicit spatial locations. Separate regressions were done of r_q on patch indices, v_{iaq} , and gap indices, v_{jaq} . Note that since both v_{iaq} and v_{jaq} are independent of aphid density any relationship found is a response to true clustering, rather than to isolated single units with excessively large or small populations.

Finally, we verified the effect of the predator on prey populations by regressing the aphid intrinsic rate of increase (r_m) against predator activity-density, measured by beetle abundance in pitfall traps.

Results

The sampling occasions spanned the peaks in seasonal activity of all three species (Table 1). Both aphid species showed significant clustering into different spatial patterns, and for both the clusters were located in small patch and relatively larger gap areas that were ephemeral in space and time (examples in Figure 1 for near maximal population densities, further details in Table 2). *P. melanarius* clustered in larger areas, which were more persistent after initial large-scale change in activity-density (Figure 1, Table 2).

Local association displayed considerable spatial structure, with clearly separated regions of association and dissociation (examples in Figure 2a,b, for near maximal population densities; other maps had similar form). From the overall association within each map, we constructed interpolated surface plots of the overall associations, for all combinations of simultaneous and lagged occasions through time (Figure 2c,d). The empirically-derived surfaces had a characteristic and similar shape for both prey

species, with contours predominantly in vertical and horizontal, rather than diagonal directions. Simultaneous samples (on main diagonal) show a chronological sequence of null, negative and then positive associations between predator and prey. Statistically significant lagged associations on off-diagonals show *P. melanarius* was predominantly *positively* associated with preceding aphid spatial pattern, whilst aphids were *negatively* associated with preceding *P. melanarius* spatial pattern. The method introduced here for measuring spatial association through clustering indices had relatively large power for the data considered, compared to the more traditional approach of correlating densities. Of the 40 correlations between beetle and aphids calculated by the standard *r*-statistic based on logarithmically-transformed counts, 10 had absolute values between 0.1 and 0.2 and none exceeded 0.2; 4 were significant by a two-tailed *z*-test at the 5% level. By contrast, for the SADIE correlation *X*, 10 had absolute values between 0.1 and 0.2 and 6 exceeded 0.2; 15 were significant by the two-tailed randomization-test at the 5% level. Of course, a full power analysis would require simulations beyond the scope of this paper.

A simple conceptual predator-prey model could be constructed to predict the form of spatial association that might be expected in each of a sequence of phases that occur in an area of undefined size, evolving over an undefined time period (Figure 3). Initially, prey patches form (indicated by red shading, Figure 3), contingent on the spatial location of aphid colonizers, whilst the predator distribution (white shading) is independent of its prey. After a time interval, prey patches are sufficiently apparent to cause an aggregative ('attraction'; phase 0-1) response by the predator, forming a (red)

patch. This leads either to a gap cluster in prey numbers (blue shading) through the direct effects of the predator ('predation'; phase 1-2), or allows the formation of prey patches elsewhere, or both. The consequent reduction in predator activity-density ('dispersal'; phase 2-3) results in a predator gap, which subsequently allows the re-establishment of a prey patch ('prey recolonisation'; phase 3-4). When all combinations of the phases for each trophic type are considered, the predicted spatial association forms a surface through time with simultaneous and lagged phases, analogously to those shown in Figure 2c,d. Similar predator and prey cluster types (red-red or blue-blue) yield positive spatial association (violet shading in Figure 3); dissimilar types (red-blue or blue-red) negative dissociation (green shading). The dynamic spatio-temporal association surface resulting from this model (Figure 3) bears a striking similarity to those from our field observations (Figure 2c,d), especially in the lack of diagonal contours, and in the initially unexpectedly strong vertical and horizontal block patterning.

Local phase-plane trajectories are mapped in Figure 4a. Considerable clustering of vector trajectories occurred, demonstrating spatial autocorrelation, typically on a scale of 4 grid cells each 24 metres square, i.e. of about 2000m². Separate regressions fitted to positive (red) patch indices, v_i , ($t_{38} = 3.48$, $P = 0.01$) and negative (blue) gap indices, v_j , ($t_{22} = 2.11$, $P = 0.046$) showed that increases in activity-density of beetle was related positively to clustering into patches of immediately previous aphid population and negatively to aphid gap clusters, *independently* of aphid density (Figure 4b).

The effect of *P. melanarius* on the population dynamics of *S. avenae* and *M. dirhodum* was confirmed by significant regressions of intrinsic rate of aphid increase (r_m) on predator activity-density (Winder *et al.*, 2000). Negative relationships were evident for *M. dirhodum* between 27 May and 7 June ($r_m = 0.168-0.038 ME_{7/6}$, $P=0.038$) and 21 June to 5 July ($r_m = -0.098-0.048ME_{21/6}$, $P=0.016$; $r_m = -0.093-0.031 ME_{5/7}$, $P=0.041$) and for *S. avenae* between 27 May and 7 June ($r_m = 0.100-0.044 ME_{7/6}$, $P=0.039$) where $ME = \log_{10}(Pterostichus\ melanarius)$ and subscripts indicate sampling occasion. This demonstrates that the predatory beetles had a measurable retardant effect on the rate of aphid population increase.

Discussion

When prey are relatively immobile, predator responses should dominate and consequently spatial distributions should be positively correlated (Sih 1984) and lagged (Turchin 1999), which we have observed in this system. Models predict that foraging causes dynamic change in predator and prey distributions; a patch response mechanism being area-restricted search or 'preytaxis' (Kareiva & Odell 1987; Grunbaum 1998) that may cause pattern spontaneously in a homogeneous domain. Both models and experiments show variability in prey consumption, dependent on prey distribution (e.g. Cappuccino 1987; Holmes *et al.* 1990; Kareiva 1990; Hastings *et al.* 1997; Yasuda & Ishikawa 1999; Bohan *et al.* 2000).

Given that *P. melanarius* is a generalist predator, it is noteworthy that we can detect spatial and temporal linkage with prey items that form only a proportion of the

predator's diet. Additionally, this linkage is sufficiently strong to cause a reduction in aphid intrinsic rate of increase providing evidence of their value as biological control agents. It has been shown that an individual insect's response to aphid density may be extremely weak, but that the cumulative effect of many individuals can produce strong aggregation in areas of high prey density (Ives *et al.* 1993). The scale of movement of 100m² over a 4 week period (Firle *et al.* 1998) and lifespan (>1 year) of *P. melanarius* is consistent with association being mediated by changes in predator activity-density alone. It is also noteworthy that despite the spatial patterns of the two aphid prey species being noticeably different (Figure 1) they yielded similar association surfaces (Figure 2 *c& d*); too little is known of alternative food sources to speculate in detail concerning their likely densities and effects on the interactions described here.

We have demonstrated considerable transient spatial structure both in individual species distributions and in their spatio-temporal dynamic associations. It is difficult to imagine any exogenous factors operating at these scales that could generate spatial heterogeneity to allow predator and prey species to follow the spatio-temporal trajectories demonstrated here. Hence, we conclude that we have provided evidence that the predator-prey field populations are dynamically coupled. Four separate aspects of our observations support this contention: evidence of lagged and unlagged spatial association (Figures 2 *c & d*); spatial autocorrelation (Figure 4a); significant relationships between predator population growth rate and prey cluster indices (Figure 4b); significant negative relationships between prey intrinsic rate of increase and predator activity-density. Additionally, there is concordance between our conceptual model (Figure 3) and our field observations (Figure 2 *c & d*). In order to investigate these observations further, individual-based studies could be undertaken to isolate the

activity- and density- components of the predator's behaviour (Thomas *et al.*, 1998).

Such studies would allow the behavioural components of the conceptual model (Figure 3) to be quantified by characterising the spatial scale and temporal periods over which the phases defined within the model operate.

The results also confirm the utility of studying such dynamics through the evolution of spatial structure in time, and the continuing need for methods that make full use of the spatial information in ecological count data. Further field work is required to establish whether or not the dominant scales of the clusters described here represent the size of areas within which local population regulation occurs, although it must be emphasized that the results described here do not depend on this in any way. Equally, similar outcomes from the model would derive either from movement of the predator or from a purely numerical response; further field work is required to distinguish between these two possible mechanisms.

These results confirm the value of spatially-explicit, large-scale field studies in ecology (Schindler 1998) which support both our theoretical understanding and help the development of applied solutions to pest management problems. They remind us that even such apparently homogeneous environments as cereal monocultures may appear strongly heterogeneous to the species that inhabit them. The ability to locate and measure shapes and sizes of prey and natural enemy patches and gaps offers the prospect of advances in the application of IPM to precision agriculture and the furtherance of environmentally-sensitive, optimally-targeted crop protection measures.

Acknowledgements

IACR-Rothamsted receives grant-aided support from the Biotechnology and Biological Sciences Research Council of the United Kingdom. This study was supported by a BBSRC research grant. We would like to thank three unnamed referees for their help in preparing this manuscript. We thank Barry Green, Jon Mellings, Sarah Oakes, Wayne Sweeting and Paul Thacker for assistance with field work and Roger Wills for generously providing the field site.

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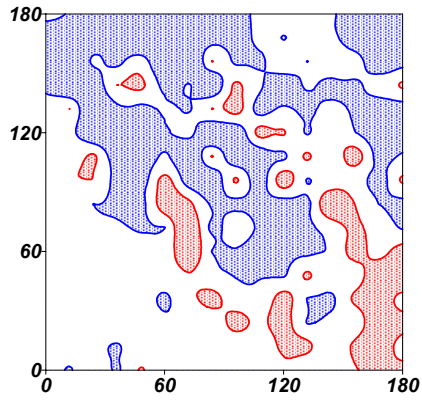
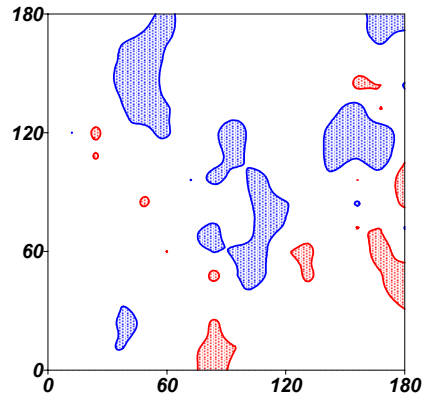
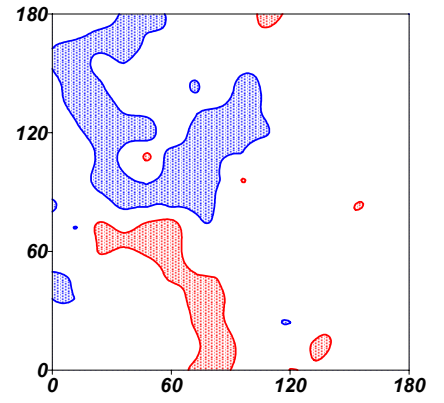
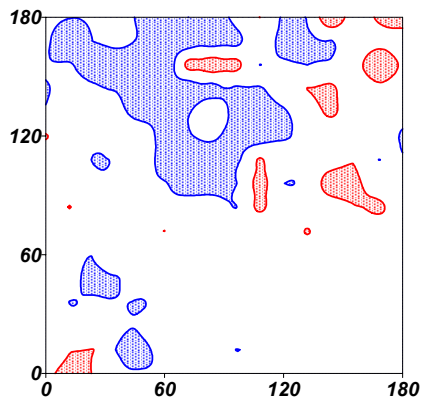
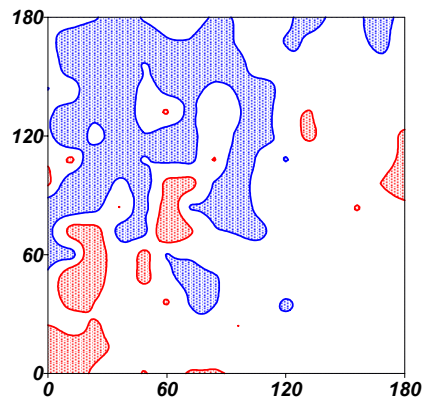
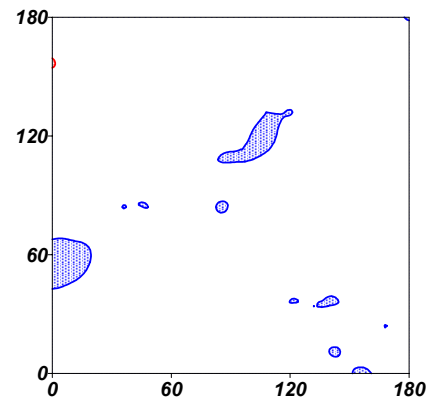
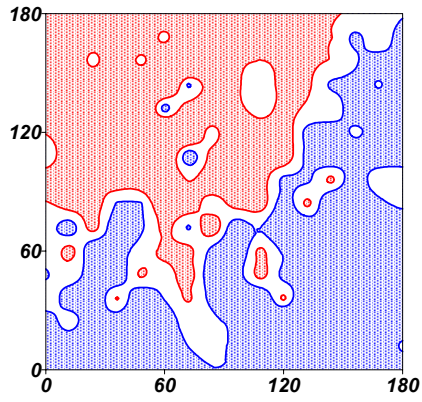
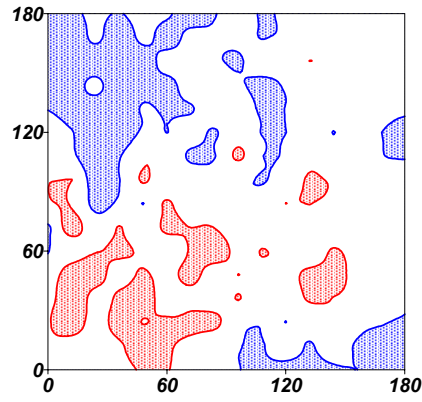
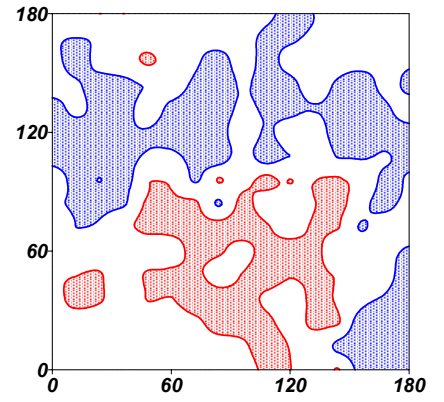
Legends to Figures

Figure 1. Examples of spatial pattern of clustering for two aphid prey species, *S. avenae* (a,b,c) and *M. dirhodum* (d,e,f), and for beetle predator *P. melanarius* (g,h,i), for the middle three sampling occasions on 7 (a,d,g) and 21 (b,e,h) June and 5 July (c,f,i) 1999. The maps indicate clusters of relatively large counts (red 'patches', for which $v_i > 1.5$) and small counts (blue 'gaps', $v_j < -1.5$). Clusters were relatively small and ephemeral for aphids; larger and more persistent after 21 June for the beetle. Further details in Table 2. Axes indicate coordinates in metres.

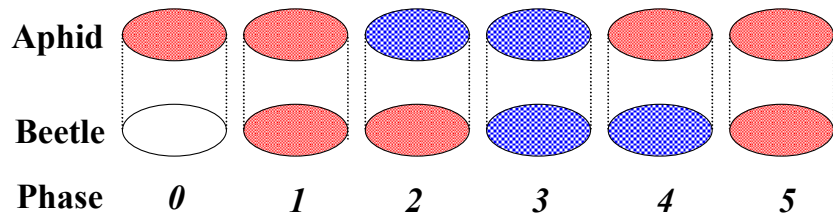
Figure 2. Spatio-temporal association between predator and prey. Association and dissociation are represented in violet and green respectively. **a**, Contour map of local association between *P. melanarius* on 7 June (occasion 2) and *M. dirhodum* on 21 June (occasion 3) shows overall negative dissociation ($x = -0.41$, $P < 0.001$) with considerable spatial structure. Axes indicate coordinates in metres. **b**, as a, but for *P. melanarius* and *S. avenae* on 21 June (occasion 3) showing overall positive association ($x = 0.29$, $P < 0.001$) with considerable spatial structure in similar areas. **c**, Interpolated surface of unlagged (main diagonal) and lagged (above and below main diagonal) associations between *M. dirhodum* (y -axes) and *P. melanarius* (x -axis) with significance indicated by bold contours (six dates omitted due to small population densities). **d**, as c, but for *S. avenae* and *P. melanarius*, shows association surface of similar form.

Figure 3. Simple conceptual model of predator-prey interactions in a local region of arbitrary dimensions, evolving over an undefined time period. Phases indicate periods during which densities of predator and prey are average (white), relatively large (red) or small (blue). Interactions at simultaneous and all lagged phases between predator and prey are measured qualitatively through coincidence or dissonance in the colours representing densities relative to average values, and are displayed on the surface below. Surface shows qualitative degree of expected spatial association, and is positive (violet shading) if phase colours coincide and negative (green shading) if they differ. Compare resulting spatial association surface at various lags with very similar shapes of those from observed data in Figure 2c,d.

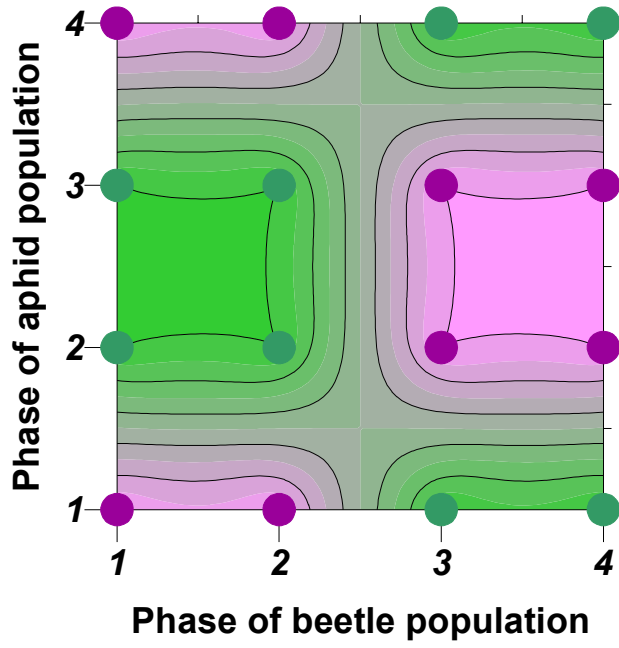
Figure 4. Spatial relationships in population trajectories. **a**, Map of trajectory vectors for combined aphid *M. dirhodum*, and beetle *P. melanarius* populations between 7 and 21 June. Yellow trajectories indicate relative increase in beetle density, blue indicate decrease; lighter shading indicates relative increase in aphid density, darker indicates decrease. Changes in population at a sample unit are therefore expressed relative to other sample units. Axes indicate coordinates in metres. **b**, Regressions of population growth rate for beetle *P. melanarius* between 7 and 21 June, on SADIE cluster indices for aphid *M. dirhodum* on 7 June. Red and blue values relate to patch ($v_i > 1.5$) and gap ($v_j < -1.5$) cluster indices respectively.

A)**B)****C)****D)****E)****F)****G)****H)****I)**

A)



B)



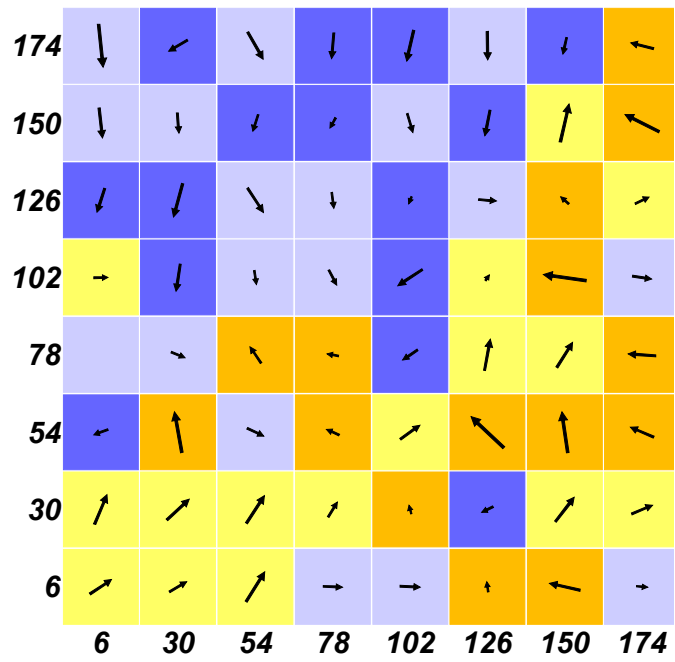
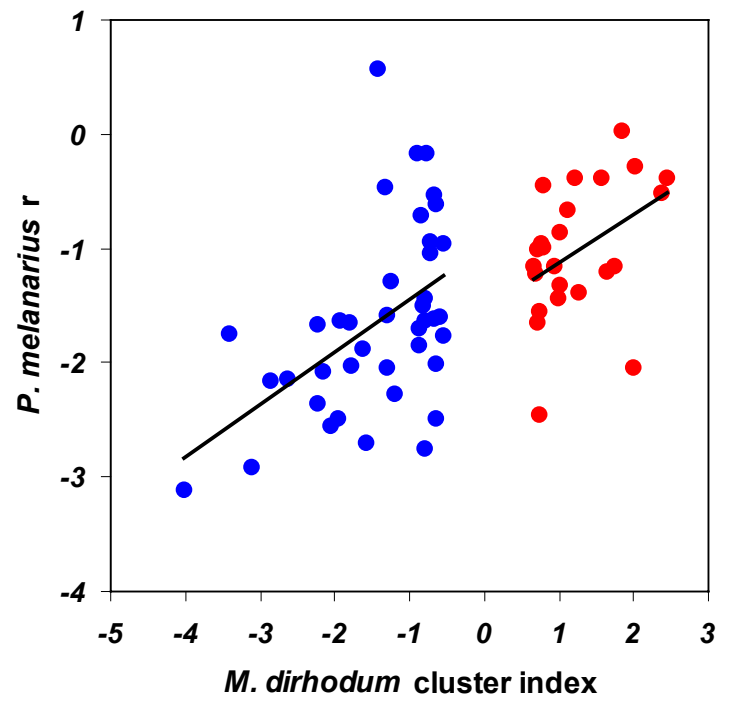
A)**B)**

Table 1. Summary statistics of beetle (*P. melanarius*) predator and aphid prey (*S.avenae* and *M. dirhodum*) showing mean, standard error (s.e.m.) and variance for each species on 5 sampling occasions.

Occasion	<i>P. melanarius</i>			<i>S. avenae</i>			<i>M. dirhodum</i>		
	mean	s.e.m.	variance	mean	s.e.m.	variance	mean	s.e.m.	variance
1	1.82	0.10	2.3	1.17	0.12	3.9	0.11	0.06	0.8
2	14.8	0.61	87.7	3.32	0.31	24.0	3.27	0.35	31.7
3	2.88	0.20	10.4	8.33	0.48	58.0	12.01	0.81	167.1
4	10.8	0.60	91.2	6.32	0.37	27.5	1.67	0.26	13.9
5	7.29	0.50	63.8	2.68	0.21	11.1	0.02	0.01	0.03

Table 2 Mean cluster index, \bar{v}_i for patches and \bar{v}_j for gaps, with associated probability, P , from randomization test, for beetle predator and aphid prey; also, number, N , and mean area (m^2) of identified clusters, for aphids recorded on 5 sampling occasions.

Occasion	Cluster Type	<i>P. melanarius</i>			<i>S. avenae</i>			<i>M. dirhodum</i>					
		Cluster Index	P	Cluster Index	P	N	Mean Area	s.e.m.	Cluster Index	P	N	Mean Area	s.e.m.
1	patch	1.40	0.013	1.32	0.033	14	62	33	-	-	-	-	-
1	gap	-1.49	0.006	-1.28	0.056	6	1239	831	-	-	-	-	-
2	patch	3.98	<0.001	2.12	<0.0002	22	154	80	1.45	0.011	13	107	32
2	gap	-3.92	<0.001	-2.17	<0.0002	11	1033	759	-1.36	0.0263	13	479	380
3	patch	1.55	0.002	1.18	0.097	13	81	35	1.63	0.0015	16	144	59
3	gap	-1.80	<0.001	-1.15	0.144	12	313	119	-1.81	<0.0002	7	1211	1065
4	patch	1.57	0.002	1.28	0.047	7	269	236	0.89	0.735	1	8	-
4	gap	-1.90	<0.001	-1.22	0.083	7	665	634	-0.89	0.744	12	76	41
5	patch	2.46	<0.001	1.22	0.072	10	146	54	-	-	-	-	-
5	gap	-2.60	<0.001	-1.13	0.156	21	124	61	-	-	-	-	-