# Population dynamics of cereal aphids: Influence of a shared predator and weather

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# Population dynamics of cereal aphids: influence of a shared predator and weather

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**Abstract**

1 Aphid populations may show strong year-to-year fluctuations, but questions remain regarding the dominance of factors that cause this variation, especially the role of natural enemies. To better understand the dynamics of aphid species that occur as pests in cereals, we investigated the relative influence of top-down control by a predator and weather (temperature and precipitation) on population fluctuations of three cereal aphid species.

2 From 1987 to 2005, populations of *Metopolophium dirhodum*, *Sitobion avenae* and *Rhopalosiphum padi* in insecticide-free stands of winter wheat were monitored in the Praha-Ruzyné region of the Czech Republic. Densities of an aphidophagous predator, the ladybeetle *Coccinella septempunctata*, were recorded from an overwintering site in the landscape. Weather was quantified using historical records.

3 A significant bottom-up effect of densities of aphids on those of *C. septempunctata* was found, but evidence of direct top-down regulation of aphids by *C. septempunctata* was only significant in the case of *R. padi*. There was no significant periodicity in the dynamics of the aphid or *C. septempunctata*, suggesting that there was no clear predator-prey cycle. Combinations of *C. septempunctata* and weather variables could be used to explain *M. dirhodum* and *R. padi* per capita rate of change. There were also indications that weather directly affected peak density of *M. dirhodum*.

4 We conclude that regional estimates of *C. septempunctata* densities are not sufficient to determine whether aphid population dynamics are driven by predator–prey interactions. Feasibility of time series analysis as an investigative tool in aphid population dynamics studies is discussed.

**Keywords** *Coccinella septempunctata*, *Metopolophium dirhodum*, partial rate correlation function, predator-prey interaction, population dynamics, *Rhopalosiphum padi*, *Sitobion avenae*, time series analysis.

## Introduction

Explaining and modelling the processes that drive population dynamics of pests is a central issue in pest management. Aphids are major pests in many crops throughout the world and their populations often show strong year-to-year fluctuations (Blackman & Eastop, 2000). Aphid population dynamics are affected simultaneously by a range of biotic and abiotic factors. For example, it is well established that temperature (Xia *et al.*, 1999; Kuo *et al.*, 2006), natural enemies (Landis & van der Werf, 1997; Costamagna & Landis, 2006), pathogens (Karley *et al.*, 2004) and plant quality (van den Berg *et al.*, 1997; Williams *et al.*, 1999; Karley *et al.*, 2004) can affect aphid population dynamics. Although each factor may have the potential to substantially affect aphid populations, some factors may be stronger or act more frequently, governing the overall dynamics of aphid populations to a larger extent, whereas other factors may contribute more to the 'noise'. Although Dixon (1990) identified competition for host resources as the main cause of

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seasonal fluctuations in monoecious tree-dwelling aphids, less is known about what factors are the main drivers of population fluctuations of heteroecious aphids, some of which are notorious pests in agricultural crops.

Numerous investigations have examined the influence of bottom-up (i.e. host quality) and top-down (i.e. natural enemies) forces shaping within-season aphid population growth by manipulating environmental factors to isolate these effects. Studies focusing on bottom-up forces include effects of planting density (Honěk & Martinková, 1999) and water availability (Moran & Whitman, 1988). Poor plant quality leads to increased intra-specific competition among aphids, which limits the carrying capacity for aphids. Studies focusing on top-down effects often utilize exclusion cages, and have effectively highlighted the capacity of natural enemies to hinder aphid population development (Landis & van der Werf, 1997; Costamagna & Landis, 2006). Only a few studies have tried to separate out and quantify the relative importance of top-down versus bottom-up forces shaping aphid population dynamics (Stadler, 2004; Costamagna & Landis, 2006). When Costamagna & Landis (2006) compared the effects of different soybean production regimes (bottom-up effect) and predator exclusion (top-down effect) on the development of soybean aphid populations, they found that natural enemies had a stronger effect on aphid population development than host quality.

Such manipulative experimentation is useful for testing hypotheses regarding the underlying mechanisms driving aphid population growth. However, it difficult to test whether these mechanisms can be used to sufficiently explain ‘real world’ aphid population dynamics over longer time scales. Although it is nearly impossible to use experimentation to investigate aphid fluctuations at decadal or multidecadal time scales, time series analysis of long-term data sets represents a complementary approach to manipulative experimentation that may provide us with a better understanding of aphid dynamics (Turchin, 2003). Long-term measurements of aphid densities and the environmental factors that may be regulating their dynamics are rare and the paucity of long-term data sets is exacerbated in agricultural settings by the frequency of changes in agricultural land use (Yamamura *et al.*, 2006). Therefore, when available, such data sets present a unique opportunity to examine patterns in natural populations. Time series analyses can act as a bridge between short-term mechanistic experimentation and process-based modelling; they can be used to validate results from manipulative experiments and also provide ‘truthing’ data for process based models that can then be used more confidently when scaling up temporally or spatially.

In the present study, we used times series analysis of long-term data sets of aphid densities and a shared predator from the Czech Republic to examine patterns and predator-prey relationships in natural settings. We present an 18-year time series of densities of three cereal aphid species, *Metopolophium dirhodum* (Walker), *Sitobion avenae* (Fabricius) and *Rhopalosiphum padi* (L.), and a coccinellid predator, *Coccinella septempunctata* (L.). These aphid species are common in cereal crops of central and western Europe (Vickerman & Wratten, 1979; Dixon, 1987) and re-colonize cereal fields each year by migrating from their respective winter hosts: rose (*M. dirhodum*), wild grasses (*S. avenae*) and bird cherry (*R. padi*). *Coccinella septempunctata* is a common predator in cereal fields and feeds on all three aphid species (Hauge *et al.*, 1998). In the Czech Republic, *C. septempunctata* has one generation per year and hibernates in aggregations on hilltops in the study region, where their densities provide a reliable estimate of population numbers in the surrounding fields during the preceding summer (Honěk, 1989; Honěk & Martinková, 2005).

In addition to the coccinellid data, we collected historical temperature and precipitation data, which allowed us to examine the influence of both weather variables and predation on long-term aphid dynamics. Weather affects aphids in a density independent manner and is unlikely to cause aphid dynamics to operate on any detectable cycle. By contrast, top-down control of aphids by natural enemies often involves time-delayed density-dependent interactions, which may generate population cycles (Turchin, 2003). The presence of population cycles can therefore indicate strong top-down control, although the lack of predator–prey population cycles does not necessarily mean that predation is not important, which could be explained in a combined model.

Based on the available data, we investigate four hypotheses of what drives long-term cereal aphid dynamics: (i) predation by *C. septempunctata* is the main factor driving aphid population fluctuations; (ii) direct effects of temperature and precipitation are the main factor driving aphid population fluctuations; (iii) both predation by *C. septempunctata* and direct effects of temperature and precipitation drive aphid population fluctuations; or (iv) the null hypotheses that predation, temperature and precipitation do not drive aphid population fluctuations, implying that they are instead driven by unidentified or stochastic phenomena. These hypotheses are hereafter referred to as ‘predation’, ‘weather’, ‘combined’, and ‘noise’, respectively.

We assessed the credibility of the hypotheses by performing six statistical analyses that may provide weight of evidence for each hypothesis, based on how aphid populations would theoretically respond to each. It is important to note that, although we tested these hypotheses statistically, biologically we are investigating the existence of patterns. The analyses focused on: (i) synchrony in between-year fluctuations of the three aphid species; (ii) the relationship between aphid peak density and *C. septempunctata* overwintering densities; (iii) the relationship between *C. septempunctata* overwintering densities and aphid per capita rate of change from 1 year to the next; (iv) the presence of population cycles for aphids and *C. septempunctata*; (v) the relationship between aphid peak densities and temperature and precipitation; and (vi) a final multiple regression analysis incorporating *C. septempunctata* densities, temperature and precipitation to detect the relative effects of each of these factors.

Our philosophical approach to the analyses and how they relate to the hypotheses are detailed below. Analysis (i) was used to establish whether the three aphid species’ dynamics are synchronous, indicating that they are probably responding to environmental factors or a shared predator in a similar fashion. Analyses (ii) and (iii) tested the predation hypothesis by looking at the top-down and bottom-up relationships between the aphids and *C. septempunctata*. Analysis (iv) indirectly examined the possibility of a density-dependent predator–prey relationship by looking for statistically significant cycles in the aphid dynamics that would not be expected if a stochastic force, such as weather, was driving the dynamics. Analysis (v) tested the weather hypothesis by examining direct relationships between weather variables (temperature and precipitation) and aphid peak densities. Lastly, analysis (vi) considered multiple factors driving aphid dynamics, thus testing our combined hypothesis. The most plausible hypothesis was identified by comparing the expected outcomes for each of the hypotheses and the actual results of the analyses (Table 1).

## Materials and methods

### Aphid counts

Aphid counts were made from 1987 to 2005 in production stands of winter wheat at Praha-Ruzyně (50°05′N, 14°10′E, 340 m a.s.l.) in the western Czech Republic. The cereals were cultivated in accordance with recommended agriculture practices (Honěk & Martinková, 2005). No insecticides were applied during the study, and fungicides and liquid fertilizers were sprayed early in the season before aphids and coccinellids arrived. Every year, 5 × 5-m sampling plots were established in a line transect across several adjacent wheat fields located at the Crop Production Institute in Praha-Ruzyně. Within a field, plots were 30–50 m apart, with a 30 m minimum distance from the field margin. The number of plots varied but, in most years, there were three replicates. Each summer, weekly aphids counts were conducted on 50–300 tillers per plot during the 6–10 weeks that they were present in the wheat. Data were recorded as aphids per tiller within each replicate and mean weekly densities were calculated by averaging across replicates. Analyses were based on annual peak density ($A_t$) for each species, where '$t$' is an index for year. Annual peak densities were calculated from 3-week moving averages. A previous study showed that peak density is strongly correlated with aphid load, which is the area under the abundance curve (Honek, 1992). A value of 0.0011 was added to all aphid density records to eliminate zeroes (with 0.0011 being the lowest possible density if one aphid was found in a sampling period) and values were then log-transformed for all analyses. Aphid per capita rate of change from 1 year to the next was calculated as $\ln(A_{t+1}/A_t)$ and is referred to hereafter as $r_t$.

### Coccinellid counts

Overwintering densities of *C. septempunctata* were assessed every autumn from 1987 to 2005 by counting the number of adults in 300 to 800 grass tussocks at the top of the hill, Rana (50°24′N, 13°46′E, 400 m a.s.l.; Honěk, 1989). The study area is a homogenous wheat-growing region, and Rana, the highest point of elevation in the region, is a permanent grassy steppe that is conducive to long-term monitoring of overwintering coccinellids. As *C. septempunctata* adults aggregate at this site from the surrounding area, these counts provide a reliable estimate of *C. septempunctata* density at the landscape scale (Honěk, 1989; Honěk & Martinková, 2005). Data were recorded as *C. septempunctata* per grassy tussock, denoted as $C_{t+1/2}$ because densities were recorded in the autumn interceding aphid counts in the summer, represented by $A_t$ and $A_{t+1}$.

### Statistical analysis

Synchrony among the yearly fluctuations of the three aphid populations was assessed through regression of aphid peak densities for each pair of aphid species. A significant positive correlation indicates (a degree of) synchrony in the year-to-year dynamics of the aphids. To examine the predator-prey relationship between the aphids and *C. septempunctata*, we first examined the bottom-up effect of aphids serving as food resource for *C. septempunctata*, by regressing $C_{t+1/2}$ on $A_t$, which examines how *C. septempunctata* overwintering density was influenced by the preceding peak aphid density. To diagnose a possible top-down effect of *C. septempunctata* feeding on aphids, we regressed $r_t$ on $C_{t+1/2}$, which examined how *C. septempunctata* density may have influenced aphid per capita rate of change. All regressions were made separately

**Table 1** The expected outcomes and test results for six analyses investigating various hypotheses explaining population fluctuations of aphids in winter wheat ($C_{t+1/2}$ = overwintering density of *Coccinella septempunctata*; $A_t$, Aphid peak density; $r_t$, per capita rate of change of aphid population)

| | Hypotheses | | | | |
|---|---|---|---|---|---|
| Analysis | Predation | Weather | Combined | Noise | Test result |
| Fluctuations in aphid populations are synchronous | Yes | Yes | Yes | – | Yes |
| $C_{t+1/2}$ is positively correlated with $A_t$ | Yes | No | Yes | No | Yes[a] |
| $r_t$ is negatively correlated to $C_{t+1/2}$ | Yes | No | Yes | No | Yes[a] |
| Delayed density-dependent feedback in aphid population dynamics | Yes | No | – | – | No |
| Relationship between $A_t$ and weather conditions | No | Yes | Yes | No | Yes[a] |
| Both weather and C7 in multiple regression analysis | No | No | Yes | No | No |

An overview of four hypotheses is shown: predation (predation by *C. septempunctata* as main driving factor); weather (temperature and precipitation as main driving factors); combined (both predation by *C. septempunctata* and temperature and precipitation as main driving factors); noise (null hypothesis; year to year fluctuations in densities driven by unidentified or stochastic phenomena).

[a] Conclusion based on significant result for at least one aphid species.

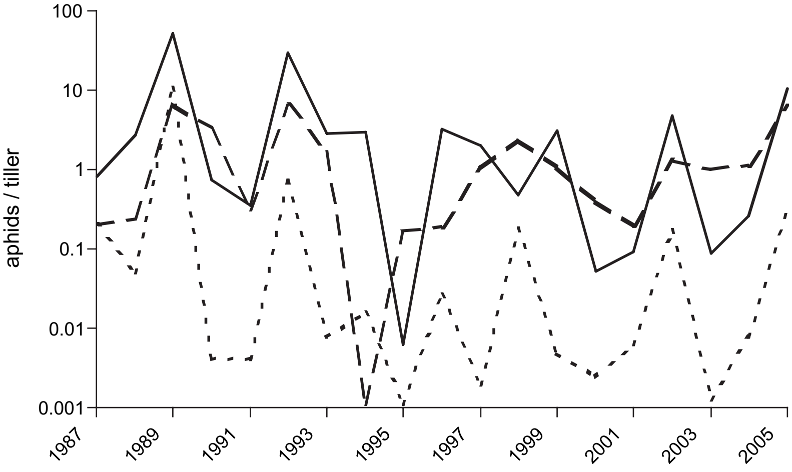

**Figure 1** Observed peak densities (log scale) of three aphid species in winter wheat in the Praha-Ruzyné region of the Czech Republic from 1987–2005. Solid line, *Metopolophium dirhodum*; dashed line, *Sitobion avenae*; dotted line, *Rhopalosiphum padi*.

for each aphid species as well as for pooled peak densities, representing peak total aphid density. Both linear and quadratic components of the predictors were tested via regression analysis in SAS, version 9.1 (SAS Institute, 2006).

The influence of temperature and precipitation on aphid population dynamics was assessed by regressing $A_t$ on average temperature and cumulative precipitation during the aphid infestation period in wheat (May and June). Again, regressions were performed separately for each species as well as for peak total aphid density. Both the linear and quadratic components of temperature and precipitation were tested using SAS, version 9.1 (SAS Institute, 2006). Quadratic effects with a significant negative regression coefficient indicate that there is an optimal value of weather variables for aphid development. Weather data were retrieved from the historical weather records of the Research Institute for Crop Production (Czech Republic) or www.tutiempo.net. Because both temperature and precipitation were used independently as predictors, we first examined the potential of multicollinearity before conducting the regression analyses.

Regulation and feedback in aphid and coccinellid population fluctuations over the years that could be indicative of a predator–prey cycle were assessed with partial rate correlation function (PRCF) using Non-Linear Time Series Modeling (NLTSM) software (Turchin, 2003). PRCF examines periodicity in a population times series by comparing per capita rate of change times series to log-transformed population density time series at lagged intervals, and removes the effect of smaller lags on larger lags by performing stepwise regression (Berryman & Turchin, 2001; Turchin, 2003). Using cross-validation, the NLTSM program proposes the process order (i.e. number of lag structures needed to explain dynamics) for the statistical model and quantifies the ability of the proposed model to predict values one time step ahead, which is expressed in the coefficient of prediction ( $R^2_{\text{pred}}$ ). An $R^2_{\text{pred}}$ value equal to 1 indicates perfect prediction whereas an $R^2_{\text{pred}}$ of zero or less indicates a prediction no better than the mean of the time series (Turchin, 2003).

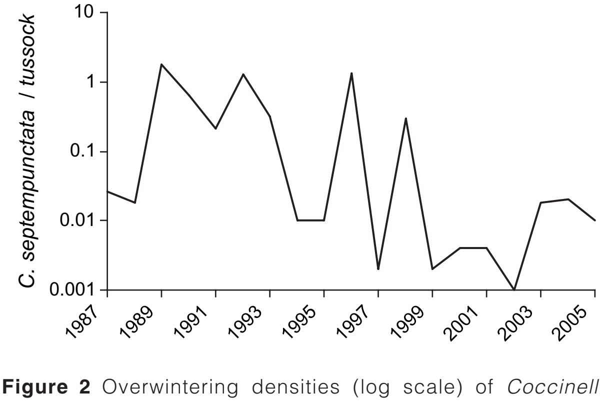

**Figure 2** Overwintering densities (log scale) of *Coccinella septempunctata* in the Praha-Ruzyné region of Czech Republic from 1987–2005.

For results indicating first-order density dependence in the aphid population dynamics (significant negative PRCF value at time step of 1 year), a randomization (rts) procedure in R version 2.4.1 (R Development Core Team, 2006) was used to check against spurious correlation. The randomization procedure, developed by Pollard and Lakhani (1987), compares the negative correlation between $r_t$ and $\log(A_t)$ from the empirical data ($x_1$) with the correlation coefficients generated from the time series randomized 1000 times ($y_i$, for *i* in 1:1000). The results are calculated as *P*-values based on the proportion of times $x_1 > y_i$.

Finally, we tested the combined hypothesis using a series of multiple regression analyses with $A_t$ or $r_t$ (for each species individually and total peak aphid density) as the response variable and *C. septempunctata* overwintering density, temperature (both linear and quadratic terms) and precipitation (both linear and quadratic terms) as regressors.

## Results

### Aphid and coccinellid population dynamics

The 18-year time series of peak densities for each of the three aphid species was in the range 51.01–0.0011 aphids/tiller, often with strong fluctuations from 1 year to the next (Fig. 1). The dominance distribution of the three aphid species was fairly consistent from year to year, with *M. dirhodum*

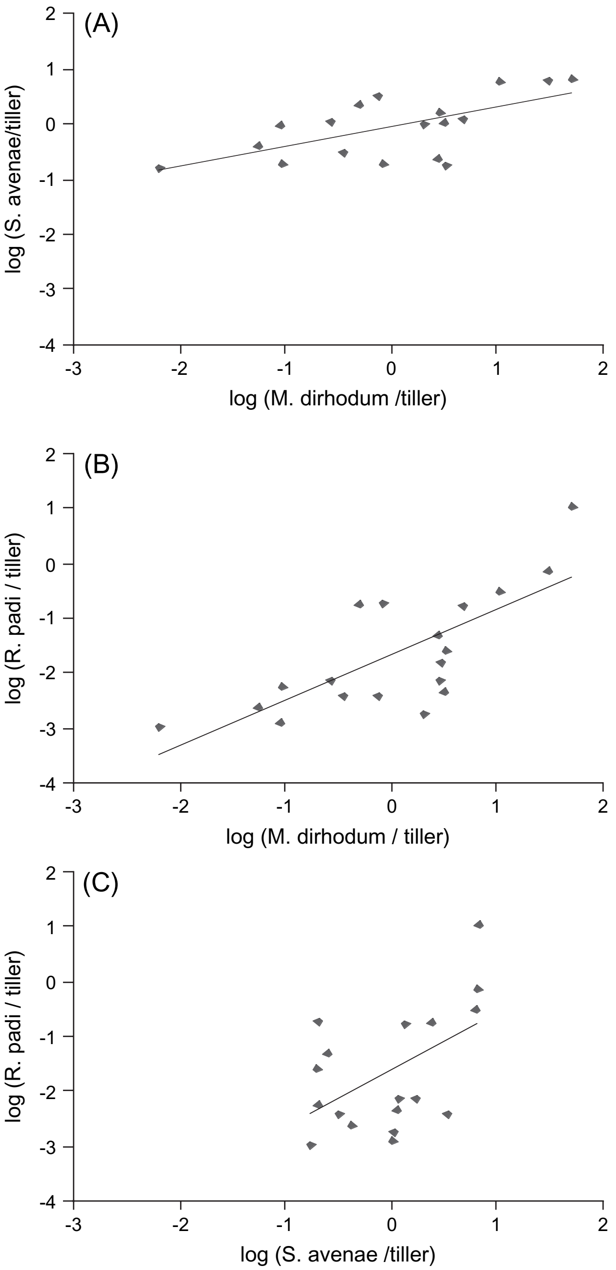

**Figure 3** Pairwise comparisons of log-transformed peak densities of (A) *Metopolophium dirhodum*, (B) *Sitobion avenae* and (C) *Rhopalosiphum padi* in winter wheat.

usually the most abundant, *S. avenae* the second most abundant, and *R. padi* the least abundant (Fig. 1). Three years (i.e. 1989, 1992 and 2005) stood out as 'outbreak' years, with pooled peak aphid density exceeding 15 aphids per tiller. In 1989, pooled peak aphid density reached the highest observed level: 68.6 aphids per tiller. The overwintering density of *C. septempunctata* also varied greatly between years with densities in the range 0.001–1.72 *C. septempunctata* adults per tussock (Fig. 2). The time series also revealed a declining trend in log-transformed *C. septempunctata* densities over the 18 years ($F = 6.73$, $P = 0.019$, $R^2 = 0.28$).

## Patterns in aphid and *C. septempunctata* population dynamics

Regression analyses indicated that all aphid species displayed synchronous population fluctuations over the years (Fig. 3), suggesting that all responded to similar external factors. All comparisons between peak densities of each pair of species yielded significant positive correlations, with *R. padi* and *M. dirhodum* exhibiting the greatest synchrony (*S. avenae* versus *M. dirhodum*: $F_{1,16} = 10.6$, $P = 0.005$, $R^2 = 0.40$; *R. padi* versus *M. dirhodum*: $F_{1,17} = 21.37$, $P = 0.0002$, $R^2 = 0.56$; *R. padi* versus *S. avenae*: $F_{1,16} = 5.84$, $P = 0.028$, $R^2 = 0.27$).

Because both the aphid and *C. septempunctata* populations exhibited large fluctuations over the years, we examined the possibility that this may be driven by a predator-prey relationship. Overwintering densities of *C. septempunctata* were affected by the peak aphid density in the preceding summer, indicating a bottom-up effect from the aphid food source (Fig. 4). The overwintering density of *C. septempunctata* was significantly positively correlated with quadratic components of the peak density of each aphid species (except for *S. avenae*) and total aphid peak density in the preceding summer (*M. dirhodum*: $F_{2,16} = 7.51$; $P = 0.005$; $R^2 = 0.48$; *S. avenae*: $F_{2,16} = 2.47$; $P = 0.12$; $R^2 = 0.23$; *R. padi*: $F_{2,16} = 7.22$; $P = 0.006$; $R^2 = 0.47$; Total: $F_{2,16} = 9.91$; $P = 0.002$; $R^2 = 0.55$).

When examining top-down effects of *C. septempunctata* on aphid per capita rate of change, a weaker relationship than the bottom-up effect was found (Fig. 5). Aphid per capita rate of change was negatively correlated to overwintering *C. septempunctata* densities; however, this relationship was only significant for *R. padi* ($F_{1,16} = 10.8$; $P = 0.005$; $R^2 = 0.40$) and marginally significant for total aphid growth rate ($F_{1,16} = 3.69$; $P = 0.07$; $R^2 = 0.19$). The relationship was not significant for *M. dirhodum* ($F_{1,16} = 2.04$; $P = 0.17$; $R^2 = 0.11$) and *S. avenae* ($F_{1,16} = 0.72$; $P = 0.41$, $R^2 = 0.08$).

Additional evidence of a predator–prey relationship was examined by looking for population cycles using PRCF. PRCF showed no long-term cycles except for a significant negative correlation at a time lag of 1 year for each aphid species individually and total peak aphid densities (Fig. 6). However, further investigation of the PRCF analysis indicated that the results were caused by a spurious negative correlation between aphid per capita rate of change and densities at a time lag of 1 year. This spurious correlation was evident by the negative $R^2_{\text{pred}}$ values in NLTSM and the results of the randomization procedure where the negative correlation from the empirical data was compared with correlations from the time series randomized 1000 times. In all cases, no species seemed to be operating in a significant first-order density-dependent fashion (*M. dirhodum*: $P = 0.362$; *S. avenae*: $P = 0.839$; *R. padi*: $P = 0.275$; pooled aphid species: $P = 0.525$). PRCF for *C. septempunctata* showed a significant negative correlation at a time lag of 1 year (Fig. 7). As with most of the aphids, the $R^2_{\text{pred}}$ was negative and the randomization procedure indicated lack of first-order density dependence ($P = 0.59$).

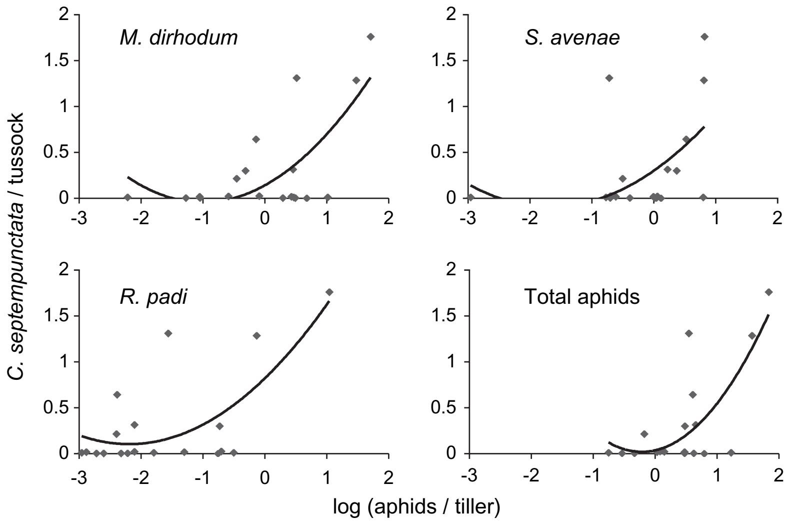

**Figure 4** Relationship between overwintering densities of *Coccinella septempunctata* and log-transformed peak densities of three aphid species and total aphid peak density in the preceding summer.

## Weather

Peak total aphid densities exhibited a quadratic relationship with precipitation (Fig. 8) and temperature. This relationship was marginally significant for cumulative precipitation ($F_{2,15} = 3.19$, $P = 0.07$, $R^2 = 0.30$), but was not significant for average temperature in May and June ($F_{2,15} = 1.98$, $P = 0.17$, $R^2 = 0.21$). For individual aphid species, only the relationship between *M. dirhodum* and precipitation (both linear and quadratic components) was significant ($F = 4.73$, $P = 0.026$, $R^2 = 0.39$). In general, years with very high or low cumulative precipitation and temperatures tended to result in low aphid densities and, conversely, in the 3 years of aphid outbreaks, temperature and precipitation were in the middle of their respective ranges. One data point (precipitation = 208.7 mm; log aphid peak density = −0.75) in the precipitation analysis represented a possible outlier (Fig. 8). We tested the impact of the data point as a multivariate outlier by assessing its Mahalanobis distance. Chi-square with two degrees of freedom at $P < 0.001$ was used as a criterion (Meyers *et al.*, 2005) and the analysis indicated that the data point was not a multivariate outlier. Consequently, it was retained in all the analyses.

To assess whether the bottom-up and top-down relationships between aphids and *C. septempunctata* may have been confounded with weather effects, we also examined the relationship between *C. septempunctata* and weather conditions. The density of *C. septempunctata* was not significantly related to precipitation or temperature (Precipitation: $F = 0.59$, $P = 0.56$, $R^2 = 0.07$; Temperature: $F = 0.16$, $P = 0.86$, $R^2 = 0.02$). This result suggests that the relationship between aphid and *C. septempunctata* densities is not driven by weather effects on *C. septempunctata* density.

## Multiple regression analysis

To test the combined effect hypothesis, a series of multiple regression analyses were run with $A_t$ or $r_t$ as the response variable and *C. septempunctata* overwintering density, precipitation (linear and quadratic components) and temperature

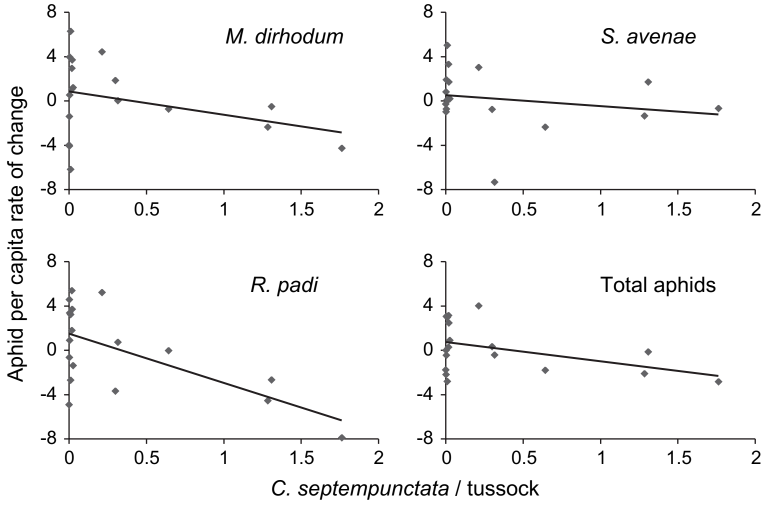

**Figure 5** Relationship between overwintering density of *Coccinella septempunctata* and population growth rates of the three individual aphid species and total aphid per capita rate of change. Aphid per capita rate of change was calculated from the change in peak density from 1 year to the next ($\log N_{t+1} - \log N_t$).

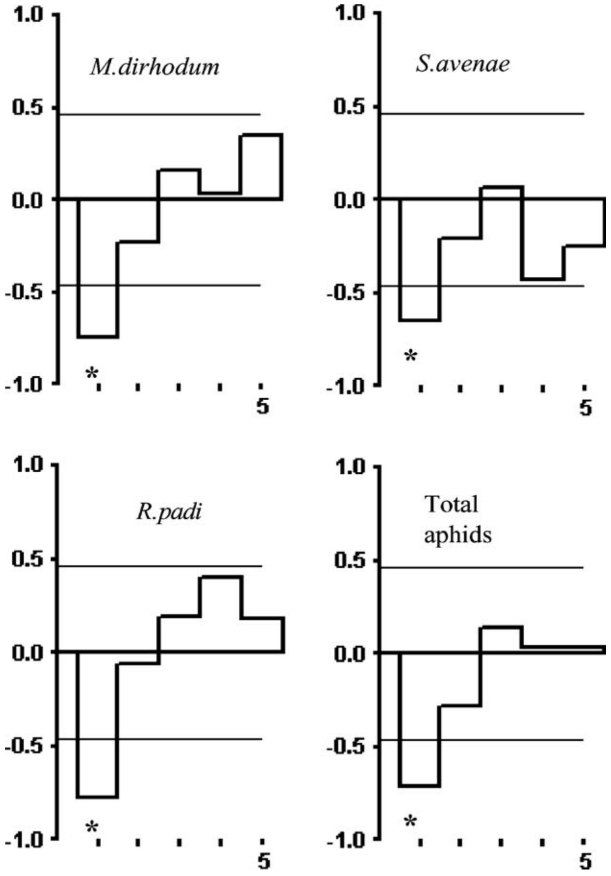

**Figure 6** Partial rate correlation function (PRCF) for peak densities of *Metopolophium dirhodum*, *Sitobion avenae* and *Rhopalosiphum padi* and the combined aphid species in winter wheat. Significant correlations at time step of 1 year is indicated with an asterisk ($P < 0.05$).

(linear and quadratic components) as regressors. When $A_t$ was the response variable, only weather variables were significant predictors (Table 2). However, when $r_t$ was used as a response variable, both *C. septempunctata* and weather variables were significant (Table 3). In the case of *S. avenae*, no predictors were significant in either model.

## Discussion

In the present study we tested three hypotheses (predation by *C. septempunctata*, direct effects of temperature and precipitation, and both predation by *C. septempunctata* and direct effects of temperature and precipitation) against the null hypothesis of random noise to explain the fluctuations in aphid dynamics by conducting a series of analyses that may support each of the hypotheses (Table 1). One out of four test results supported the noise hypothesis, four out of the six test results supported predation and weather hypothesis, and four out of five supported the combined predation and weather hypothesis. We conclude therefore that both predation and weather factors influence aphid population dynamics.

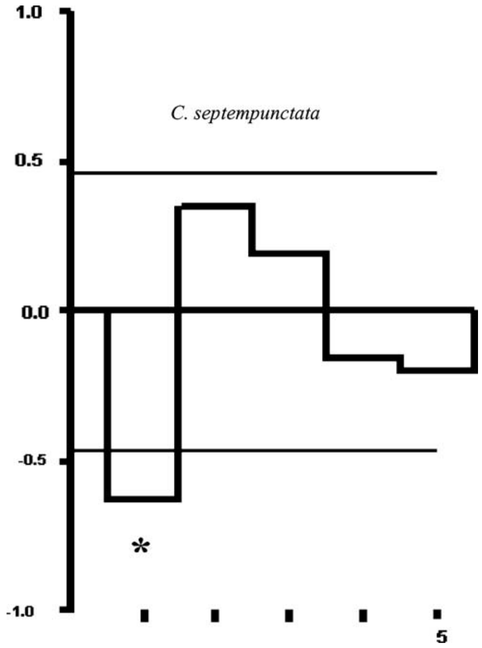

**Figure 7** Partial rate correlation function (PRCF) for *Coccinella septempunctata*. Significant correlation at time step of 1 year is indicated with an asterisk ($P < 0.05$).

In our examination of the 18-year data set, we found evidence of a predator–prey interaction between field populations of cereal aphids and one of their major predators, *C. septempunctata*. This was primarily revealed by a bottom-up relationship between *C. septempunctata* and the aphids as a food resource (Fig. 4). We also found evidence that *C. septempunctata* played a role in regulating the aphid populations in a top-down manner, especially for *R. padi* (Fig. 5; Table 3) and, to a lesser extent, for *M. dirhodum* (Table 3). Despite documented evidence that *C. septempunctata* can play an important role in suppressing aphid population growth (Rautapää, 1972), our regional estimates of

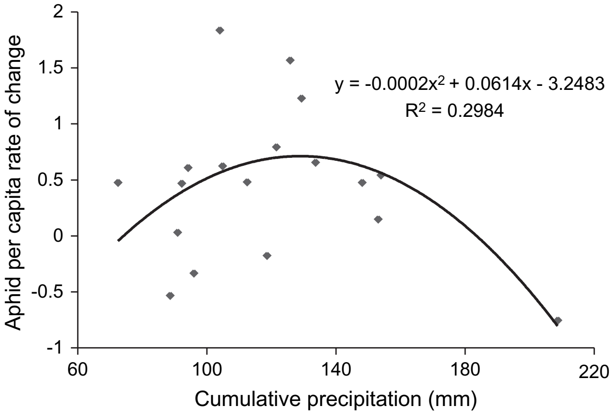

**Figure 8** Relationship between log-transformed peak aphid density and cumulative precipitation in May and June during the aphid population growth period in winter wheat.

**Table 2** Results of multiple regression analysis for densities of three aphid species individually and all combined

| | *Metopolophium dirhodum* | *Sitobion avenae* | *Rhopalosiphum padi* | Total |
|---|---|---|---|---|
| C7 | 0.086 | 0.256 | –0.320 | 0.102 |
| Prec | 3.396$^a$ | 1.875 | 2.794$^b$ | 2.950$^a$ |
| Prec$^2$ | –3.658$^a$ | –1.722 | –2.928$^a$ | –3.086$^a$ |
| Temp | 6.328$^b$ | 0.352 | 6.070$^b$ | 6.073 |
| Temp$^2$ | –6.392$^b$ | –0.010 | –6.089$^b$ | –5.943 |
| | $F_{5,\,12} = 3.01$ | $F_{5,\,12} = 0.68$ | $F_{5,\,12} = 2.31$ | $F_{5,\,12} = 2.04$ |
| | $P = 0.055$ | $P = 0.64$ | $P = 0.11$ | $P = 0.145$ |
| | $R^2 = 0.56$ | $R^2 = 0.22$ | $R^2 = 0.49$ | $R^2 = 0.46$ |

Regression coefficients of overwintering densities of *Coccinella septempunctata* (C7), precipitation (Prec) and its quadratic component (Prec$^2$), and temperature (Temp) and its quadratic component (Temp$^2$), as well as *F*, *P* and $R^2$ values are indicated.
[a]Regression coefficients are significant at $P < 0.05$;
[b]regression coefficients are significant at $P < 0.10$.

*C. septempunctata* densities were not suitable for detecting regulation of all aphid species at our study site. However, finding any connection between *C. septempunctata* densities and aphid dynamics using long-term data sets is notable, as it has been observed that the relationship between aphids and their natural enemies in the field can be unstable (Ankersmit & Carter, 1981).

The variable significance of top-down regulation of aphids by *C. septempunctata* may also have been dependent on timing of predation, which we could not investigate because our *C. septempunctata* data were limited to overwintering densities. Timing of predation has been noted in other studies, where predators have the potential to substantially reduce aphid densities when predation occurs during the early stages of population growth, thus limiting time of exponential growth (van der Werf, 1995; Ives & Settle, 1996). In another long-term study of aphids and natural enemies, Rautapää (1976) found that aphid maximums in midsummer could be predicted by the ratio of first generation *C. septempunctata* adults and aphids early in the season. Conversely, second generation *C. septempunctata* adults, arriving later in the summer had no effect on aphid maximum (Rautapää, 1976).

**Table 3** Results of multiple regression analysis of per capita rate of change for three aphid species individually and all combined

| | *Metopolophium dirhodum* | *Sitobion avenae* | *Rhopalosiphum padi* | Total |
|---|---|---|---|---|
| C7 | –0.356$^c$ | –0.078 | –0.671$^a$ | –0.434$^c$ |
| Prec | 3.341$^b$ | –1.037 | 1.944 | 2.528$^c$ |
| Prec$^2$ | –3.584$^a$ | 1.560 | –2.146$^c$ | –2.669$^c$ |
| Temp | 5.576$^c$ | 1.980 | 3.464 | 6.140$^c$ |
| Temp$^2$ | –5.876$^c$ | –1.712 | –3.724 | –6.210$^c$ |
| | $F_{5,\,12} = 3.87$ | $F_{5,\,12} = 1.08$ | $F_{5,\,12} = 3.8$ | $F_{5,\,12} = 2.70$ |
| | $P = 0.025$ | $P = 0.42$ | $P = 0.027$ | $P = 0.074$ |
| | $R^2 = 0.62$ | $R^2 = 0.31$ | $R^2 = 0.61$ | $R^2 = 0.53$ |

Regression coefficients of overwintering densities of *Coccinella septempunctata* (C7), precipitation (Prec) and its quadratic component (Prec$^2$), and temperature (Temp) and its quadratic component (Temp$^2$), as well as *F*, *P* and $R^2$ values are indicated.
[a]Regression coefficients are significant at $P < 0.01$;
[b]regression coefficients are significant at $P < 0.05$;
[c]regression coefficients are significant at $P < 0.10$.

One of the most useful aspects of long-term data sets is that they provide the possibility to detect cycles in population dynamics, which often represent biotic interactions. For example, some aphid populations have been documented to exhibit first-order dynamics (on a yearly time scale), or alternating high and low densities between years, which has been referred to as a 'see-saw effect' (Dixon, 1970). These alternating cycles have been attributed to natural enemies (Way, 1967) or competition for host resources and limiting nutrients (Dixon, 1990). In the present study, the first-order dynamics (Figs 6, 7) found with PRCF appears to be more the result of a spurious correlation that occurs when comparing growth rates with log-transformed densities at a time lag of 1 year, stemming from the fact that the density $N_t$ occurs both as regressor and as divisor in the calculation of the dependent variable $r_t = \ln (N_{t+1}/N_t)$. Pearson (1897) documented spurious correlations in ratio variables over a century ago and, despite subsequent reminders (Jackson & Somers, 1991), can still be the cause of erroneous conclusions. Needless to say, care should be taken when interpreting results of PRCF at a time lag of 1 year. Randomization procedures are a good tool to verify first-order density dependence (Pollard and Lakhani, 1987; Maudsley *et al.*, 1996), as in this case, where we determined that neither the aphids nor the coccinellid were operating in statistically significant first-order fashion. Therefore, although *C. septempunctata* undoubtedly plays a role in aphid dynamics, the predator–prey relationship was not strong enough to produce statistically convincing cycles, as seen in other predator–prey systems (e.g. Elton & Nicholson, 1942).

The lack of periodicity in the aphid dynamics can be seen as evidence that a larger complex of factors are involved in governing the aphid dynamics (Turchin, 2003), which can include stochastic effects such as weather. We found some indication that weather conditions during aphids' presence in wheat affected population dynamics of the aphids because precipitation (both linear and quadratic components) had a significant relationship with *M. dirhodum* peak densities, the most abundant aphid species in our study. Additionally, in our combined models, weather variables were found to be important predictors of peak density for all species, except *S. avenae*. Although potential effects of weather factors, such as temperature (Dean, 1974; Turak *et al.*, 1998), drought (Pons & Tatchell, 1995) frost accumulation (Parish & Bale, 1993), humidity (Leather, 1985) or rain (Araya, 1991) have been demonstrated, direct relationships between aphid dynamics and weather are scarce.

There is a longstanding discussion on the importance of natural enemies in controlling pest populations. Initially, the vast fluctuations in the dynamics of the cereal aphids and *C. septempunctata* in our study system seemed to be the result of a predator–prey interaction. In fact, in most years, aphid densities were maintained at relatively low levels without the use of insecticides. However, our ability to use *C. septempunctata* densities to predict aphid densities or per capita rate of change was only partially successful and may have been compromised by our inability to determine the timing of predation by *C. septempunctata* at our study site, or other exogenous factors that were not measured. It is likely that other regulating factors were involved, especially during the later years of the study when the aphid populations continued to fluctuate after the abundance of *C. septempunctata* decreased across the landscape (Fig. 2).

The use of time series analysis versus short-term mechanistic experimentation represents a trade off between the ability to look for long-term patterns and gathering data at a resolution needed to confidently detect biotic interactions between aphids and predators. For example, despite the relatively lengthy nature of our data set (i.e. 18 years), each variable used in the analyses was inevitably reduced to 18 data points from which to examine patterns. It would seem that long-term times series used in conjunction with short-term high-resolution data will provide the most comprehensive understanding of factors influencing aphid dynamics. However, it is much easier to conduct short-term mechanistic experiments than collect data from natural populations on multidecadal time scales. Other approaches, such as a comparison of population dynamics between regions to look for similar patterns, may comprise one method of bypassing this problem. Tracking populations of pests and natural enemies for several years at multiple spatially-distinct sites would quickly provide a robust data set for examining predator–prey dynamics. Time series analysis could also be improved by directing monitoring to times of crucial pest-natural enemy interactions, such as during early-season immigration into crop fields, when pest population growth has been shown to be most influenced by natural enemies.

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