The landscape context of cereal aphid–parasitoid interactions

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Analyses at multiple spatial scales may show how important ecosystem services such as biological control are determined by processes acting on the landscape scale. We examined cereal aphid–parasitoid interactions in wheat fields in agricultural landscapes differing in structural complexity (32–100% arable land). Complex landscapes were associated with increased aphid mortality resulting from parasitism, but also with higher aphid colonization, thereby counterbalancing possible biological control by parasitoids and lastly resulting in similar aphid densities across landscapes. Thus, undisturbed perennial habitats appeared to enhance both pests and natural enemies. Analyses at multiple spatial scales (landscape sectors of 0.5–6 km diameter) showed that correlations between parasitism and percentage of arable land were significant at scales of 0.5–2 km, whereas aphid densities responded to percentage of arable land at scales of 1–6 km diameter. Hence, the higher trophic level populations appeared to be determined by smaller landscape sectors owing to dispersal limitation, showing the 'functional spatial scale' for species-specific landscape management.

Keywords: biological control; wheat; landscape structure; spatial ecology; temporal changes

1. INTRODUCTION

Understanding of population dynamics needs analyses of trophic interactions at multiple spatial and temporal scales (Kareiva 1990; Pimm 1991; Wiens *et al.* 1993; Kareiva & Wennergren 1995; Pickett & Cadenasso 1995; Rosenzweig 1995; Holt 1996; Roland & Taylor 1997; Wiens *et al.* 1997; Tischendorf & Fahrig 2000; Cadenasso & Pickett 2000; Ricketts 2001; Menalled *et al.* 2003; Tscharntke & Brandl 2004). Spatial and temporal dynamics should be particularly important in agricultural landscapes, which are dominated by arable fields. Annual harvesting and soil cultivation almost completely erase herbivores and their natural enemies, so that arable fields have to be recolonized from surrounding habitats yearly. Nevertheless, annual crops can exhibit strong regulation of herbivore populations by natural enemies (Halaj & Wise 2001), this being improved by both changing agricultural practices within crop fields (Wratten & van Emden 1995; Van Driesche & Bellows 1996), and the management of agricultural landscapes (Altieri 1995; Burel & Baudry 1995; Van Driesche & Bellows 1996; Matson *et al.* 1997; Menalled *et al.* 1999; Thies & Tscharntke 1999; Tscharntke & Kruess 1999; Tscharntke 2000; Östman *et al.* 2001; Tscharntke *et al.* 2002; Van Nouhuys & Hanski 2002*a*). A basic understanding of the mechanisms of naturally occurring biological control may contribute to the management of environmentally sound crop production systems that use ecosystem services and reduce external effects such as those due to pesticides (Tilman *et al.* 2002).

In winter wheat fields (*Triticum aestivum* L.) in northern Germany, the herbivore community is dominated by three species of cereal aphid (Homoptera, Aphididae), *Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker) and *Rhopalosiphum padi* (Linnaeus). Outbreaks of aphid populations causing economic damage have been recorded since the early 1970s. They have been related to increased applications of nitrogen fertilizers in combination with applications of growth regulators and fungicides, which protect the leaf structure (Hanisch 1980; Ankersmit 1988; Honek 1991). The role of natural enemies in preventing cereal aphid outbreaks is emphasized in several studies (e.g. Wratten & Powell 1991; Levie *et al.* 2000; Kindlmann & Dixon 2001; Sigsgaard 2002; Schmidt *et al.* 2003), but little is known about whether variability of bio-control can be explained by the surrounding landscape (but see Östman *et al.* 2001). The landscape context connects to local processes via dispersal and thereby should be expected to filter differences in the species traits such as body size, foraging range, resource specialization, population size variability and trophic position (Holt 1996; Tscharntke & Brandl 2004).

In this three-year study, we analysed changes in the population size of cereal aphids and their mortality owing to parasitism at multiple spatial scales. Our former analyses of experimental exclusion of aphid enemies showed that parasitoids (Hymenoptera: mainly Aphidiidae) that are specialized on one or several aphid host species (Sigsgaard 2002), could best explain differences in aphid densities (Schmidt *et al.* 2003). However, flying and ground-dwelling predators can also be important (see Holland *et al.* 1996; Holland & Thomas 1997; Östman *et al.* 2001; Lang 2003). The fields were located in agricultural landscapes characterized by a gradient from structurally complex landscapes to structurally simple ones (32–100% arable land that was closely correlated with habitat type diversity). The influence of landscape context on aphid–parasitoid interactions was tested from small to large landscape scales, in that we tested seven circular landscape sectors ranging from 0.5 to 6 km diameter. We expected that (i) aphid parasitism would decrease and aphid densities increase with increasing percentage of arable land in a landscape and (ii) that

aphids and their parasitoids would respond to landscape context at different spatial scales.

2. MATERIAL AND METHODS

The three-year study was conducted in 40 conventionally managed winter wheat fields in the vicinity of the city of Göttingen (51°32′ N, 9°56′ E; see Steffen-Dewenter *et al.* (2002); Thies *et al.* (2003)), Lower Saxony (North Germany) in 2001 ($n = 18$ fields), 2002 ($n = 10$ fields) and 2003 ($n = 12$ fields), which differed between years owing to crop rotation. The area is dominated by arable fields with intensive agricultural land use (*ca.* 75% of the region) and patchily distributed fragments of forest, grassland, fallow, hedge and other semi-natural habitats. The area under cultivation was composed of cereals (71%), sugar beets (12%), oilseed rape (8%) and corn (4%) (I. Roschewitz, unpublished data). The average temperature (°C) and total rainfall (mm) during the study periods from June to July differed considerably (June 2001: 13.9 °C, 59.9 mm; June 2002: 16.6 °C, 71.4 mm; June 2003: 18.1 °C, 47.7 mm; and July 2001: 18.4 °C, 68.8 mm; July 2002: 17.3 °C, 95.2 mm; July 2003: 18.7 °C; 46.9 mm; data from the meteorological station in Göttingen).

The study sites were located in a gradient from structurally simple landscapes (up to 100% arable land) to structurally complex landscapes (less than 35% arable land). The distribution of landscapes of different complexity did not show any north–south or east–west pattern, to avoid spatial autocorrelation in abiotic factors such as soil fertility. For each of the fields the surrounding proportion of habitat types was measured at seven circular sectors of increasing diameter (∅ 0.5 km; ∅ 1 km; ∅ 2 km; ∅ 3 km; ∅ 4 km; ∅ 5 km; ∅ 6 km), representing a nested set of landscape sectors at seven spatial scales. Landscape data were available for 39 (out of the 40) landscape sectors. We quantified the area of arable land, grassland, forest, hedgerow, garden land and settlement using official digital thematic maps (ATKIS–Digitales Landschaftsmodell 25/1; Landesvermessung und Geobasisinformation, Hannover, Germany 1991–1996) and the Geographical Information System ArcView 3.1 (ESRI Geoinformatik GmbH, Hannover, Germany) at these seven spatial scales. The percentage of arable land per landscape was used as an indicator of landscape complexity as annual ploughing and harvesting in crops may greatly affect most organisms, and this simple parameter has been shown to be a good predictor for other landscape metrics such as habitat type diversity and habitat isolation (Thies & Tscharntke 1999; Steffan-Dewenter *et al.* 2002).

Land-use intensity of the fields, i.e. the amount of nitrogen fertilizers (kg N per hectare) and pesticides (number of applications of herbicides, fungicides, insecticides and growth regulators per year), which was recorded in a questionnaire to farmers in 2001 ($n = 18$ fields), was not related to landscape complexity. For example, percentage of arable land in a landscape sector of 1 km diameter was not related to (i) nitrogen: 208.1 ± 28.1 kg N per hectare, $r_S = 0.282$, $p = 0.244$; (ii) herbicides: 1.9 ± 0.5 applications per year, $r_S = 0.218$ to $p = 0.369$; (iii) fungicides: 1.9 ± 0.8 applications per year, $r_S = 0.336$, $p = 0.167$; (iv) insecticides: 0.7 ± 0.6 applications per year, $r_S = 0.288$, $p = 0.235$; or (v) growth regulators: 1.7 ± 0.7 applications per year, $r_S = 0.207$, $p = 0.394$ (mean $\pm$ s.d.; Spearman's rank correlation (r_S); I. Roschewitz, unpublished data).

Aphids and parasitized aphids (mummies) were quantified visually on an insecticide-free area of 800 m² in each of the 40 fields on 100 wheat shoots per field at wheat flowering in June (after the main period of aphid colonization of the fields), and on 100 wheat shoots per field at wheat milk ripening in July (after the main period of aphid reproduction in the fields). Each of the 80 samples consisted of four sub-samples of 25 shoots from different locations, which totalled 100 shoots. In the first year, aphid mummies were additionally sampled (2 h per field) and taken into the laboratory for rearing and identification of the parasitoid genera. The effects of the predictor variables: 'year', 'host plant density' and 'percentage of arable land' on aphid densities, and the effects of the predictor variables: 'year', 'host density' and 'percentage of arable land' on aphid parasitism were analysed individually for each of the seven spatial scales (i.e. landscape sectors) using general linear models (following Wiegand *et al.* 1999; Steffan-Dewenter *et al.* 2002; Thies *et al.* 2003; for theoretical background, see Hanski 1998; Legendre & Legendre 1998; Turner *et al.* 2001; Holland *et al.* 2004). Model assumptions were tested by examining the normality of the residuals (Sokal & Rohlf 1995). The skewness and/or kurtosis of the data was compensated by $\log_{(X+1)}$-transformation of aphid densities, and arcsine($\sqrt{x}$)-transformation of parasitism rates. In addition, Spearman's rank correlations (r_S) were used to analyse the relationship between aphid population growth (the proportion of aphid density at wheat milk ripening (d_{wmr}) and aphid density at wheat flowering (d_{wfl}) = d_{wmr}/d_{wfl}) and percentage of parasitism at the second sample date. Arithmetic means $\pm$ s.d. are given.

3. RESULTS

A total of 12 234 cereal aphid individuals was counted in 40 winter wheat fields, of which 69.4% were *Sitobion avenae*, 27.4% *Metopolophium dirhodum* and 3.2% *Rhopalosiphum padi*. Aphids were attacked by five genera of parasitoids (mainly *Aphidius*; Aphidinidae) and the latter by three genera of hyperparasitoids (mainly *Dendrocerus*; Megaspilidae). The population densities of aphids and their parasitoids are summarized in table 1; they varied considerably between the 40 study sites. Aphid and parasitoid densities were positively correlated at wheat flowering ($F_{1,38} = 10.0$, $p = 0.003$, $n = 40$, $R = 0.456$), but not at wheat milk ripening ($F_{1,38} = 0.01$, $p = 0.913$, $n = 40$, $R = 0.031$).

Aphid densities averaged 111.6 ± 127.8 individuals per 100 shoots at wheat flowering and 194.3 ± 258.8 individuals per 100 shoots at milk ripening. They increased from wheat flowering to milk-ripening stage in 2001 and 2003, but not in 2002 (table 1), thereby exceeding the threshold level of economic damage (3–5 per shoot; Pflanzenschutzamt Hannover 2002) in 0% of the fields in 2001, 40% of the fields in 2002, and 100% of the fields in 2003. Aphid densities differed significantly between years on both dates (table 2). At wheat flowering, they correlated negatively with percentage of arable land at scales between ∅ 1 km and ∅ 6 km. At milk ripening, this relationship was not significant at any scale (table 2; figure 1*a–c*).

Aphid parasitism was low at wheat flowering with an average of 2.6 ± 5.6% and increased at wheat milk ripening to 15.9 ± 15.8% (for absolute densities, see table 1). At wheat milk ripening, parasitism differed significantly between years, and correlated negatively with percentage of arable land and host density (table 2). In contrast to aphid abundance, the variation in parasitism explained by percentage of arable land was only significant between scales of ∅ 0.5 km and ∅ 2 km diameter of landscape sector (table 2; figure 1*d–f*). At the smallest spatial scale (∅ 0.5 km), the negative effect of percentage of arable land on

Table 1. Densities of cereal aphids and parasitoid mummies (individuals per 100 shoots) in winter wheat fields in three consecutive years.
(Arithmetic mean ± s.d., minima and maxima are given for 18 fields in 2001, for 10 fields in 2002 and for 12 fields in 2003.)

	mean ± s.d.	minimum	maximum
number of aphids at wheat flowering			
2001	23.7 ± 14.5	1	53
2002	257.6 ± 161.7	30	596
2003	121.7 ± 63.9	7	229
number of aphids at wheat milk ripening			
2001	46.9 ± 32.2	13	140
2002	101.6 ± 63.9	18	228
2003	492.6 ± 297.4	258	1371
number of mummies at wheat flowering			
2001	0.9 ± 1.5	0	5
2002	5.8 ± 5.4	0	14
2003	0.3 ± 0.6	0	2
number of mummies at wheat milk ripening			
2001	8.8 ± 6.4	0	23
2002	13.2 ± 8.1	4	26
2003	8.0 ± 6.0	0	23

parasitism occurred mainly when host density was low (interaction: arable land × host density), and differed between years, being marked only in 2001 and 2002 (interaction: year × arable land). At scales of ∅ 1 km and 2 km, arable land and host density accounted for the main effects, but the effect of local host densities also differed between years, being marked in 2001 and 2002 (interaction: year × host density).

Aphid population growth correlated negatively with parasitism (figure 2). Aphid populations decreased between wheat flowering and milk ripening at parasitism rates higher than 27%, which were found in landscapes with more than 30% non-crop area. The negative correlation between aphid population growth and parasitism rate occurred in each year (2001: $p = 0.019$, $n = 18$, $r_S = -0.571$; 2002: $p = 0.031$, $n = 10$, $r_S = -0.720$; 2003: $p = 0.060$, $n = 12$, $r_S = -0.566$); 34% of the mummies reared in the laboratory were hyperparasitoids.

4. DISCUSSION

The analyses of population density and parasitism of cereal aphids showed that trophic interactions in wheat fields varied greatly between years and were associated with the landscape context at different spatial scales. Non-crop area in the complex landscapes appeared to support larger parasitoid populations, but aphids also profited from complex landscapes, thereby counterbalancing possible biological control of aphids by parasitoids. Aphid densities, after colonization at wheat flowering stage, were higher in structurally complex landscapes than in structurally simple landscapes. However, they only increased substantially between wheat flowering and milk ripening in structurally simple landscapes, thereby resulting in no differences in aphid densities between landscapes after aphid reproduction. As high rates of parasitism could be found only in structurally complex landscapes with a relatively small area of annual crop fields, the parasitoid wasps were most likely to have contributed to the suppression of aphid densities in these landscapes. This implication is supported by the overall negative correlation between aphid population growth and parasitism, and by recent field experiments in our landscapes indicating the great importance of naturally occurring cereal aphid parasitoids (Schmidt *et al.* 2003). A regulation of cereal aphids by parasitoids released into field cages was also found by Levie *et al.* (2000), and suggested by other studies reporting similar high rates of cereal aphid parasitism (e.g. Sigsgaard 2002). However, our results showed that parasitism strongly decreased with host density, and parasitoids therefore should be expected to successfully control the aphids only in situations of lower aphid densities. The rates of hyperparasitism that we found reached 34%. Hyperparasitoids mainly act later in the season, namely in the period when aphid population densities break down owing to decreasing resource quality. Nevertheless, they may influence primary parasitoid densities in the following year (Sunderland *et al.* 1997). Several studies suggest that hyperparasitoids reduce the potential control of herbivore populations by primary parasitoids (reviewed by Rosenheim 1998).

Both aphid populations and their parasitoids appeared to have profited from structurally complex landscapes owing to a high availability of perennial habitats providing shelter from disturbances by agricultural practices, overwintering sites, and alternative host. The cereal aphid *S. avenae* hibernates on perennial grasses (Leather 1993), which represent a dominant plant family in many perennial habitats. *M. dirhodum* and *R. padi* are host alternating on *Rosa* spp. and *Prunus padus*, respectively, which are common plant species only in structurally rich landscapes. In addition, other aphid species could be expected to act as a reservoir of cereal aphid parasitoids. For example *Acyrthosiphum pisum*, which is a key aphid on legumes and known to be highly parasitized by *Aphidius* sp. (Stary 1976, 1978). Therefore, undisturbed perennial areas should support both high aphid densities and large parasitoid populations, whereas high proportions of arable land should disadvantage

Table 2. *F*-values and levels of significance from general linear models relating aphid densities and aphid parasitism rates in wheat fields to three predictive factors: (i) the year of the survey (A), (ii) the percentage of arable land per landscape sector at seven spatial scales (B), and (iii) host plant density (C) and host density, respectively.

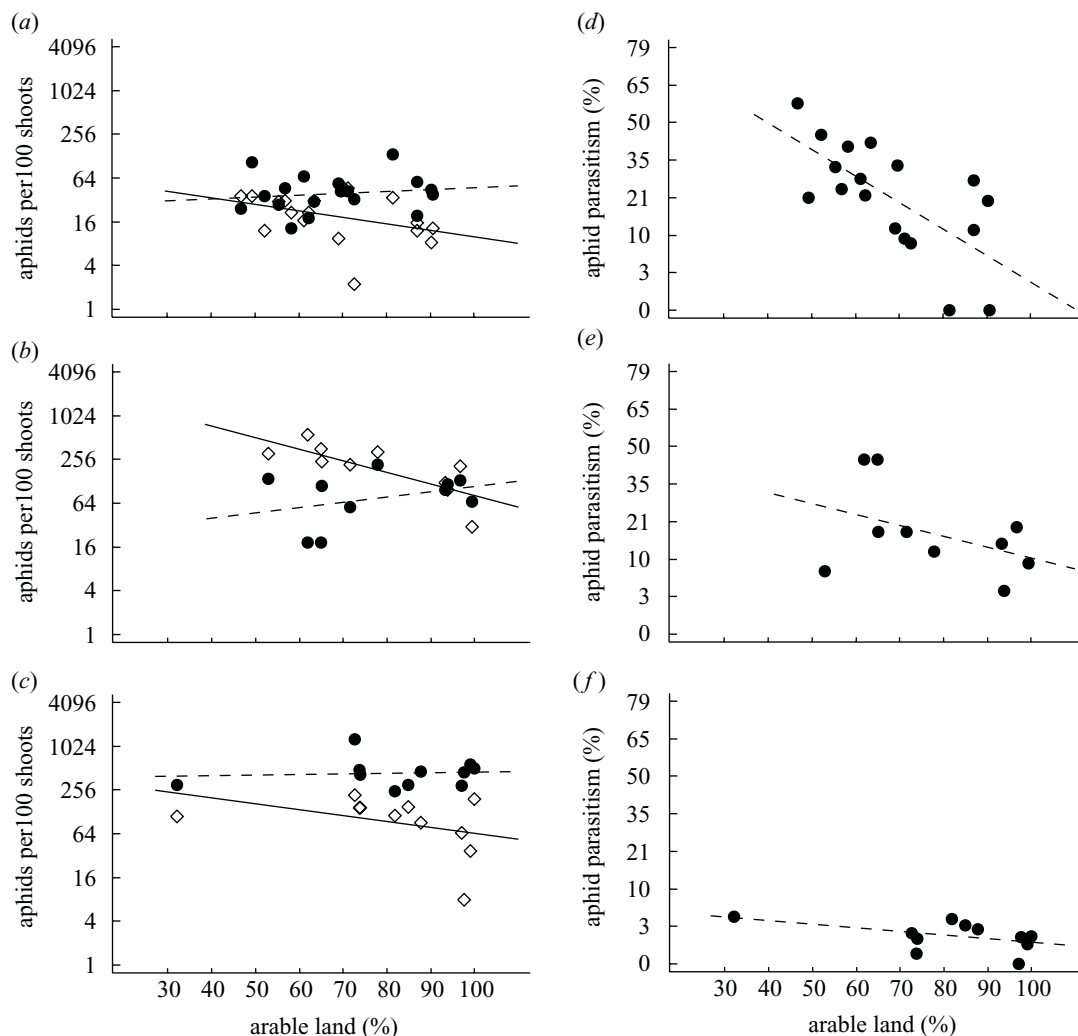|				diameter of landscape sector (km)			
	0.5	1	2	3	4	5	6
aphids per 100 shoots at wheat flowering							
A	28.3***	39.1***	40.5***	37.1***	36.6***	36.5***	34.8***
B (%)	n.s.	10.2**	12.3**	9.9**	9.4**	9.5**	8.9**
C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
A×B	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
A×C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
B×C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
model	28.3***	26.1***	27.9***	25.9***	25.5***	25.6***	25.0***
aphids per 100 shoots at wheat milk ripening							
A	53.1***	53.1***	53.1***	53.1***	53.1***	53.1***	53.1***
B (%)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
A×B	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
A×C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
B×C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
model	53.1***	53.1***	53.1***	53.1***	53.1***	53.1***	53.1***
aphid parasitism (%) at wheat milk ripening							
A	7.2**	3.9*	3.8*	n.s.	n.s.	n.s.	n.s.
B (%)	n.s.	12.3**	9.6**	n.s.	n.s.	n.s.	n.s.
C	n.s.	18.8***	18.4***	57.2***	57.2***	57.2***	57.2***
A×B	6.9*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
A×C	n.s.	5.6*	5.4*	n.s.	n.s.	n.s.	n.s.
B×C	34.9***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
model	19.8***	18.6***	15.9***	57.2***	57.2***	57.2***	57.2***

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Figure 1. Dependence of cereal aphid densities (*a–c*) and percentage of parasitism (*d–f*) on the percentage of arable land within circular landscape sectors of 1 km diameter in three consecutive years: (*a,d*) 2001; (*b,e*) 2002; (*c,f*) 2003. Open quadrats and solid lines: wheat flowering stage in June (after the main period of aphid colonization of the fields); filled points and dashed lines: wheat milk-ripening stage in July (after the main period of aphid reproduction in the fields). Regression lines are shown for descriptive purposes. See table 2 for statistics. Note the logarithmic scale for aphid densities.

these organisms. Overwintering sites for parasitoids adjacent to crop fields are known to increase egg parasitism of grape leafhoppers (Corbett & Rosenheim 1996) and larval parasitism of the rape pollen beetle (Thies & Tscharntke 1999). Moreover, our structurally complex landscapes provide more nectar sources for adult parasitoids owing to a larger cover of flowering plants (Steffan-Dewenter *et al.* 2001), and there are several examples of enhanced parasitism and extended parasitoid lifetimes by augmented nectar resources (Powell 1986; Wäckers & Swaans 1993; Wratten & van Emden 1995; Wäckers 1994; Wäckers & Steppuhn 2003).

Cereal aphid populations are expected to profit from higher temperatures causing higher immigration and reproduction rates, but to suffer from rainfall events resulting in lower survival rates (Triltsch *et al.* 1998; Gosselke *et al.* 2001; for other host–parasitoid systems, see Godfray *et al.* 1994; Kaitaniemi & Ruohomaki 1999; Van Nouhuys & Lei 2004). In accordance with these findings, our results showed mean aphid densities to be higher in 2002 and

2003, years with higher average temperatures, and population development to be lower in 2002, possibly owing to heavy rainfall in June and July 2002 (two events with 38.5 mm and 36.7 mm per day, respectively, in the period of aphid reproduction). The relative role of interannual weather changes (e.g. Palmer & Räisänen 2002; Hansen 2004) for aphid–natural enemy interactions is not yet well known, but changing temperatures and rainfall events might be expected to be important, because they were related to aphid densities (negatively density-dependent parasitism). Weather conditions are also suggested to influence the aphid control by generalist predators early in the season (Chiverton *et al.* 1986; Lang 2003).

The geographical scale analyses supported the expectation that species experience the spatial scale of landscape complexity differentially. The predictive power of landscape complexity for aphid parasitism was only significant within smaller landscape sectors of 0.5–2 km diameter. This is in support of the hypothesis that parasitoids often show dispersal limitation (Kruess & Tscharntke 1994, 2000; Tscharntke & Kruess 1999; With *et al.* 1999, but see
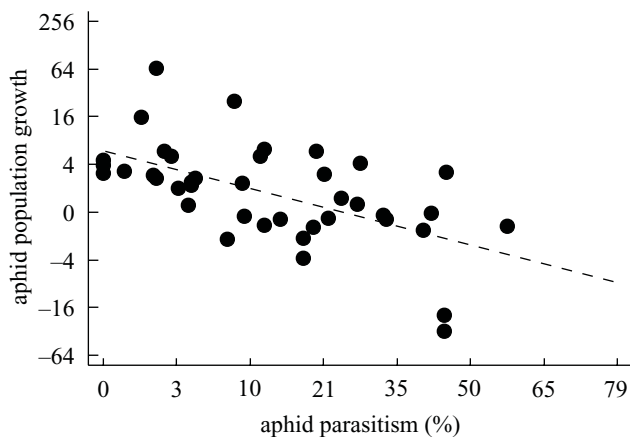
Figure 2. Relation of aphid population growth (the proportion of aphid density at wheat milk ripening (d_{wmr}) and aphid density at wheat flowering (d_{wfl}) = d_{wmr}/d_{wfl}) to percentage of parasitism. Spearman's rank correlation: $p < 0.001$, $n = 40$, $r_S = -0.547$.

Van Nouhuys & Hanski 2002*b*), and could be related to the relatively small body size of the parasitoids, which is a general predictor of how organisms acquire resources in space (Roland & Taylor 1997; Ritchie & Olff 1999). By contrast, the cereal aphids responded to differences in landscape context within landscape sectors up to 6 km. This is in line with expectations from host-alternating species like cereal aphids (but not parasitoids), as such multi-habitat use should be associated with high dispersal abilities. In addition, this supports findings of other studies that ascribed much importance to long-distance dispersal of aphids of tens or even hundreds of kilometres (Taylor 1977; Halber *et al.* 1990; Riley *et al.* 1995).

In conclusion, structurally complex landscapes showed the highest rates of aphid parasitism, but they also enhanced aphid populations, thereby counterbalancing possible control of this major pest, and resulting in an overall neutral effect of landscape context. Hence, the often-stressed argument for conservation or recreation of undisturbed perennial habitats in agricultural landscapes may not generally hold for biological control. Further, parasitoid populations responded to changes of landscape context at smaller scales than their aphid hosts, thereby supporting the idea that spatially explicit approaches may provide a perspective to identify 'functional spatial scales' at which species experience their environment, and at which species-specific landscape management may be arranged to enhance biological control. The striking differences in aphid abundance and their interactions with parasitoids between years call for more long-term experiments to better understand the relative role of spatial and temporal factors that shape local ecological processes.

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