Effects of landscape context on herbivory and parasitism at different spatial scales

Carsten Thies, Ingolf Steffan-Dewenter and Teja Tscharntke

Local community structure and interactions have been shown to depend partly on landscape context. In this paper we tested the hypothesis that the spatial scale experienced by an organism depends on its trophic level. We analyzed plant-herbivore and herbivore-parasitoid interactions in 15 agricultural landscapes differing in structural complexity using the rape pollen beetle (*Meligethes aeneus*), an important pest on oilseed rape (*Brassica napus*), and its parasitoids. In the very center of each landscape a patch of potted rape plants was placed in a grassy field margin strip for standardized measurement. Percent non-crop area of landscapes was negatively related to plant damage caused by herbivory and positively to the herbivores' larval mortality resulting from parasitism. In a geographic scale analysis, we quantified the structure of the 15 landscapes for eight circular sectors ranging from 0.5 to 6 km diameter. Correlations between parasitism and non-crop areas as well as between herbivory and non-crop area were strongest at a scale of 1.5 km, thereby not supporting the view that higher trophic levels experience the world at a larger spatial scale. However, the predictive power of non-crop area changed only slightly for herbivory, but greatly with respect to parasitism as scales from 0.5 to 1.5 km and from 1.5 to 6 km diameter increased. Furthermore, the effect of non-crop area tended to be stronger in parasitism than herbivory suggesting a greater effect of changes in landscape context on parasitoids. This is in support of the general idea that higher trophic levels should be more susceptible to disturbance.

C. Thies, I. Steffan-Dewenter and T. Tscharntke, Agroecology, Georg-August Univ., Waldweg 26, DE-37073 Goettingen, Germany (c.thies@uaoe.gwdg.de).

There is increasing recognition that community structure, species abundance and biotic interactions may depend on scales much larger than a single habitat. This demands the use of a landscape perspective, considering area, spatial arrangement and connectivity of habitats in determining local ecological patterns and processes (Kareiva 1990, Turner and Gardner 1991, Kareiva and Wennergren 1995, Pickett and Cadenasso 1995, Polis et al. 1997, Roland and Taylor 1997, Gonzales et al. 1998, Menalled et al. 1999, Thies and Tscharntke 1999, Wiegand et al. 1999, Tischendorf and Fahrig 2000, Cadenasso and Pickett 2000, Ricketts 2001). Landscape context does not influence all species equally, and interacting communities are made up of species with different spatial strategies (Kareiva 1990,

Holt 1996, With et al. 1999, 2002). Perception of spatial scale of landscape complexity and responses to landscape structure facilitating or impeding movement among habitat patches are species specific (Taylor et al. 1993, Wiens et al. 1997). Accordingly, we have to consider how different organisms perceive their landscape, and to include components and metrics relevant to the target species. Quantification of spatial heterogeneity is a prerequisite to understanding the relationship between landscape structure and species-specific responses (Forman 1995, Gustafson 1998, Tischendorf and Fahrig 2000, Turner et al. 2001).

Biological control involving parasitoids as antagonists of pest insects is also linked to landscape context (Corbett and Rosenheim 1996). Parasitoids are impor-

tant natural enemies of many crop pests and may act as keystone species in ecosystems (LaSalle 1993). Their population dynamics in agricultural landscapes have received much attention in the last decades (Hawkins 1994, Hawkins and Cornell 1994, Hawkins et al. 1999, Hochberg and Ives 2000). The efficiency of parasitoids and other natural enemies of crop pests may be improved by both changing agricultural practices within crop fields (Wratten and Van Emden 1995, Van Driesche and Bellows 1996), and the management of agricultural landscapes (Burel and Baudry 1995, Van Driesche and Bellows 1996, Matson et al. 1997, Tscharntke and Kruess 1999, Tscharntke 2000). Few studies have shown, using replicated landscape sectors, how landscape context directly affects local plant-herbivore-parasitoid interactions, viz Roland and Taylor (1997), Menalled et al. (1999), Thies and Tscharntke (1999), Östman et al. (2001). Further evidence include studies on scale-dependence of the aggregative responses of parasitoids which has been shown for meal moths (*Plodia interpunctella*) (Waage 1979), the holly leaf-miner (*Phytomyza ilicis*) (Heads and Lawton 1983), and the cabbage root fly (*Delia radicum*) (Jones and Hassell 1988). De Roos et al. (1991) found with individual-based models that features of population dynamics in predator-prey models are linked to a characteristic spatial scale imposed by individual mobility (see also McCauley et al. 1993).

In this paper, we analysed plant-herbivore-parasitoid interactions and the "functional spatial scale" at which the organisms respond to landscape context using the rape pollen beetle *Meligethes aeneus* (Col. Nitidulidae) and its specialized parasitoid species (Hym. Ichneumonidae), which are known to be affected by landscape context (Thies and Tscharntke 1999). We experimentally tested the hypothesis that the spatial scale experienced by an organism depends on its trophic level (Holt 1996; Fig. 1). According to this idea, the abundance of a plant species is mainly determined by its microhabitat. Herbivore populations are wider-ranging, but confined within the local community. Predator populations encompass several prey populations and have to be mobile enough to switch between patches colonized by the prey. This is why Holt (1996) expects the density of species of higher trophic levels to be determined at larger spatial scales than that of species of lower trophic levels. We tested the effects of landscape context on trophic-level interactions using 15 landscapes characterized by a gradient from extremely simple and structurally poor landscapes to complex and structurally rich ones with up to 50% uncultivated habitats. In each landscape, we analyzed effects of 8 spatial scales, namely circular landscape sectors ranging from 0.5 to 6 km diameter. We experimentally placed a patch of potted oilseed rape (*Brassica napus*) in the center of each of the 15
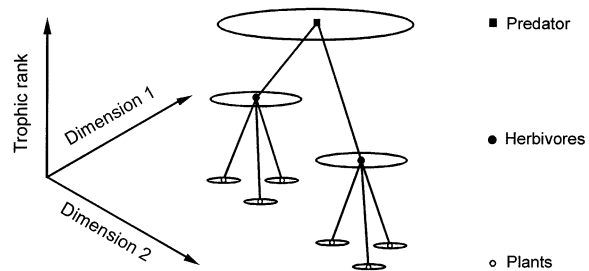

Fig. 1. Food webs in space. The spatial domain pertinent to population dynamics of each type of species are described by ovals, indicating different spatial scales for trophic levels in communities. Plant species occupy distinct microhabitats. Herbivore species have larger spatial domains, but are relatively confined within local communities. Predator dynamics encompass the range of several herbivore populations (after Holt 1996).

landscapes to study insect colonization and plant-herbivore-parasitoid interactions.

Methods

Study area and landscape structure

The study area is located in the agricultural landscapes of southern Lower Saxony around the city of Göttingen (Germany). The region mainly consists of cropland-grassland mosaics, dominated by intensive agricultural land use (covering on average about 75% of the region), and by patchily distributed fragments of near-natural habitats such as fallows, grasslands, hedges and few forest remnants. We selected 15 independent landscape sectors which covered a gradient from extremely simple and structurally poor landscapes ($< 3\%$ of non-crop area, i.e. area that is not converted to annual crops) to complex and structurally rich landscapes ($> 50\%$ non-crop habitats). For each of the 15 landscapes, structure was estimated in eight circular sectors ($\varnothing$ 0.5 km, $\varnothing$ 1 km, $\varnothing$ 1.5 km, $\varnothing$ 2 km, $\varnothing$ 3 km, $\varnothing$ 4 km, $\varnothing$ 5 km, $\varnothing$ 6 km), representing a nested set of landscape sectors at eight spatial scales (Fig. 2). We used the official digital thematic maps (ATKIS – Digitales Landschaftsmodell 25/1; Landesvermessung und Geobasisinformation, Hannover, Germany 1991–1996) to measure the area of arable land, grassland, forests, hedgerows, garden land and settlement. For each of the eight nested spatial scales the percentage of non-crop area per landscape, i.e. the area not ploughed annually for the cultivation of annual crops such as
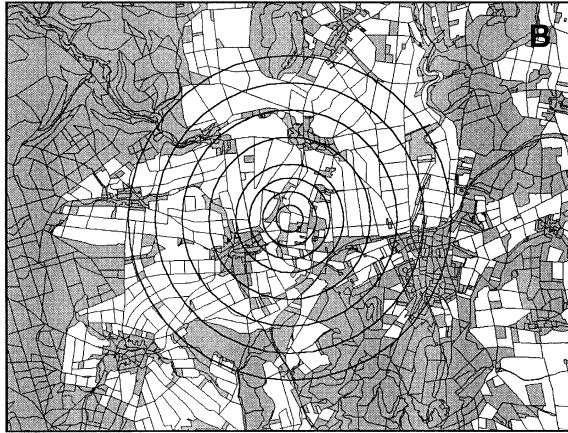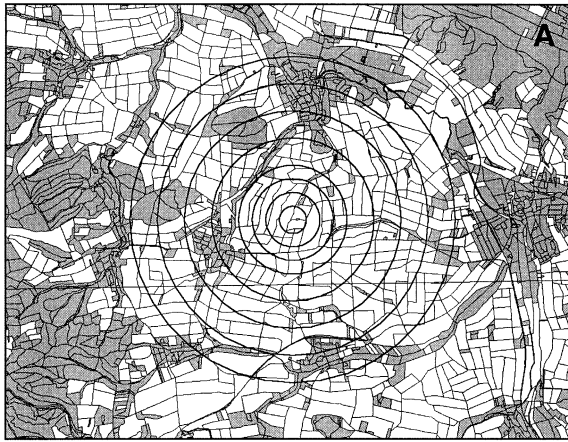
Fig. 2. Two landscape sectors illustrating the experimental design. In the center of each landscape sector a patch of potted rape plants was placed. The circles show the eight circular sectors ($\varnothing$ 0.5 km, $\varnothing$ 1 km, $\varnothing$ 1.5 km, $\varnothing$ 2 km, $\varnothing$ 3 km, $\varnothing$ 4 km, $\varnothing$ 5 km, $\varnothing$ 6 km), representing a nested set of landscape sectors at eight spatial scales. (A) Structurally simple landscape ($\varnothing$ 1500 m: 97.7% annual crops; white area). (B) Structurally more complex landscape ($\varnothing$ 1500 m: 56.0% annual crops; white area).

Experimental species

The focal plant used in this study was summer oilseed rape (*Brassica napus*), which is decended from the wild cruciferous species *Brassica campestris* and the cabbage *Brassica oleracea*. Oilseed rape is an important cultivated plant species in Germany covering about 1.2 million ha (Saaten-Union 1999). The expansion of rape area in the last decades has been followed by an increase of rape pollen beetle abundance (Paul 1988), so plant protection professionals recommend farmers to use insecticides in rape fields in most years (Pflanzenschutzamt Hannover 1999). The rape pollen beetle *Meligethes aeneus* (Coleoptera: Nitidulidae) is one of the most important pest species on rape (Hoffmann and Schmutterer 1983, Paul 1988). Pollen feeding of the adult beetles on young rape buds prevents pod and seed development leading to damage levels of great economic importance. The number of adults and the number of destroyed buds are known to be closely correlated (Hoffmann and Schmutterer 1983). Larvae of rape pollen beetle develop in rape flowers into the last instar and are attacked by three specialized univoltine larval parasitoids, *Tersilochus heterocerus*, *Phradis interstitialis*, and *P. morionellus* (Hymenoptera: Ichneumonidae), of which the last is rare. *Phradis interstitialis* mostly attacks host larvae in the second instar while *T. heterocerus* attacks host larvae mostly in the third instar. Both parasitoid species kill their host larvae after they drop to the ground before pupation in the soil (Jourdheuil 1960). A few species of insect predators, such as ladybeetles, lacewings and malachiid beetles, are known but generally rare (Jourdheuil 1960).

Experimental design

We established a patch of potted summer rape (*Brassica napus*) in the center of each of the 15 landscape sectors (two 30 l pots per landscape, five plants per pot) in May. We used potted plants to standardize our measurements, because landscape complexity is related to many characteristics such as the intensity of agricultural practices and soil nutrient richness (Thies et al., unpubl.). These rape pots were established in the same local environment (grassy field margins adjacent to cereal fields), had the same soil type, nutrient and water availability (standardized garden soil; watered weekly), and were planted with the same crop variety (Lisonne®; Deutsche Saatenveredelung).

cereals, sugar-beets or oilseed rape, was quantified using the Geographical Information System ARC View 3.1 (ESRI Geoinformatik GmbH, Hannover, Germany). Additionally, we estimated the area cultivated with oilseed rape in each of the 15 landscapes by intensive field inspections, but only in five circular landscape sectors ($\varnothing$ 0.5 km, $\varnothing$ 1 km, $\varnothing$ 1.5 km, $\varnothing$ 2 km, $\varnothing$ 3 km).

By using the percentage of non-crop area, our estimation of landscape structure was rather simple. However, this factor has been shown to be a robust parameter for the quantification of landscape complexity as percent non-crop area was closely correlated with other landscape metrics such as habitat-type diversity ($R^2 = 0.91$, $P < 0.001$, $N = 15$; Thies and Tscharntke 1999). The changes of landscape context at different spatial scales are in detail given in another publication (Steffan-Dewenter et al. 2002).

Analysis of plant damage and parasitism

Levels of parasitism were analyzed during summer rape

flowering in June. All flowers of five of the potted rape plants were collected in each landscape. The flowers (438 ± 40 mean ± SE per plot) and the larvae (104 ± 18 mean ± SE per plot) were stored in polyethylene bags in a freezer at −22°C. Rates of parasitism were measured by dissection of the last instar larvae of rape pollen beetle. Parasitoid species identification was based on egg shell characteristics, either black (*T. heterocerus*) or white (*Phradis* spp.) pigmented (Osborne 1960). Young beetle larvae (< 3 mm length) were discarded from this measurement, because our earlier studies have shown that their parasitism is very low. Plant damage caused by adult beetle feeding was quantified at peak ripeness of the summer rape in August on the remaining five experimental potted rape plants in each of the 15 landscapes. The number of pods, as well as the number of destroyed buds, which did not develop into pods and appeared as typically podless stalks, were assessed.

Statistical analysis

After an arcsine-square-root transformation of the proportional data to meet the residual assumptions of the statistical models (Sokal and Rohlf 1995), our statistical analyses were separated in two steps. In the first step, we carried out stepwise regression analyses to examine the effects of landscape structure on herbivory and parasitism at an appointed spatial scale of ∅ 1.5 km, which is known to influence this specific plant-herbivore-parasitoid system (Thies and Tscharntke 1999). We examined the effects of percent non-crop area and percent rape crop area on the percentage of destroyed buds (herbivory), and the effects of percent non-crop area, percent rape crop area and host density on the percentage of parasitism. In the second step, we examined the effects of landscape context on herbivory and parasitism at seven further spatial scales ranging from ∅ 0.5 km–∅ 6 km, because it is not a priori clear at which spatial scale landscape structure has the strongest effect. In stepwise regression analyses we examined (i) the effects of percent non-crop area and percent rape crop area on herbivory damage and (ii) the effects of percent non-crop area, percent rape crop area and host density on parasitism at spatial scales ∅ 0.5 km, ∅ 1 km, ∅ 2 km, ∅ 3 km, ∅ 4 km, ∅ 5 km and ∅ 6 km (but data of rape crop area were missing at the three largest scales). We plotted the correlation coefficients for each of the eight scales with the n = 15 landscapes (following Wiegand et al. 1999, Fig. 2) to illustrate scale-dependent effects of landscape structure on plant-herbivore-parasitoid interactions at these eight analysed spatial scales.

Results

The oilseed rape plants were characterized by high damage due to feeding from adult *Meligethes* spp. (97% out of 498 adults were identified as *M. aeneus*). The percentage of destroyed buds was on average 60.1% ± 4.4% (min: 35%; max: 92.2%, N = 15 landscapes). Only 182.3 ± 30.3 buds/plant developed into pods, whereas 255.5 ± 25.3 buds/plant were destroyed and appeared as podless stalks. The number of destroyed buds due to feeding from adult *Meligethes* spp. and the number of *Meligethes* spp. larvae did not correlate (R = −0.20, P = 0.48), showing a high variability of reproductive success. Total rate of larval parasitism was 29.7% ± 6.4% (min: 0%; max: 74.4%, N = 15 landscapes). *P. interstitialis* contributed with 16.5% ± 5.1% parasitism (min: 0%; max: 62.5%, N = 15 landscapes) and *T. heterocerus* with 16.7% ± 4% parasitism (min: 0%; max: 50%, N = 15 landscapes).

In multiple regression analyses, herbivory and parasitism were correlated with percent non-crop area in the 15 agricultural landscapes using a spatial scale of ∅ 1.5 km. The percentage of destroyed buds decreased (Fig. 3A) and the percent parasitism increased (Fig. 3B) as the percentage of non-crop area increased. Parasitism by each of the two main parasitoid species responded positively to landscape complexity, without any evi-
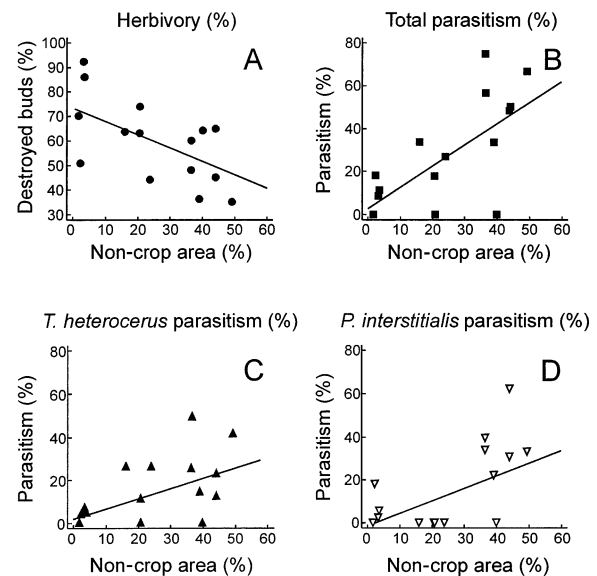
Fig. 3. Dependence of plant-herbivore and herbivore-parasitoid interactions on the percentage of non-crop area (i.e. landscape complexity) within circular landscape sectors of 1.5 km diameter. (A) Herbivory (%), i.e. the percentage of destroyed rape buds. (B) Total parasitism (%) due to *T. heterocerus* and *P. interstitialis*. (C) Parasitism (%) due to *T. heterocerus*. (D) Parasitism (%) due to *P. interstitialis*. Statistics see Table 1.

dence of a threshold. Rate of parasitism by *T. heterocerus* increased from 6% to 50% (Fig. 3C), and by *P. interstitialis* from 3% to 65% (Fig. 3D). Percentage of rape crop per landscape did not significantly contribute to the explanation of plant damage ($R = -0.33$, $P = 0.23$). Rates of parasitism were neither related to larval host density (Total parasitism: $R = -0.03$, $P = 0.93$; *Tersilochus* parasitism: $R = 0.10$, $P = 0.73$; *Phradis* parasitism: $R = -0.19$, $P = 0.49$) nor to the percentage of rape crop fields per landscape (Total parasitism: $R = 0.02$; $P = 0.66$; *Tersilochus*-parasitism: $R < 0.01$, $P = 0.99$; *Phradis*-parasitism: $R = 0.18$, $P = 0.53$).

These effects of non-crop area on herbivory and parasitism were calculated using landscape sectors with a diameter of 1.5 km. In addition, we tested smaller and larger diameters of landscape sectors to examine whether interactions between the first and the second trophic level (herbivory) as well as the second and the third trophic level (parasitism) were affected at different spatial scales. The predictive power of non-crop area for herbivory and parasitism differed in dependence on the spatial scale considered ($\varnothing$ 0.5 km, $\varnothing$ 1 km, $\varnothing$ 2 km, $\varnothing$ 3 km, $\varnothing$ 4 km, $\varnothing$ 5 km, $\varnothing$ 6 km), thereby indicating scale-dependence for both plant-herbivore and herbivore-parasitoid interactions (Table 1, Fig. 4). At all spatial scales, the predictive power of non-crop area was higher for herbivory than parasitism (Table 1, Fig. 4). However, this may be due to the three sites with zero parasitism. In contrast to our expectations, both herbivory and parasitism showed the best correlations with non-crop area at the same spatial scale, a landscape sector of 1.5 km diameter. Coefficients of determination (R^2) changed only slightly for herbivory (Fig. 4A), but greatly for parasitism (Fig. 4B) as scales from 0.5 to 1.5 km and from 1.5 to 6 km diameter increased (Table 1) suggesting a reduced susceptibility to spatial scale in the herbivores. Furthermore, slopes of the regressions tended to be steeper in parasitism than in herbivory suggesting a stronger effect of landscape changes on parasitism. The percentage of rape crop fields per landscape was not related to the percentage of destroyed buds ($\varnothing$ 0.5 km: $R = -0.31$, $P = 0.27$; $\varnothing$ 1 km: $R = -0.36$, $P = 0.19$; $\varnothing$ 2 km: $R = -0.33$, $P = 0.23$, and $\varnothing$ 3 km: $R = -0.50$, $P = 0.06$). Larval host density (see above) as well as percent rape crop area did also not significantly contribute to the explanation of parasitism (Total parasitism: $\varnothing$ 0.5 km: $R = 0.24$, $P = 0.40$; $\varnothing$ 1 km: $R = 0.12$, $P = 0.95$; $\varnothing$ 2 km: $R = 0.16$, $P = 0.56$, and $\varnothing$ 3 km: $R = 0.32$, $P = 0.25$; *Tersilochus* parasitism: $\varnothing$ 0.5 km: $R = 0.22$, $P = 0.44$; $\varnothing$ 1 km: $R = 0.12$, $P = 0.67$; $\varnothing$ 2 km: $R = 0.09$, $P = 0.75$ and $\varnothing$ 3 km: $R = 0.26$, $P = 0.34$; *Phradis* parasitism: $\varnothing$ 0.5 km: $R = 0.11$, $P = 0.71$; $\varnothing$ 1 km: $R = 0.21$, $P = 0.46$; $\varnothing$ 2 km: $R = 0.12$, $P = 0.68$ and $\varnothing$ 3 km: $R = 0.20$, $P = 0.48$.

Table 1. Dependence of plant-herbivore and herbivore-parasitoid interactions on the percentage of non-crop area (i.e. landscape complexity) in 15 agricultural landscapes at eight spatial scales: (a) percentage of destroyed rape buds ("herbivory"), (b) total percentage of parasitism due to *T. heterocerus + P. interstitialis*, (c) percentage of parasitism due to *T. heterocerus*, (d) percentage of parasitism due to *P. interstitialis*. F-values, correlation coefficients (R) and levels of significance ("stars") are from simple linear regressions with arcsine-transformed proportions (arcsine $\sqrt{p} \times 10/9$ where p is a proportion), each with $N = 15$ landscape sectors.

Factor	F	R	Regression model
Herbivory (%)			
Scale: 0.5 km	8.1	-0.62 *	$Y = 66.32 - 0.46X$
Scale: 1 km	9.0	-0.64 *	$Y = 69.15 - 0.48X$
Scale: 1.5 km	9.6	-0.65 **	$Y = 73.71 - 0.53X$
Scale: 2 km	6.2	-0.57 *	$Y = 74.47 - 0.50X$
Scale: 3 km	5.5	-0.54 *	$Y = 79.66 - 0.54X$
Scale: 4 km	3.9	-0.48 (*)	$Y = 76.79 - 0.44X$
Scale: 5 km	3.2	-0.45 (*)	$Y = 75.48 - 0.40X$
Scale: 6 km	3.2	-0.44 (*)	$Y = 76.33 - 0.41X$
Parasitism (%)$_{Total}$			
Scale: 0.5 km	2.2	0.38	$Y = 22.34 + 0.51X$
Scale: 1 km	4.9	0.52 *	$Y = 14.68 + 0.71X$
Scale: 1.5 km	6.5	0.58 *	$Y = 5.84 + 0.85X$
Scale: 2 km	5.0	0.53 *	$Y = 3.31 + 0.84X$
Scale: 3 km	2.7	0.41	$Y = 1.60 + 0.74X$
Scale: 4 km	1.7	0.34	$Y = 7.44 + 0.57X$
Scale: 5 km	1.1	0.27	$Y = 12.11 + 0.44X$
Scale: 6 km	1.0	0.27	$Y = 11.28 + 0.45X$
Parasitism (%)$_{T. heterocerus}$			
Scale: 0.5 km	1.4	0.32	$Y = 16.79 + 0.31X$
Scale: 1 km	3.2	0.44 (*)	$Y = 12.03 + 0.43X$
Scale: 1.5 km	4.5	0.51 (*)	$Y = 6.01 + 0.54X$
Scale: 2 km	3.4	0.45 (*)	$Y = 4.78 + 0.52X$
Scale: 3 km	2.0	0.37	$Y = 3.01 + 0.47X$
Scale: 4 km	1.4	0.31	$Y = 6.08 + 0.40X$
Scale: 5 km	0.8	0.23	$Y = 10.35 + 0.27X$
Scale: 6 km	0.7	0.23	$Y = 9.80 + 0.28X$
Parasitism (%)$_{P. interstitialis}$			
Scale: 0.5 km	2.6	0.42	$Y = 9.71 + 0.51X$
Scale: 1 km	5.4	0.54 *	$Y = 2.65 + 0.69X$
Scale: 1.5 km	5.0	0.53 *	$Y = -2.75 + 0.73X$
Scale: 2 km	4.1	0.49 (*)	$Y = -5.36 + 0.73X$
Scale: 3 km	1.8	0.35	$Y = -4.78 + 0.59X$
Scale: 4 km	1.0	0.27	$Y = 1.58 + 0.42X$
Scale: 5 km	0.9	0.26	$Y = 1.91 + 0.39X$
Scale: 6 km	0.9	0.26	$Y = 0.89 + 0.41X$

** $P < 0.01$; * $P < 0.05$; (*) $P < 0.1$.

Discussion

In this study, we analyzed the effects of landscape context on plant-herbivore-parasitoid interactions and addressed the question whether landscape context influences herbivory and parasitism at different spatial scales. Low plant damage caused by the rape pollen beetles and high beetle mortality due to parasitism could only be found in landscapes with a high percentage of non-crop area, i.e. in structurally complex landscapes with relatively little area converted to annual crop fields. Non-crop area supported large parasitoid populations which greatly contributed to the reduction of rape pest populations. When the non-crop area dropped below a value of approximately 20%, percent
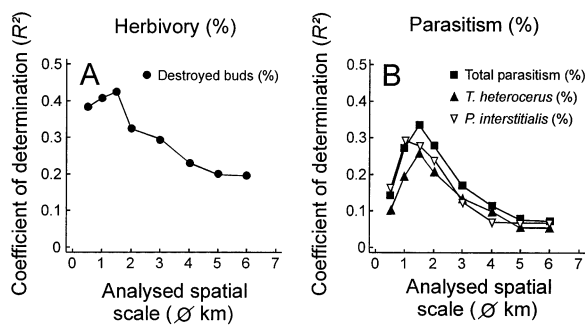
Fig. 4. Correlation of plant-herbivore and herbivore-parasitoid interactions versus the percentage of non-crop area (i.e. landscape complexity) at eight spatial scales. (A) Coefficients of determination (R^2) for herbivory (%), i.e. the percentage of destroyed rape buds. (B) Coefficients of determination (R^2) for total parasitism (%) due to *T. heterocerus* and *P. interstitialis*, partial parasitism (%) due to *T. heterocerus*, and partial parasitism (%) due to *P. interstitialis*. Statistics see Table 1.

parasitism was observed to drop below the threshold value of 32–36%, below which successful classical biological control has never been reported (Hawkins and Cornell 1994).

Parasitoid populations of rape pollen beetle may have profited from high percentage of non-crop areas, i.e. the availability of perennial habitats in complex landscapes, in three ways. First, the parasitoids hibernate in the soil and are known to be negatively affected by ploughing which reduces their emergence by 50–100% (Nilsson 1985). Undisturbed areas should better enable populations to built up over years, whereas a high proportion of annual fields should disadvantage these parasitoids. Overwintering refuges for parasitoids adjacent to crop fields were also found to increase egg parasitism of grape leafhoppers (Corbett and Rosenheim 1996), and tillage is known to kill 95% of the parasitoids attacking cereal leaf beetles (Ellis et al. 1988). Second, complex landscapes support alternative hosts and host plants, and thereby, may enhance parasitoid populations. In particular, wild Brassicaceae are known as alternative host plants of the rape pollen beetle and its parasitoids (Frenzel and Brandl 1998, Tommes et al. 1998), and several *Meligethes* species feeding on non-cruciferous herbs, such as *Lamium* spp. and *Symphytum* spp., are also hosts of the parasitoids attacking rape pollen beetles (Horstmann 1981). These alternative host plants mainly occurred on fallows, field margins, extensively managed grasslands and hedges, which represent > 20% of the total area in our structurally complex landscapes. Third, complex landscapes provide more nectar resources due to a larger cover of flowering plants (Steffan-Dewenter et al. 2001). The reviews of Powell (1986) and Wratten and Van Emden (1995) give examples of parasitism enhanced by augmented nectar resources and thereby, extended parasitoid lifetime. Wäckers and Swaans (1993) and Wäckers (1994) show that the "hunger state" of a female parasitoid is decisive whether a parasitoid is searching for food or hosts.

The expectation that the spatial scale recognized by an organism is largely influenced by its trophic level (Fig. 1) was not supported in our study. Landscape context was most strongly correlated with both herbivory and parasitism within a diameter of 1.5 km (Fig. 4). We suggest three possible reasons. First, body size did not increase with trophic level as is often the case in predator-prey interactions (for example, with vertebrate predators attacking vertebrate or invertebrate prey). Body size is a predictor of how organisms acquire resources in space (Roland and Taylor 1997, Ritchie and Olff 1999). The similar body size of the pollen beetles and their parasitoids does not justify the expectation of different home ranges or dispersal abilities encompassing landscape sectors of different diameters. Second, specialized parasitoids may be temporally and spatially more closely related to host dynamics than less specialized predators. Generalist predators depend on several prey species which may even inhabit different (micro)habitats, and may encompass a larger area than parasitoids depending on only one host species. Third, switching between prey or host populations should be more important in a heterogeneous landscape than in a more homogeneous landscape. Patchy but not continuous prey or host distribution may cause high dispersal rates of natural enemies. Oilseed rape is cultivated in large crop fields supporting huge herbivore and parasitoid populations, so parasitoids do not need to switch between fragmented host populations, and higher dispersal rates than their hosts may not be advantageous. In contrast, spatially or temporally fluctuating host or prey populations may lead to higher dispersal of natural enemies. Behavioral studies on relative movement of a tephrid fly and its parasitoid wasps on marsh thistles indicate that within-patch dispersal of four parasitoids was consistently greater than that of the host (Jones et al. 1996). In situations of local prey or host losses and the necessity to switch between variable host or prey patches, natural enemies have been shown to suffer from dispersal limitation and to depend more on connected habitats than their victims (Zabel and Tscharntke 1998, Walde and Nachman 1998, Tscharntke and Kruess 1999).

In conclusion, spatial scale of landscape context determining populations dynamics does not appear to generally increase with trophic level. However, the parasitoid populations appeared to respond more sensitively to the spatial scale of landscape context than the herbivores, which is in support of the general idea that higher trophic levels should be more susceptible to disturbance (Kareiva 1990, Kruess and Tscharntke 1994, 2000, Holt et al. 1999). We are just at the beginning to understand how different habitats and their location in a landscape connect to tritrophic interactions. This is in contrast to the great effects of

landscape context on local community structure and interactions shown by the few studies with replicated landscapes (Roland and Taylor 1997, Thies and Tscharntke 1999, Menalled et al. 1999, Östman et al. 2001). Understanding how landscape context affects populations requires a spatially explicit and organism-centered point of view (Wiens et al. 1993, With et al. 1999) to link the species-specific use of space and the spatial scale experienced with population dynamics and ecological processes. We urgently need more case studies and well-designed experiments on a landscape scale that take spatial aspects of trophic interactions into account.

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