

Landscape complexity is not a major trigger of species richness and food web structure of European cereal aphid parasitoids

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Abstract In fragmented farmland landscapes structural complexity and low agricultural intensification should decrease the abundance of crop aphids due to increased abundances and species diversity of aphid enemies, including hymenopteran parasitoids. Here we study the effects of landscape structure and agricultural intensification on parasitism rates, abundances, and species richness of aphids and their parasitoids in five different regions in Europe. While total aphid numbers did not differ significantly among regions, we observed marked differences between Scandinavian and central European sites with respect

to the species composition of aphids and their parasitoids and parasitism rates. In the cross country comparison landscape complexity and agricultural intensification did not significantly affect total aphid densities, although we observed species-specific reactions to land use. We also observed a tendency towards increased parasitoid species richness at low agricultural intensification but not at high landscape structure.

Keywords Landscape ecology · Aphid parasitoids · Aphididae · Cereal crops · Biological control

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Introduction

Landscape complexity increases species richness of many animal taxa, such as birds (Geiger et al. 2010a), bees (Holzschuh et al. 2008), spiders (Schmidt et al.

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2005), and ground beetles (Purtauf et al. 2005a, b). A number of studies also reported landscape complexity to differentially affect proportions of polyphagous and monophagous species (Jonsen and Fahrig 1997; Kassen 2002; Batáry et al. 2007). Richness of polyphagous species was found to decline at lower levels of landscape structure.

Aphids (Bianchi et al. 2006; Tscharrntke et al. 2007) as well as their hymenopteran parasitoids (Landis et al. 2000; Schmidt et al. 2005; Thies et al. 2005; Tscharrntke et al. 2005) are two taxa heavily influenced by landscape structure. A number of authors have argued that diverse landscapes have a higher aphid and parasitoid biodiversity than homogeneous ones (Schmidt et al. 2005; Tscharrntke et al. 2005; Holland et al. 2008). Other authors argued that the occurrence of species-rich guilds of aphid natural enemies is promoted by the diversity of non-crop habitats around cereal fields (Pankanin-Franczyk 1994; Schmidt et al. 2005; Thies et al. 2011). Consequently, higher complexity of rural landscape is considered an important factor promoting the effectiveness of aphid parasitoids (Kruess and Tscharrntke 2000). Additionally, parasitoid colonization and, therefore, parasitism rates are also affected by the distance between local host aphid populations and the size of aphid colonies, suggesting that spatial processes are important in this system (Rauch and Weisser 2007; Pareja et al. 2008).

Another critical determinant of effectiveness of aphid biocontrol is the ratio of polyphagous (generalist) to oligo- or monophagous (specialist) species within the different enemy guilds. Contrary to the common opinion on the superiority of specialists as biocontrol agents, generalist natural enemies such as spiders, can limit aphids more effectively because of their earlier appearance in crop fields during the

growing season (Settle et al. 1996; Snyder and Ives 2003).

Primary and secondary parasitoids have been less frequently involved in specialist-generalist comparisons within and between trophic levels (Snyder and Ives 2003; Brewer and Elliott 2004). With few exceptions, primary hymenopteran aphid parasitoids are host specialists (Mackauer and Starý 1967; Stilman et al. 2008). For example, *Aphidius uzbekistanicus* (Luzhetski) and *A. rhopalosyphi* (DeStefani-Peres) are mostly restricted to cereal aphids *Sitobion avenae* (F.), *Rhopalosiphum padi* (L.) and *Metopolophium dirhodum* (Walker). Some other parasitoid species have a broader host range. For instance, *Ephedrus plagiator* (Nees) and *Praon volucre* (Haliday) attack aphids associated with forest edges and orchards, but they can also attack aphids on herbaceous plants (Ölmez and Ulusoy 2003; Rakhshani et al. 2006). Therefore, more complex landscapes, consisting of forest and semi-natural habitats should provide more alternative hosts for polyphagous primary parasitoids. In turn, secondary parasitoids are mainly host generalists and are divided into more specialized true hyperparasitoids and polyphagous “pseudohyperparasitoids” (mummy parasitoids) (Müller et al. 1999). The ratio of specialists to generalists in both groups of secondary aphid parasitoids may be another important factor for biocontrol effectiveness. For example, Monmany and Aide (2009) found higher parasitism rates of herbivorous insects in some Argentinian forests as a result of higher numbers of generalist primary parasitoids. These differences between and within guild, as well as landscape structure and agricultural intensification might influence food chain structure and therefore total parasitism rates and biocontrol effectiveness (Mackauer and Völkl 1993).

Higher landscape complexity and its associated higher proportions of generalist parasitoids might increase the effectiveness of parasitoids in biocontrol. In this respect, complex landscapes and low agricultural intensification might (1) increase abundance and species richness of parasitoids in general (Fahrig et al. 2011), (2) increase parasitism rates by primary parasitoids (Thies et al. 2003; Rand et al. 2012), and (3) favor polyphagous primary parasitoids and mummy parasitoids (Jonsen and Fahrig 1997).

To date, no published study has tested these hypotheses simultaneously. Therefore, it is still

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unknown how the trade-offs between heterogeneity, species richness, and species host preferences influence parasitism rates and, therefore, crop protection. Using spatially explicit data on parasitoid attack on crop aphids from five European regions with different environmental conditions and species composition of aphids and their parasitoids, we investigated if and how species richness of parasitoids, their abundance, host range, and parasitism rates were linked to landscape complexity and agricultural intensification. This study design allowed us to disentangle the effects of landscape and food chain structure on crop protection.

Materials and methods

In 2008 in each of five European regions (Göttingen and Jena, Germany; Warsaw, Poland; Uppsala and Skåne, Sweden) (Supplementary data Fig. S1) eight cereal fields were chosen, of which four were managed at low levels of agricultural intensification and located in structurally complex landscapes, and four at high levels of agricultural intensification in simple landscapes. Fields were a minimum of one hectare, located at least one kilometer apart (Supplementary data table S2). Each of the five study areas was between $30 \times 30 \text{ km}^2$ and $50 \times 50 \text{ km}^2$ to minimize differences in the regional species pools among farms within each area (Geiger et al. 2010a, b). Winter wheat (*Triticum aestivum* L.) grew on the German and Polish sites and spring barley (*Hordeum vulgare* L.) in Sweden. These two crops were found to have a similar species composition of aphids and their parasitoids (Sigsgaard 2002). Sampling was synchronized between regions using phenological stages of cereals.

In this study, we used the classification of Geiger et al. (2010a, b), who estimated the degree of agricultural intensification of fields within thirty farms per region by pesticide and fertilizer use, the number of soil disrupting management events, cereal yield, the percentage of arable land and the Shannon index of habitat diversity in surrounding landscapes. The thirty fields were ranked according to these parameters, values of which were related to the particular rank. Subsequently, we summed all ranks to obtain the final rank for each field. From among these 30 fields, we selected the four fields with the highest ranks and the four lowest ranked fields. As recommended by Thies

et al. (2003) landscape structure was quantified as the proportion of individual habitat types (grassland, forest and arable land) at two spatial scales: within a circle of 500 m radius (area of about 78.5 ha included) and within a circle of 1,000 m radius (about 314 ha) around each focal field.

Data on the abundance and species composition of aphids came from field counts of aphids on 20 randomly chosen cereal shoots at five sampling points, along a transect going from the edge to the center of each field (100 cereal shoots in total per field). Counting was done twice, at flowering and milk ripening stages of the cereals, i.e. at phenological stages following colonization of the crops by aphids and the main period of aphid reproduction, respectively (for details see Thies et al. 2005).

The species composition and abundance of aphid parasitoids were assessed from aphid mummies, collected at random in the whole field, during two-hour surveys at the milk ripening stage of the crop. Mummies were taken to the laboratory and kept individually in small vials. After emergence, adult parasitoids were identified to species level. Among all sites we found only two species with single occurrences (Supplementary data table S1), indicating that our surveys were sufficiently complete to focus on observed species richness without the need for additional richness estimation.

Parasitism rate was calculated in each field at both phenological stages (cereal flowering and milk ripening) as the proportion of mummified aphids to the total number of aphids (living and mummified) on 100 cereal shoots (the same as above). Rates of hyperparasitism and mummy parasitism were calculated as the proportion of secondary parasitoids (hyperparasitoids and mummy parasitoids, respectively) to all parasitoids hatched from mummies collected during 2 h at milk ripening stage of the crop.

Because the error structures of our data did not significantly deviate from a normal approximation we used one-way analysis of variance (ANOVA) and general linear model analysis of covariance (ANCOVA as implemented in Statistica 9.0) to relate landscape complexity, region, and agricultural intensification to aphid abundance and parasitism rates. Pair-wise comparisons were based on Tukey post-hoc tests. The region of Uppsala (at both scales) and Skåne (solely at the 1000 m scale) were the only regions where agricultural intensification and landscape

heterogeneity were dependent (ANOVA: $F_{1,6} = 12.2$, $P < 0.05$ for Skåne at 1000 m scale; $F_{1,6} = 116.7$ and 232 for Uppsala at 500 and 1000 m scale respectively, both $P < 0.01$). In most cases such relationships were not significant. Therefore, we treated agricultural intensification and landscape structure as independent variables.

Results

In total we recorded 11 primary parasitoid species, four hyperparasitoid and seven mummy parasitoid species, of which *Aphelinus abdominalis* (Dalman) and *Alloxysta macrophadna* (Hartig) were found only once (Supplementary data table S1). In the Jena region, primary parasitoid richness was lowest with the overwhelming dominance of a polyphagous *Ephedrus* species. A specialized *Aphelinus* sp. was exclusively restricted to the Swedish regions whilst *Ephedrus* sp. and *Praon* sp. were quite rare there. The abundance of the specialist *Aphidius* sp. was similar in the fields of Warsaw, Göttingen and Skåne (ANOVA: $F_{2,21} = 0.31$, $P > 0.05$) (Fig. 1; Supplementary data table S1). Richness and abundance of hyperparasitoids were highest in Skåne (Tukey post-hoc test: $P < 0.01$ for both variables), and lowest in the regions of Jena and Uppsala (Tukey post-hoc test: $P < 0.05$ for both regions). The Uppsala was also the only region where mummy parasitoids were not recorded at all (Fig. 2; Supplementary data tables S1, S3).

The common cereal aphid species *S. avenae*, *R. padi* and *M. dirhodum* occurred at all study sites (Supplementary data tables S1, S3) but differed significantly in

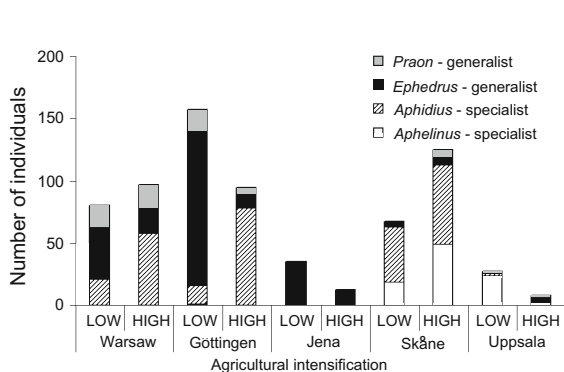


Fig. 1 Numbers of individuals of particular genera of primary parasitoids recorded in the eight study fields, with low and high agricultural intensification in each region

abundance among our study regions (Table 1, Supplementary data table S4, ANOVA: $F_{4,35} = 10.4$ and 9.3 for *S. avenae* flowering and milk ripening stage of cereal, respectively, both at $P < 0.0001$; $F_{4,35} = 5.8$, $P < 0.01$ for *M. dirhodum* at cereal flowering; $F_{4,35} = 3.2$ and 2.6 for *R. padi* at cereal flowering and milk ripening, respectively, both at $P < 0.05$). In the two Swedish regions, *R. padi* clearly dominated at both aphid censuses, while in Göttingen and Jena the most abundant species were *S. avenae* and *M. dirhodum*, respectively. In the Warsaw region, *S. avenae* and *M. dirhodum* co-dominated attaining similar population levels. In all but one region (Göttingen), aphid abundance was higher at crop flowering than at milk ripening stage (Supplementary data table S1). Total aphid numbers at flowering and milk ripening stages did not significantly differ among regions (ANOVA: $F_{4,35} = 1.3$ and 1.4, respectively, both at $P > 0.05$). We also found no clear relationship between species richness of primary parasitoids and landscape heterogeneity (ANCOVA: $F_{1,29} = 0.22$ and 0.0005 at 500 and 1000 m scale, respectively, both at $P > 0.05$).

We found significant, although incongruent differences in the parasitism rates of primary, mummy, and hyperparasitoids at milk ripening stage among the regions (Table 2, Supplementary data table S4). At milk ripening stage of the crop, primary parasitism was lowest in Göttingen and highest in Warsaw, hyperparasitism highest in Skåne and lowest in Jena, and mummy parasitism highest in Jena and lowest in Uppsala (Supplementary data table S1).

At both spatial scales we found only a weak indication that aphid abundances were influenced by landscape

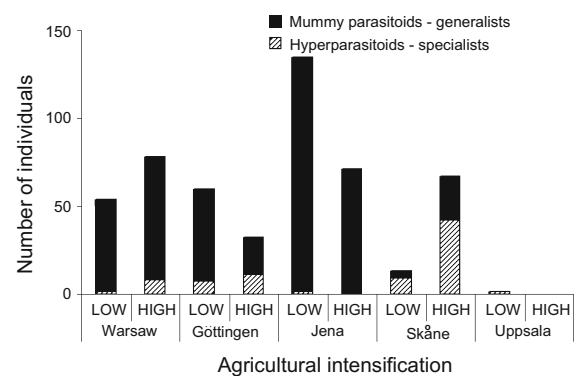


Fig. 2 Numbers of individuals of hyperparasitoids and mummy parasitoids recorded in the eight study fields, with low and high agricultural intensification in each region

Table 1 Statistical results (ANCOVA) for the influence of landscape diversity (500 and 1000 m radius), region, and agricultural intensification (AI) on the abundance of particular aphid species at flowering and milk ripening stages of crop, N = 40

Predictor	df (effect, error)	Abundance											
		<i>Sitobion avenae</i>				<i>Metopolophium dirhodum</i>				<i>Rhopalosiphum padi</i>			
		Flowering		Milk ripening		Flowering		Milk ripening		Flowering		Milk ripening	
		F	P	F	P	F	P	F	P	F	P	F	P
Landscape heterogeneity 500 m	1, 38	2.13	0.16	3.21	0.08	4.12	0.05	0.04	0.85	0.58	0.45	0	0.98
Region	4, 35	11.16	<0.01	11.81	<0.01	7.71	<0.01	0.59	0.67	3.42	0.02	2.26	0.09
AI	1, 38	0.5	0.48	0.18	0.67	6.78	0.01	3.08	0.09	0.99	0.33	0.23	0.64
Region×AI	4, 35	1.15	0.35	3.74	0.01	1.72	0.17	0.74	0.58	1.77	0.16	0.25	0.91
Landscape heterogeneity 1,000 m	1, 38	5.02	0.03	2.29	0.14	4.16	0.05	0.23	0.63	0.27	0.61	0	0.98
Region	4, 35	12.14	<0.01	9.57	<0.01	8.07	<0.01	0.56	0.69	3.41	0.02	2.24	0.09
AI	1, 38	0.05	0.82	0.2	0.66	7	0.01	2.34	0.14	0.76	0.39	0.24	0.63
Region×AI	4, 35	1.76	0.16	3.5	0.02	1.69	0.18	0.72	0.58	1.79	0.16	0.24	0.91
% of arable land 500 m	1, 38	3.35	0.08	5.96	0.02	3.5	0.07	0	0.99	0.16	0.69	0.01	0.93
Region	4, 35	11.8	<0.01	11.12	<0.01	7.88	<0.01	0.59	0.67	3.37	0.02	2.26	0.09
AI	1, 38	0.32	0.58	0.03	0.87	6.26	0.02	3.47	0.07	0.65	0.43	0.2	0.66
Region×AI	4, 35	1.24	0.32	4.22	0.01	1.67	0.18	0.73	0.58	1.7	0.18	0.25	0.91
% of arable land 1,000 m	1, 39	7.44	0.01	6.59	0.02	5.56	0.03	0	0.98	0.18	0.68	0.06	0.81
Region	4, 35	13.52	<0.01	9.56	<0.01	8.88	<0.01	0.59	0.68	3.38	0.02	2.25	0.09
AI	1, 39	0.02	0.88	0.01	0.94	7.91	0.01	3.35	0.08	0.66	0.42	0.13	0.72
Region×AI	4, 35	2.04	0.12	4.76	<0.01	1.8	0.16	0.73	0.58	1.75	0.17	0.2	0.94

Statistically significant values of the associated F-tests ($P < 0.05$) are in bold

complexity (Table 1, Supplementary data table S4). Only *S. avenae* seemed to be negatively influenced by the percentage of arable land and reached higher abundances in structurally more diverse landscapes (Tukey post-hoc test: $P < 0.01$). Abundances of the aphid *M. dirhodum* were positively correlated with agricultural intensification (Table 1, Supplementary data table S4).

High agricultural intensification did not significantly reduce parasitoid species richness (matched pairs test: $P > 0.1$). However, there was a weak tendency to increased species numbers (Fig. 3a: six data points below and three above the 1:1 regression line, P (binomial distribution) = 0.25) and parasitism rates (Fig. 3b: eight data points below and four above the 1:1 regression line, P (binomial distribution) = 0.19) at low agricultural intensification.

Parasitism rates by hyperparasitoids were independent of the rates of primary parasitoids (Fig. 4a), while parasitism rates by mummy parasitoids increased with those by primary parasitism (Fig. 4b). They were also

independent of agricultural intensification and landscape structure in all cases (Table 2, Supplementary data table S4).

Discussion

Our study does not corroborate common hypotheses on the influence of landscape heterogeneity on parasitoid abundance and their effectiveness as bio-control agents (Kruess and Tscharrntke 2000; Thies et al. 2003, 2005). These hypotheses state that high primary parasitoid abundances in complex landscapes should increase parasitism rates and reduce pest numbers (Altieri and Letourneau 1982). For example Gagic et al. (2011) reported a higher rate of aphid parasitism in areas with more diverse vegetation. However some authors challenged this view, showing that complex landscape (Menalled et al. 1999) as well as the species richness of the food web (Montoya et al.

Table 2 Statistical results (ANCOVA) for the influence of landscape diversity (500 and 1000 m radius), region, and agricultural intensification (AI) on parasitism rates of primary, hyperparasitoids, and mummy parasitoids at flowering and milk ripening stages of crop, N = 40

Predictor	df (effect, error)	Parasitism rates							
		Primary parasitoids				Hyperparasitoids		Mummy parasitoids	
		Flowering		Milk ripening		Milk ripening		Milk ripening	
		F	P	F	P	F	P	F	P
Landscape heterogeneity 500 m	1, 38	0.37	0.55	0.09	0.7	0.07	0.8	2.72	0.11
Region	4, 35	0.84	0.51	3.69	0.02	1.68	0.18	24.57	<0.01
AI	1, 38	0.26	0.61	0.38	0.54	0	1	3.62	0.07
Region×AI	4, 35	1.5	0.23	0.55	0.7	1.76	0.16	1.25	0.31
Landscape heterogeneity 1000 m	1, 38	2.94	0.1	0.26	0.61	0.1	0.75	2.25	0.14
Region	4, 35	0.58	0.68	3.72	0.01	1.66	0.19	24.27	<0.01
AI	1, 38	1.35	0.26	0.54	0.47	0	0.96	3.41	0.07
Region×AI	4, 35	1.36	0.27	0.6	0.67	1.79	0.16	1.3	0.29
% of arable land 500 m	1, 38	0.7	0.41	0.09	0.77	0.04	0.84	2.1	0.16
Region	4, 35	0.76	0.56	3.63	0.02	1.68	0.18	24.22	<0.01
AI	1, 38	0.39	0.54	0.38	0.54	0	0.98	3.19	0.08
Region×AI	4, 35	1.58	0.21	0.55	0.7	1.74	0.17	1.08	0.38
% of arable land 1000 m	1, 38	2.37	0.13	0.19	0.67	0	0.99	1.22	0.28
Region	4, 35	0.6	0.67	3.59	0.02	1.69	0.18	23.21	<0.01
AI	1, 38	1.02	0.32	0.47	0.5	0.02	0.9	2.55	0.12
Region×AI	4, 35	1.38	0.26	0.58	0.68	1.7	0.18	1.12	0.37

Statistically significant values of the associated F-tests ($P < 0.05$) are in bold

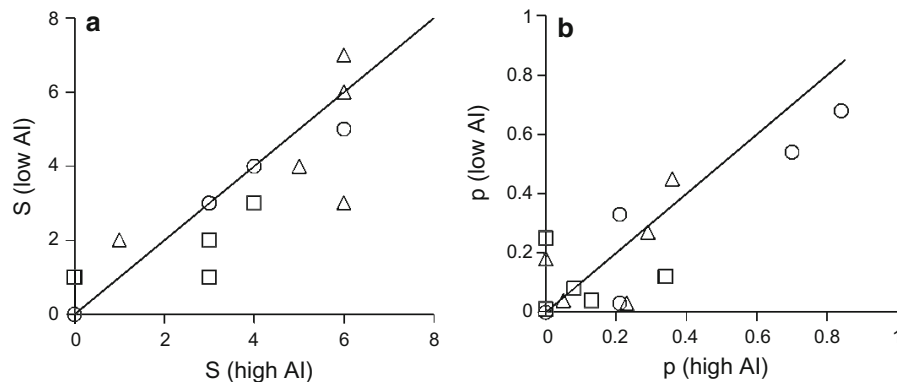


Fig. 3 Species richness *S* (**a**) and parasitism rates *p* (**b**) of primary (triangles), mummy (circles), and hyperparasitoids (squares) on fields of low and high agricultural intensification (AI) were positively correlated (**a** $r = 0.85$; permutation

$P < 0.01$; **b** $r = 0.83$; permutation $P < 0.01$) but did not significantly differ (Wilcoxon's matched pairs test (**a**) and ANOVA (**b**): both permutation $P > 0.1$). The straight lines in **a** and **b** indicate the 1:1 relationship

2003) do not enhance rates of parasitism. Similar results were obtained by Salvo et al. (2005) who showed that parasitism and parasitoid species richness were higher in simple than in complex habitats.

There was no clear relationship between species richness of primary parasitoids and landscape structure. Similar findings were reported by Marino and Landis (1996), Costamagna et al. (2004), Vollhardt

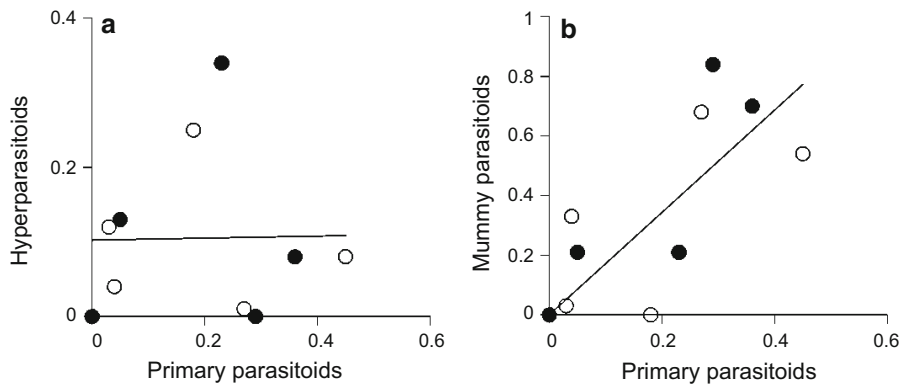


Fig. 4 Parasitism rates of hyperparasitoids were not correlated with the rates of primary parasitoids (**a** linear regression $r = 0.02$; permutation $P > 0.5$), while parasitism rates of mummy parasitoids significantly increased with those of

primary parasitoids (**b** linear regression $r = 0.73$; permutation $P = 0.01$). *Black dots* refer to high agricultural intensification (AI) fields, *open circles* to low AI fields

et al. (2008) and Rand et al. (2012), in contrast to other investigations, which have identified environmental heterogeneity as an important contributor to total species richness of different vertebrate and arthropod taxa (Kassen 2002; Schmidt et al. 2005; Bianchi et al. 2006; Öberg et al. 2007; Schüepp et al. 2011). According to previous studies, species richness of organisms was influenced particularly by the number of cover types and their spatial array (Holland and Fahrig 2000; Weibull et al. 2000), but also by the habitat age (Fahrig and Jonsen 1998; Tscharrntke and Kruess 1999), land-use intensification, cropping history (Thies and Tscharrntke 1999), soil variables, and climate (Dormann et al. 2008). Some authors (Gagic et al. 2011; Schüepp et al. 2011; Rand et al. 2012) have also suggested that parasitoids might benefit from the proximity of perennial herbaceous habitats and forest patches surrounding arable fields. Semi-natural habitats were found to increase the longevity and fecundity of parasitoids and offered them shelter from agricultural disturbances (Costamagna et al. 2004; Araj et al. 2008).

Our results do not point to any significant influence of landscape complexity on parasitoid species richness (see results section) and parasitism rate after accounting for differences among regions (Table 2, Supplementary data table S4). Therefore, the most likely explanation for these mixed results may be that studies have been conducted in different regions. Another explanation could be tied with temporal variation in the dynamics of parasitoids (Menalled et al. 2003), or simply the short period of the study. However, most

studies exploring this issue (Marino and Landis 1996; Menalled et al. 1999; Costamagna et al. 2004; Salvo et al. 2005; Monmany and Aide 2009; Gagic et al. 2011; Rand et al. 2012) lasted only one season. Moreover, some of them have tested pests that are usually controlled by generalists, rather, than more specialized parasitoids with few alternative hosts (Marino and Landis 1996; Costamagna et al. 2004; Monmany and Aide 2009). The results of this and other investigations suggest that various causes (regional differences, variability in population dynamics, duration of the studies, different studied organisms) may generate inconsistent results. Nevertheless, they concern the influence of landscape or agricultural intensification and it is justifiable to take their conclusions into account.

Our investigation strongly shows the species composition of aphids and their parasitoids, as well as the effectiveness of parasitoids as biocontrol agents, depend mainly on the geographical region, but not on the landscape heterogeneity nor on the agricultural intensification (Table 2, Supplementary data table S4). For instance, *R. padi* is known as the most abundant cereal aphid in Sweden (Leather et al. 1989; Östaman et al. 2001). The dominance of *R. padi* is associated with better suitability for cooler climates (Gianoli 1999). This fact and the high abundance of its primary host *Prunus padus* may explain the increased abundances of this aphid at the Swedish study sites. The differences in species composition of aphids and their parasitoids recorded between European and Swedish study regions, were probably not caused by

the occurrence of different host plants (Sweden – spring barley, Europe – winter wheat). According to the results of Leather and Lehti (1982), *R. padi* was equally distributed on barley, wheat and oats in colder regions like Finland. Similar results were obtained by Sigsgaard (2002), who showed no differences in aphid and parasitoid species composition between wheat and barley in Zealand (Denmark). She recorded all three aphid species, with a strong dominance of *S. avenae*, and with very low numbers of *M. dirhodum* and *R. padi* on both host plants.

These regional differences in aphid composition affected higher trophic levels. Le Ralec et al. (2011) emphasized internal defense mechanisms of *R. padi*, which result in many of its parasitoids being unable to reach later larval stages. As the spectrum of parasitoids was limited to *Aphidius* and *Aphelinus* species at the Swedish sites, more polyphagous taxa such as *Ephedrus* and *Praon*, may not have been able to break the immunological defense of *R. padi*. In turn, *Ephedrus* and *Praon* were abundant in central Europe, where *R. padi* was not so common (Fig. 1, Supplementary data table S1).

Kassen (2002) and Schüepp et al. (2011) hypothesized that complex landscapes and low intensity agriculture favor generalist organisms. In the present case, this prediction refers particularly to polyphagous mummy parasitoids. In comparison with hyperparasitoids, they are expected to exert stronger parasitism pressure on primary parasitoids in diverse landscapes due to their higher numbers in such landscapes (Tscharnke et al. 2007). However, in comparison with specialized hyperparasitoids, polyphagous mummy parasitoids might be less effective in limiting primary parasitoids because of other hosts that they can utilize (Montoya et al. 2003). In turn, simple landscapes are expected to promote an increased proportion of specialized *Aphidius* and *Aphelinus* species within primary parasitoid assemblages. It would result in higher numbers of specialized hyperparasitoids, which prefer these species as hosts. Such a situation should weaken the primary parasitoid pressure. Again, our results do not corroborate this view. We did not find significant responses of parasitoid species richness (see results section) and parasitism rates (Fig. 3; Table 2, Supplementary data table S4) to our measures of landscape heterogeneity and agricultural intensification, as well as parasitism rates by primary, hyperparasitoids, and mummy parasitoids

(Fig. 4; Table 2, Supplementary data table S4). Furthermore, we did not observe any response of hyperparasitoids to the increased abundance of their hosts. Hyperparasitoids and primary parasitism rates were independent irrespective of agricultural intensification (Fig. 4a). In turn, mummy parasitoids increased their parasitism rates at higher levels of primary parasitoid attack (Fig. 4b), again regardless of agricultural intensification. Such a linear increase might have severe consequences for the population dynamics of the primary parasitoids and might indicate density-dependent prey mortality (Varley et al. 1974; van Veen et al. 2002). Our data do not allow for a direct test of this prediction as we did not measure parasitism rates directly. However, the correlation between mummy and primary parasitoid attack rates (Fig. 4b) is expected if parasitoid effectiveness in biological control were independent from landscape heterogeneity and agricultural intensification and mainly triggered by host availability.

In line with the above argument, landscape complexity and agricultural intensification did not significantly affect total aphid population densities in the cross country comparison although we found significant species-specific differences in regional abundance (Table 1, Supplementary data table S1). *Metopolophium dirhodum* seems to be affected by agricultural intensification, whilst *Sitobion avenae* by landscape structure (Table 1, Supplementary data table S4). The latter finding is in line with Thies et al. (2005) who showed a positive influence of landscape heterogeneity on the dominant *S. avenae* and explained this by the food preferences of *S. avenae*, and its association with grassy habitats.

In conclusion, our results did not reveal a dominant influence of landscape structure and agricultural intensification on aphid—parasitoid food webs. However, we found significant differences in abundance and species richness of aphids and their parasitoids, and parasitism rates between geographical regions across Europe. Patterns of parasitoid attack and, therefore, their effectiveness in the control of aphid crop pests appeared to be largely independent from the landscape parameters we quantified.

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