Agricultural intensification, biological pest control and spatio-temporal changes in food web structure

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Chapter 1

Introduction: Agricultural intensification, biological pest control and spatio-temporal changes in food web structure

Agricultural intensification, biodiversity and ecosystem functioning

In the face of increasing food demand for a growing human population, agriculture has been intensified at local and landscape scales, often leaving homogenous landscapes with only few and fragmented semi-natural habitats, such as calcareous grasslands, meadows and forests (Stoate *et al.* 2001, Robinson & Sutherland 2002). Agro-ecosystems now cover 65 per cent of terrestrial land (Jackson *et al.* 2009), while 60% of human food is comprised of three cereals: wheat, corn and rice (Tilman *et al.* 2002). In addition, management at field scales became more intensive due to machine-driven farming with higher inputs of fertilizers and pesticides, lower crop diversity and increased sizes of arable fields, resulting in the reduction of habitat diversity and quality for most species (Matson *et al.* 1997, Tscharntke *et al.* 2005).

Agricultural intensification (AI) is currently a major threat to biodiversity (Matson *et al.* 1997, Tscharntke *et al.* 2005). However, structurally complex landscapes and organic agriculture may compensate for biodiversity losses due to AI (Benton *et al.* 2003, Hole *et al.* 2005, Bianchi *et al.* 2006), with organic fields being mainly beneficial for biodiversity in structurally simple landscapes (Bengtsson *et al.* 2005, Tscharntke *et al.* 2005), but often situated in landscapes containing large amounts of semi-natural vegetation (Gibson *et al.* 2007). Furthermore, by altering the composition of ecological communities and decreasing biodiversity, AI affects related ecosystem services, such as biological control (Hooper *et al.* 2005). Being outside the market, ecosystem services are often ignored and undervalued, although they contribute greatly to human welfare (Constanza *et al.* 1997). For example, Constanza *et al.* (1997) estimated biological control to be worth US$400 billion per year.

Plethora of different quantitative and qualitative biodiversity measures (such as species richness, evenness, community composition, species turnover, food web indices etc.), while often essential to address different questions, complicate drawing general conclusions on the relationship between AI, biodiversity and ecosystem functioning. Although species richness is commonly used as predictor variable, species interactions can be as important in determining biodiversity-ecosystem functioning relationship (Woodward 2009), but remained largely unexplored in field studies. Furthermore, AI often induces simultaneous and mutually dependant changes in more than one trophic level or functional group. For example, abundances and diversity of natural enemies often decrease in highly intensified fields, while pest species, such as cereal aphids, can benefit from higher amounts of nitrogen fertilisers combined with loss of natural enemies (Honek 1991, Bianchi *et al.* 2006). Thus, studies that combine analyses at multiple trophic levels and functional groups are needed to improve our knowledge on pest and their natural enemy communities in dynamic agricultural landscapes. Furthermore, given that agricultural practices induce uniformity in both space and time (Benton *et al.* 2003) effects of AI on biodiversity and ecosystem functioning cannot be fully understood unless appropriate spatio-temporal scales at which species and communities operate are taken into account. In my studies, I focused on the effects of AI on biodiversity and ecosystem functioning comparing multiple trophic levels and functional groups in spatiotemporally changing environments.

Study design and organisms

The studies were carried out in winter wheat fields in Germany in the vicinity of the city of Göttingen (Lower Saxony). Winter wheat is the major crop in Germany and its area of cultivation constantly increases (14% increase in Germany during last decade), while that of most other crops, such as barley decreases (as reported in 2009 by Federal Statistical Office, Germany, www.destatis.de). The region of Göttingen is dominated by arable crops interspersed with human settlements and semi-natural areas, such as grasslands, forests, fallows and hedges, but percentage of each landscape element greatly differs from one landscape to the other (Figure 1.1.).

Figure 1.1. Landscape structural complexity in the vicinity of the city of Göttingen: (left) structurally complex landscape, (right) structurally simple landscape.

Figure 1.2. Parasitoid and parasitized aphid ("mummy") on winter wheat.

The major and economically important pests in winter wheat fields in Europe are aphids (Hemoptera: Sternorrhyncha). Chemical control of aphids is possible but not satisfactory, owning to numerous negative effects of pesticides on the environment, human health, and natural enemies and other non-target groups (Willson & Tisdell 2001). Flying and ground-dwelling arthropod fauna contributing to aphid biological control is mainly composed of parasitoids (Hymenoptera: Aphidiidae), hoverflies (Diptera: Syrphidae), carabid beetles (Coleoptera: Carabidae) and several other groups, which have been shown to significantly reduce populations of aphids (Schmidt *et al.* 2003, Thies *et al.* 2005; 2011). These taxa play an important role as specialised (parasitoids, Figure 1.2.) and more generalised (predators) natural enemies, but relative importance of different enemy groups is little known and differs among regions (Thies *et al.* 2011). Furthermore, the relative importance of different enemy groups might change with AI, so that in highly intensified landscapes, organisms with high dispersal abilities, such as hoverflies, might have higher influence on local food web interactions than dispersal limited groups such as parasitoids (Tscharntke *et al.* 2005). In addition, various mechanisms, such as secondary parasitism may disrupt biological control mediated by primary parasitoids and decrease their biological control potential (Rosenheim JA 1998). Here, we address biodiversity and ecosystem functioning of the above-mentioned arthropod groups in relation to agricultural intensification.

In the first two field studies (Chapter 2 and 3), we focused on food web interactions between cereal aphids, primary-parasitoids and secondary parasitoids, and analysed parasitism as an ecosystem service and herbivory as well as hyperparasitism as disservices. In the last part (Chapter 4), we studied aphid natural enemies' community composition as influenced by AI, and their within and among-group variation. The first study (Chapter 2) has been conducted in winter wheat fields embedded in a gradient of landscape structural complexity and insects were sampled at wheat milk ripening (time of aphid reproduction in fields). In the other two parts (Chapter 3 and 4) studies are carried out in winter wheat fields under contrasting AI regimes (organic farming in complex landscapes vs. conventional farming in simple landscapes) over time. Hence, AI simultaneously varied at the local and the landscape scale. In Chapter 4 we analysed five taxa (aphids, hoverflies, carabid beetles, primary and secondary parasitoids) sampled four times during the season, starting from wheat flowering (time of aphid colonisation of fields) until wheat peak ripening (crash time of all populations). A description of the sampling methods and more information about study designs can be found in the Method sections of Chapters 2-4.

Research objectives and chapter outline

The overall aim of this research is to examine effects of agricultural intensification on communities of aphids and their natural enemies. Diversity of these taxa or identity of particular species is thought to be associated with ecosystem functioning, such as biological control, which in turn influences agricultural production. We aimed to understanding biodiversity and ecosystem functioning patterns under the influence of AI by analysing spatio-temporal changes in food-web interactions, species richness, evenness and species turnover of different feeding guilds and trophic levels.

In Chapter 2 we examined how landscape structural complexity affects aphid-parasitoid-hyperparasitoid food-web interactions and ecosystem functioning. We found that landscape complexity considerably influenced trophic link properties, but not species richness. While parasitism rates increased in structurally more complex landscapes, food web complexity decreased, thereby casting doubt on the general importance of food web complexity for ecosystem functioning.

In Chapter 3 we took a step further, by including the temporal scale in investigating how contrasting AI regimes influence aphid-parasitoid-hyperparasitoid species richness, evenness, food-web properties and parasitism rates. We found that high AI increases food web complexity and temporal variability in aphid-parasitoid food webs, while parasitism rates decreased. Contrary to primary parasitoids, secondary parasitoids exhibited a positive relationship between biodiversity (as measured by species richness, evenness and food web properties) and ecosystem functioning (hyperparsisitism rates). Hence, ecosystem functioning might not be easily predictable from biodiversity measures and its relation to biodiversity might differ among different trophic levels, thereby further complicating drawing general conclusions.

Chapter 4 addresses the relationship between AI and community composition and variability of aphid natural enemies, i.e. hoverflies, carabid beetles, primary and secondary parasitoids. We show that environmental homogeneity due to AI does not necessarily homogenize communities in space and time, and can have contrasting effects on the community variability of specialist and low-dispersive parasitoids vs. generalist and high-dispersive predators.

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Chapter 2

Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient

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Abstract

Decline in landscape complexity owing to agricultural intensification may affect biodiversity, food web complexity and associated ecological processes such as biological control, but such relationships are poorly understood. Here, we analysed food webs of cereal aphids, their primary parasitoids and hyperparasitoids in 18 agricultural landscapes differing in structural complexity (42 – 93% arable land). Despite little variation in the richness of each trophic group, we found considerable changes in trophic link properties across the landscape complexity gradient. Unexpectedly, aphid – parasitoid food webs exhibited a lower complexity (lower linkage density, interaction diversity and generality) in structurally complex landscapes, which was related to the dominance of one aphid species in complex landscapes. Nevertheless, primary parasitism, as well as hyperparasitism, was higher in complex landscapes, with primary parasitism reaching levels for potentially successful biological control. In conclusion, landscape complexity appeared to foster higher parasitism rates, but simpler food webs, thereby casting doubt on the general importance of food web complexity for ecosystem functioning.

Keywords: food webs, biological control, landscape complexity, parasitoids, hyperparasitoids

Introduction

In agricultural landscapes, the loss of semi-natural habitats and the fragmentation and degradation of remaining habitat remnants may reduce biodiversity and associated ecosystem processes (Thies & Tscharntke 1999, Robinson & Sutherland 2002, Benton 2003, Tscharntke *et al.* 2005a, Bianchi *et al*. 2006), but can also promote species groups via higher productivity or specific resources provided by agriculture (Tscharntke *et al.* 2005a, Rand *et al.* 2006). Higher trophic level organisms can be expected to be at a disadvantage in anthropogenically fragmented habitats when they exhibit traits such as a small body size and low dispersal ability, high resource specialization or high population size variability (Kruess & Tscharntke 1994, Holt *et al.* 1999). Furthermore, even when species richness is unaffected by agricultural intensification, the structure of the food web interactions may change (Tylianakis *et al.* 2007), and this may affect biological control. However, the relationship of food web structure and ecological processes, such as biological control is poorly understood and has been so far largely ignored. Moreover, it is even less clear how these relationships change across landscapes differing in structure and community composition (Loreau 2001, Memmott *et al.* 2006). There is experimental evidence for pest suppression in agricultural systems by diverse enemy communities (Cardinale *et al.* 2003, Schmidt *et al.* 2003, Snyder & Ives 2003, Letourneau *et al.* 2009), but this is also documented in simplified habitats and by less species-rich enemy communities (Hawkins *et al.* 1999, Montoya *et al.* 2003, Finke & Denno 2004). For example, Rodriguez & Hawkins (2000) found no effect of parasitoid richness on pest suppression, probably owing to a low-resource complementarity and/or strong bottom-up control. By contrast, species richness and parasitism rates are often positively related (Hawkins & Gagné 1989), but such relationships may not be causal as the dynamics of systems are often driven by one or few species (Hawkins 1994).

Biological control of aphids is an important ecosystem service as aphids are one of the major pests in cereal fields in Europe (Vickerman & Wratten 1979, Ankersmit & Carter 1981, Thies *et al.* 2005). Naturally occurring parasitoids have been shown to be important in suppressing aphid abundances (Schmidt *et al.* 2003, Thies *et al.* 2005). Their populations are enhanced in agricultural landscapes with a high percentage of semi- natural habitats providing shelter from agricultural practices, alternative hosts and flower resources (Landis *et al.* 2000, Roschewitz *et al.* 2005, Thies *et al.* 2005). However, hyperparasitoids may disrupt biological control of aphids mediated by primary parasitoids (Rosenheim 1998), and the effects of landscape complexity on this fourth trophic level remain largely unexplored. Hence, it is necessary to analyse biological aphid pest control in a multi-trophic context (Memmott *et al.* 2006, Letourneau *et al.* 2009), and more specifically, to assess the impact of the fourth trophic level on the third trophic level in changing landscapes, and whether and how these effects cascade down within food webs.

Here, we examined food webs of cereal aphids, their primary parasitoids and hyperparasitoids in 18 winter wheat fields in Germany across landscapes differing in structural complexity (42 – 93% arable land). We used recently developed quantitative, weighted descriptors of food web complexity (Bersier *et al.* 2002) that are more accurate, more robust to differences in sampling effort and less sensitive to among system differences, compared with their qualitative counterparts (Banašek-Richter *et al.* 2004, 2009). They account for variation in link magnitude and energetic importance of each species in a community. Increasingly used in the last decade, these methods have been shown to provide a powerful tool with which to explore the structure of ecological communities and their responses to environmental factors that may not be revealed by analyses of species richness *per se* (Tylianakis *et al.* 2007, Albrecht *et al.* 2007, Bukovinszky *et al.* 2008, Murakami *et al.* 2008, van Veen *et al.* 2008). Here, we analysed four of these quantitative metrics (generality, vulnerability, interaction diversity, and linkage density) as well as the mortality rates of primary and hyperparasitoids to test the functional significance of these descriptors and their response to decline in landscape complexity. We expected that: (i) a decline in landscape complexity would lead to lower species richness, with stronger effect on higher trophic levels; (ii) food web complexity would decrease as species richness decreases in simple landscapes; and (iii) the simpler the food web, the lower parasitism rates would be.

Material and methods

The organisms

The most dominant aphids (Hemiptera: Sternorrhyncha) in winter wheat in Germany are *Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker) and *Rhopalosiphum padi* (Linnaeus). Cereal aphids are attacked by primary parasitoids in the subfamily Aphidiinae (Braconidae, Ichneumonidea) and family Aphelinidae (Chalcidoidea). Larvae of each species of the primary parasitoids that are commonly found in winter wheat can develop by feeding internally in all three aphid species (Powell 1982), subsequently killing them and forming a cocoon (referred to as a 'mummy'). Primary parasitoids are attacked by secondary parasitoids including Alloxystinae (Cynipoidea, Charipidae) that feed internally on a primary larval host within the living aphid (true hyperparasitoids), as well as Pteromalidae (Chalcidoidea) and Megaspilidae (Ceraphronoidea, namely *Dendrocerus sp.)* that feed externally on the primary or secondary larval parasitoid inside the mummy (mummy parasitoids) (Sullivan *et al.* 1988). For simplicity, we will refer to both true hyperparasitoids and mummy parasitoids as hyperparasitoids in this paper.

Study design

We analysed a dataset partly used and described in detail by Thies et al. (2005), in which the focus was on the effect of landscape complexity on aphid-parasitoid population densities and parasitism rates across different spatial scales. Our study was carried out in 18 conventionally managed winter wheat fields in the surroundings of Göttingen, Lower Saxony, Germany. The most common habitats in the region are intensively used arable fields and patchily distributed semi-natural habitats, such as forest fragments, fallows and grasslands. Proportions of the habitat types were measured in the surrounding of each field. Percentage of arable land in a landscape sector has been shown to be a good indicator of landscape complexity owing to its close correlation with other landscape metrics, such as habitat type diversity (Thies & Tscharntke 1999, Steffan-Dewenter *et al.* 2002, Schmidt *et al.* 2004). We used a circle with 1 km diameter around each study field to measure landscape complexity (i.e. the percentage of arable land), as this scale has been found to be appropriate given the low dispersal abilities of cereal aphid parasitoids (Thies *et al.* 2005). Structural complexity of landscapes in this dataset ranged from 42 (structurally complex landscapes) up to 93 per cent arable land (structurally simple landscapes). Land-use intensity (i.e. the amount of nitrogen fertilizers and pesticides used) was not related to landscape complexity (see Thies *et al.* 2005). The average temperature (°C) and total rainfall (millimetres) during the study period from June to July 2001 were 13.9°C, 59.9 mm in June and 18.4°C, 68.8 mm in July (data from the meteorological station in Göttingen). Sampling was conducted in each field after the main period of aphid reproduction in July (wheat milk-ripening) in an insecticide-free area of 800 m^2, reaching 40 m along the field edge and 20 m into the fields. Aphids and mummies (parasitized aphids) were visually quantified on 100 wheat shoots per field. Additionally, aphid mummies were collected for 2 h per field during the milk-ripening period and reared in the laboratory to identify primary and hyperparasitoid genera. Hyperparasitoid - primary parasitoid genera relationships were identified using typical mummy morphologies induced by primary parasitoids (Powell 1982). Thus, links between food web members were fully quantified, which makes this economically important system a good ecological model system for investigating multi-trophic interactions (Müller & Godfray 1999).

Quantitatively weighted food web metrics (linkage density, generality, vulnerability, interaction diversity) were calculated following Bersier *et al.* 2002 (for details refer to the Supplementary Methods 2.1.). Quantitative vulnerability is the mean number of consumers per host species and quantitative generality is the mean number of host species per consumer species. Quantitative linkage density is the mean number of links per species and quantitative interaction diversity is a measure of Shannon diversity of interactions taking the number as well as the evenness of interactions into account. These metrics are often used to represent measures of food web complexity (Neutel *et al.* 2007, Banašek-Richter *et al.* 2009, Blüthgen 2010). Parasitism rates were calculated as the proportion of mummies from all aphids (including mummies) and the proportion of hyperparasitoid mummies from all mummies (including primary and hyperparasitoids).

Statistical analysis

We used general linear models to test the effect of landscape complexity on food web metrics as well as primary parasitism and hyperparasitism rates, while controlling for genera richness of hosts and consumers by including them in the models before arable land (the measure of landscape complexity) following Tylianakis et *al.* (2007). Thus, we accounted for the effect of variation in genera richness across different landscapes on food web metrics and parasitism rates. Overall variance in the response variables was quantified by using type I sum of squares. Additionally, we tested the influence of food web topologies on parasitism rates for primary and hyperparasitoids. Residuals of the models were tested for normality of errors and homogeneity of variance. (log + 1)-transformations or reciprocal transformations were used for genera richness and food web metrics, and arcsine square-root transformation for percentages (when necessary), to meet assumptions of the approach. To account for nonlinearity, models were also tested by including quadratic terms of explanatory variables. The best-fit models were chosen according to the Akaike information criterion (AIC). We found no hyperparasitoids in two fields, thus we excluded these fields from primary-hyperparasitoid food web analysis. All models were tested for spatial autocorrelation in the residuals using Moran’s I statistic, and marginally significant (p = 0.049) spatial autocorrelation was present in only one model (for the effect of generality on parasitism rates). We used a generalized least squares model with exponential spatial correlation structure (which was the best-fit choice among other correlation structures according to AIC) to successfully account for spatial autocorrelation in this model, and the model results remained very similar.

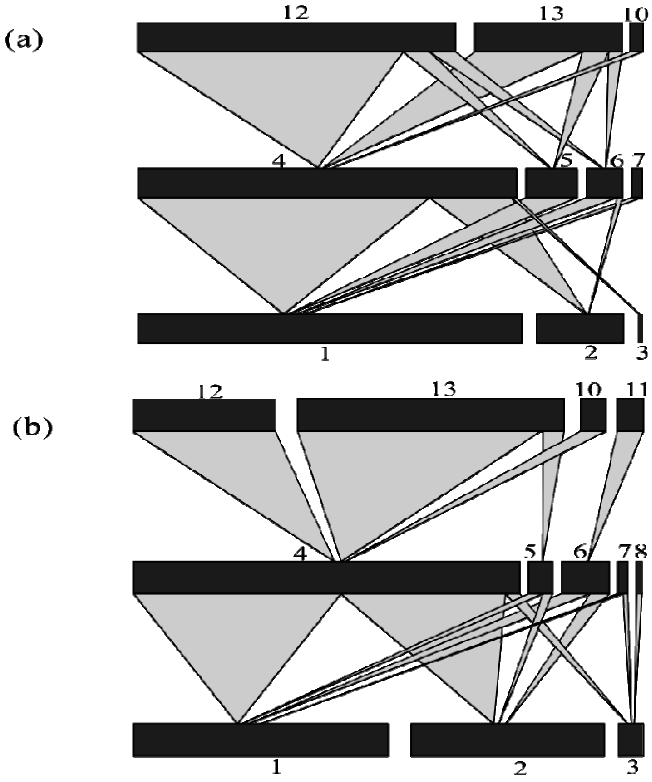

Figure 2.1. Parasitoid food webs calculated from pooled data for four landscapes with the lowest (57.6%±5.22%; mean±SE; fig. 1a) and four landscapes with the highest (90.16%±1.23%; mean±SE; fig. 1b) percentage arable land. Black bars represent relative abundances of aphids (lower bars), primary parasitoids (middle bars) and hyperparasitoids (upper bars) drawn at different scales. The numbers are genera codes from Table 1. Frequency of trophic interactions is indicated by the link width.

We used path analysis (a form of structural equation modelling (SEM)) to evaluate pathways of direct and indirect effects of landscape structural complexity on parasitism and hyperparasitism rates (see the Supplementary Methods 2.2.). Indirect effects mediated by genera richness and food web structure on parasitism rate were tested in separate models for primary and hyperparasitoids. We report these results with caution because our sample size was relatively small. In addition, we used bootstrapping methods to estimate standard errors and to avoid the large sample assumptions (Grace 2006).

Statistical analyses were performed using the statistical software R V. 2.8.0 (R Development Core Team 2008), and the packages ‘bipartite’ (for food web analysis, Dormann *et al.* 2008; 2009) and ‘SEM’ Fox 2006.

Results

Genera abundance and food web metrics varied considerably across the landscape complexity gradient (for an overview, see Table 2.1. and Supplementary Table 2.1.). Aphid communities were dominated by *S. avenae*, whose relative abundance decreased with increasing percentage of arable land (Spearman's rank correlation, $r_s = -0.57$, $p = 0.01$), while that of *M. dirhodum* increased (Spearman's rank correlation, $r_s = 0.48$, $p = 0.04$; Figure 2.1.).

Table 2.1. Arithmetic means ± standard errors, minimum and maximum values (n=18) of cereal aphid, their primary and hyperparasitoid densities (individuals per 100 shoots).([a] only one individual of *Diaeretiella sp.* was found (mummy collection data).

	Individuals per 100 shoots		
Taxa code	mean ± SE	min	max
Aphids			
1. *S. avenae*	31.74 ± 6.19	6.25	101.25
2. *M. dirhodum*	13.89 ± 2.93	0	46.25
3. *R. padi*	1.32 ± 0.29	0	3.75
Primary parasitoids			
4. *Aphidius sp.*	6.94 ± 1.26	0	19.09
5. *Ephedrus sp.*	1.10 ± 0.39	0	5.68
6. *Praon sp.*	0.63 ± 0.15	0	2.05
7. *Aphelinus sp.*	0.15 ± 0.08	0	1.17
8. *Diaeretiella sp.*[a]	<0.01		
9. *Toxares sp.*	0.68 ± 0.00	0	0.68
Hyperparasitoids			
10. *Alloxysta sp.*	0.06 ± 0.03	0	0.42
11. *Phaenoglyphis sp.*	0.07 ± 0.05	0	0.88
12. *Dendrocerus sp.*	1.33 ± 0.38	0	5.88
13. *Asaphes sp.*	1.10 ± 0.34	0	4.81
14. *Coruna sp.*	0.02 ± 0.01	0	0.23

In total, 845 aphids were recorded in all fields, of which 67.7 per cent were *S. avenae,* 29.6 per cent *M. dirhodum* and 2.8 per cent *R. padi*. Absolute aphid abundance did not differ across the landscape gradient. The dominant primary parasitoid genus in the fields was *Aphidius* with 78.7 per cent of all rearings (emerged parasitoids from mummies) dominant in all landscape types, and among hyperparasitoids, *Dendrocerus* with 51.7 per cent and *Asaphes* with 42.7 per cent of all rearings.

Relative abundances of primary parasitoid genera did not change, while relative abundance of the hyperparasitoid genus *Dendrocerus* decreased with increasing percentage of arable land (Spearman's rank correlation, $r_s = -0.64$, $p = 0.01$). Within the guild of primary parasitoids, only absolute abundance of *Ephedrus* decreased significantly with percentage of arable land ($r_s = -0.515$, $p = 0.029$) and in the guild of hyperparasitoids, only *Dendrocerus* ($r_s = -0.658$, $p = 0.006$).

We found significant difference in the food web structure across the landscape complexity gradient (Figures 2.1. and 2.2. and Table 2.2.). In aphid – primary parasitoid food webs, linkage density, generality and interaction diversity (Figure 2.2.a) increased as the percentage of arable land increased, while vulnerability did not change across the landscape gradient (Table 2.2.). Linkage density, interaction diversity and vulnerability were positively influenced by consumer (primary parasitoid) richness, while generality and linkage density were

Table 2.2. F-values and levels of significance from general linea models relating parasitism rates and food web metrics (linkag density, interaction diversity, vulnerability and generality) for aphid primary parasitoid webs and primary-hyperparasitoid webs to thre predictive factors: (1) percentage arable land, (2) aphid specie richness, (3) parasitoid (or hyperparasitoid) genera richness (Significant codes: p<0.001'***', p< 0.01 '**', p<0.05 '*', p>0.0 'n.s')

	F-value
Aphid-primary parasitoid food webs	
Linkage density	
No. of aphid species	4.74*
No. of prim. parasitoid genera	10.38**
Arable land	5.77*
Interaction diversity	
No. of aphid species	n.s
No. of prim. parasitoid genera	11.81**
Arable land	13.89**
Vulnerability	
No. of aphid species	n.s
No. of prim. parasitoid genera	9.47**
Arable land	n.s
Generality	
No. of aphid species	7.26*
No. of prim. parasitoid genera	n.s
Arable land	7.41*
Primary parasitism rate	
No. of aphid species	n.s
No. of prim. parasitoid genera	8.32*
Arable land	17.44**
Primary-hyperparasitoid food webs	
Linkage density	
No. of prim. parasitoid genera	12.84**
No. of hyperparasitoid genera	12.37**
Arable land	n.s
Interaction diversity	
No. of prim. parasitoid genera	21.37**
No. of hyperparasitoid genera	13.75**
No. of hyperparasitoid genera ^{2}	5.41*
Arable land	n.s
Vulnerability	
No. of prim. parasitoid genera	n.s
No. of hyperparasitoid genera	24.93***
Arable land	n.s
Generality	
No. of prim. parasitoid genera	49.09***
No. of hyperparasitoid genera	n.s
Arable land	n.s
Hyperparasitism rate	
No. of prim. parasitoid genera	53.18***
No. of hyperparasitoid genera	14.75**
Arable land	8.01*

positively influenced by host (aphid) richness.

In primary-hyperparasitoid food webs, food web metrics did not significantly respond to percentage of arable land (see Figure 2.2.b for correlation among interaction diversity and percentage arable land), but linkage density and interaction diversity were positively influenced by host (primary parasitoid) and consumer (hyperparasitoid) richness, while vulnerability and generality responded positively only to consumer and host richness, respectively. Richness of all three trophic levels was not correlated to landscape complexity (Spearman's rank correlations: aphid richness: $r_s = 0.29$, $p = 0.23$; primary parasitoid richness $r_s = 0.002$, $p = 0.99$; hyperparasitoid richness $r_s = 0.078$, $p = 0.76$; Supplementary Figure 2.2.).

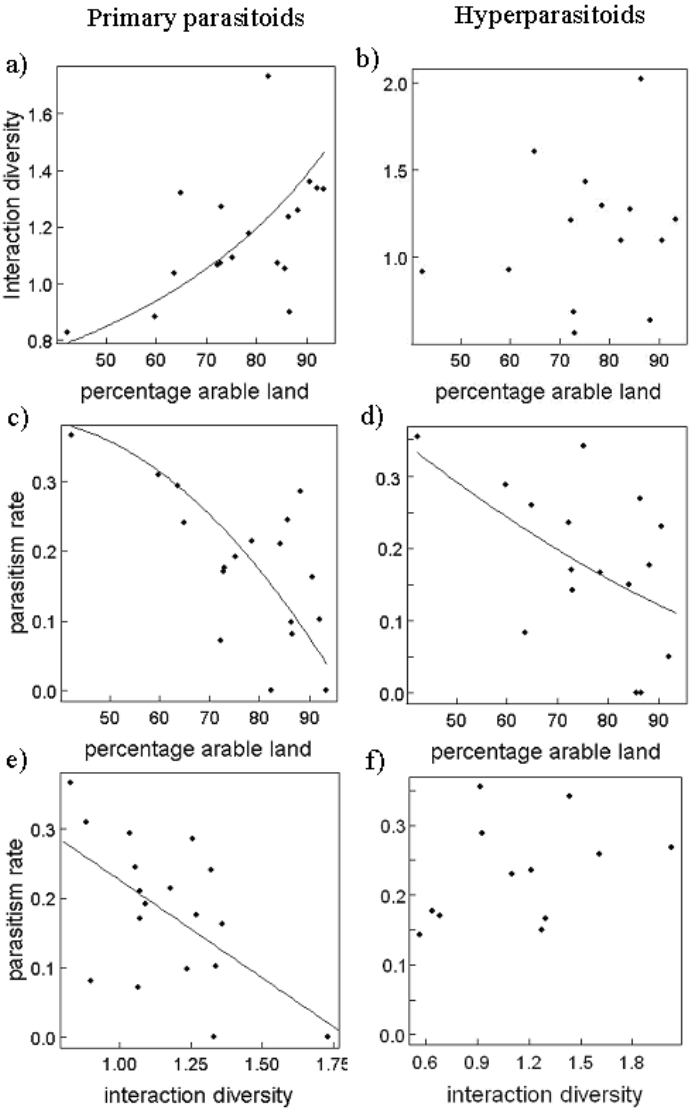

Figure2.2. Interaction diversity and parasitism rates across a landscape complexity gradient and relation of parasitism rate to interaction diversity for (a,c,e) primary and (b,d,f) hyperparasitoid webs.

Overall, *S. avenae* was the most heavily parasitized species by 67.8 per cent, *M. dirhodum* by 30.0 per cent and *R. padi* by 2.2 per cent of all parasitoids (463 mummies in total). The most hyperparasitized primary parasitoid genera were *Aphidius* 76.6 per cent, *Ephedrus* 15.3 per cent, *Praon* 6.4 per cent and *Aphelinus* 1.6 per cent (124 mummies in total). Aphid mortality owing to parasitism, as well as primary parasitoid mortality owing to hyperparasitism, significantly increased as the percentage of arable land decreased (Figure 2.2.c,d and Table 2.2.). In aphid – parasitoid food webs, parasitism correlated negatively with interaction diversity ($F_{1,16} = 8.14$, $p = 0.01$; Figure 2.2.e) and linkage density ($F_{1,16} = 5.77$, $p = 0.03$).

By contrast, in the primary parasitoid – hyperparasitoid webs, hyperparasitism correlated positively with linkage density ($F_{1,11} = 6.82$, $p = 0.02$), generality ($F_{1,11} = 7.73$, $p = 0.02$) and vulnerability ($F_{1,11} = 7.13$, $p = 0.02$), but not with interaction diversity (Figure 2.2.f).

The most parsimonious, biologically meaningful models in path analysis for the effect of landscape on parasitism and hyperparasitism rates (before and after bootstrapping), indicated that all significant effects were direct (see Supplementary Figure 2.1.). There were no indirect effects of landscape mediated by host and consumer richness or food web structural properties (linkage density and interaction diversity) on parasitism and hyperparasitism rates.

Discussion

The structure of interactions in aphid–parasitoid–hyperparasitoid communities showed distinct changes across the landscape complexity gradient and was related to host and consumer richness. In contrast to our expectations, food webs were more complex (i.e. revealed a higher interaction diversity and linkage density) in structurally simple landscapes characterized by high percentages of arable land, while host and consumer genera richness did not respond to landscape complexity. Moreover, complex food webs were negatively related to primary parasitism rate, thereby calling into question the general importance of food web complexity for ecosystem functioning.

Species richness

Ecological theory predicts that insect diversity will increase with increasing vegetation diversity and structural complexity (Murdoch *et al.* 1972, Lawton 1983, Stinson & Brown 1983), which may then spill over to adjacent habitats (Tscharntke *et al.* 2005b). In contrast to this common theory and our first hypothesis, we found no differences in richness of any trophic level across the landscape complexity gradient. This has been shown for primary parasitoids (Marino & Landis 1996, Menalled *et al.* 1999, Vollhardt *et al.* 2008), but not for hyperparasitoids. However, parasitoids and hyperparasitoids are known to respond in a similar way to many of the factors that influence their species richness (Hawkins 1994). Hence, as shown for primary parasitoids, our finding suggests that simple landscapes, dominated by cereal crops, provide large amounts of food resources that may support and sustain diverse hyperparasitoid communities.

Food web complexity

Absence of variation in trophic groups' richness leads us to dismiss our second hypothesis that food web complexity would decrease as species richness decreases in simple landscapes. Food web complexity did change across landscape complexity gradient in aphid – parasitoid webs, but contrary to our expectations, interaction diversity decreased as landscape complexity increased, mainly because of a lower number of unique interactions between aphid and parasitoid species. In particular, trophic interaction between the main aphid (*Sitobion*) and the main parasitoid genus (*Aphidius*) dominated the food webs in complex landscapes. Host use by the main parasitoid genus *Aphidius* in simple landscapes included larger proportions of *Metopolophium,* whose relative abundances increased while those of *Sitobion* decreased, resulting in more evenly distributed aphid species in simple landscapes. Landscape structural complexity is positively correlated with percentage of grassland (in our region and at the spatial scale we used for analysis, see Schmidt *et al.* 2004, Purtauf *et al.* 2005), and habitats such as grassland may provide a good source for colonization of cereals by grass-hibernating aphid species *S. avenae* (Leather 1993, Thies *et al.* 2005). Furthermore, the landscape complexity gradient had no influence on the mean number of consumers per host species (vulnerability), partly because of the absence of significant differences in parasitoid richness and in their relative abundances among landscapes. This suggests that parasitoids may be able to adjust average attack rates on each aphid species to changes in aphid relative abundances, by favouring the dominant species, and keeping vulnerability of aphids constant across landscape types. Hence, landscape complexity changes host range of parasitoids and overall food web complexity in cereal aphid – parasitoid food webs, presumably owing to changes in the structure of aphid communities, thereby triggering bottom-up effects that affect interactions with the next trophic level. This is in agreement with Hawkins (1992), who argues that parasitoid communities are likely to be bottom-up controlled (see also Scherber *et al.* 2010).

In contrast to aphid – primary parasitoid food webs, the structure of parasitoid – hyperparasitoid interactions was not influenced by landscape complexity, but by host and consumer richness. This may be related to the lack of response of parasitoid and hyperparasitoid richness to landscape complexity. In addition, relative abundances of primary parasitoids remained similar across landscapes, diminishing bottom-up effects induced by aphids that can propagate to the fourth trophic level.

Parasitism and hyperparasitism rates

The third hypothesis that the simpler the food web the lower the parasitism rates would be, was partly disproved by our results. In spite of lower food web complexity and narrow host range of primary parasitoids in structurally complex landscapes, parasitism rates in these landscapes reached values that can be effective for biological control (Hawkins & Cornell 1994; Thies *et al.* 2005). These findings are consistent with the studies showing that top-down control is often stronger in simplified food webs dominated by a single link (Hawkins 1999, Montoya *et al.* 2003, Finke & Denno 2004, Tylianakis *et al.* 2007). However, hyperparasitism rates were positively influenced by both landscape and food web complexity (except for interaction diversity), suggesting that hyperparasitoids might benefit from increased availability of alternative resources (similar to primary parasitoids, see Roschewitz *et al.* 2005, Thies *et al.* 2005), but also from increased host range. Increased parasitism and hyperparasitism rates were not the result of higher aphid densities as they did not change across landscape complexity gradient and may be related to the occurrence of the primary parasitoid genus *Ephedrus* and the most common hyperparasitoid genus *Dendrocerus,* whose abundances increased across the landscape complexity gradient. Furthermore, high rates of parasitism in structurally complex landscapes may indirectly benefit from higher relative abundances of the ear-colonizing aphid *S. avenae*, which is more easily accessible to parasitoids than leaf-colonizing aphid species, and frequently associated with the hyperparasitoid genus *Dendrocerus* (Höller *et al.* 1993). In addition, specific interactions between these particular species may be fostered owing to the closely related colonization time of wheat fields by *S. avenae* (later in the season with a time lag of two to four weeks compared with *M. dirhodum* and *R. padi*, Vickerman & Wratten 1979, Ankersmit & Carter 1981) and the main parasitoid and hyperparasitoid genera, *Aphidius* and *Dendrocerus* (Höller *et al.* 1991). However, the main effect of landscape structural complexity on parasitism and hyperparasitism rates was direct rather than indirect via host and consumer richness and food web structure, as indicated by our SEMs.

Conclusions

Despite the presence of simplified food webs in structurally complex landscapes and similar host and consumer genera richness among landscapes, complex landscapes supported higher parasitoid densities, causing higher levels of aphid biological control. Hence, food web complexity appeared to be a poor predictor of ecological functioning in aphid – primary parasitoid webs. However, aphid – parasitoid systems are typically characterized by strong population dynamics (boom and bust cycles), and changes in community composition in time (Thies *et al.* 2005, Leslie *et al.* 2009), implying dynamic changes in food web structures among years and regions. Our results represent a snap-shot of the interaction structure of this aphid – parasitoid system. More long-term research would contribute to better understanding the response of multi-trophic systems to agricultural landscape changes.

Acknowledgements

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Supplementary material

Supplementary Methods 2.1.

Food web metrics

Quantitative, weighted measures of linkage density, generality, vulnerability and interaction diversity based on Shannon's entropy were calculated following Bersier *et al.* 2002. Diversity of inflows ($H_{N,}$, diversity of host) and diversity of outflows (H_P, diversity of consumer), were calculated for each species k as:

$$H_{N,k} = -\sum_{i=1}^{S} \frac{b_{ik}}{b_{\bullet k}} \log_2 \frac{b_{ik}}{b_{\bullet k}} \qquad\qquad H_{P,k} = -\sum_{j=1}^{S} \frac{b_{kj}}{b_{k\bullet}} \log_2 \frac{b_{kj}}{b_{k\bullet}}$$

and their "reciprocals" ($n_{N,,k}$ - equivalent number of host and $n_{P,,k}$ - equivalent number of consumers) give number of genera present in equal proportion that would yield the same value of H.

$$n_{N,k} = \begin{cases} 2^{H_{N,k}} \\ 0 \end{cases} \quad \text{if} \quad b_{\bullet k} = 0 \qquad\qquad n_{P,k} = \begin{cases} 2^{H_{P,k}} \\ 0 \end{cases} \quad \text{if} \quad b_{k\bullet} = 0$$

The sum of column ($b{\bullet}k$) is the number of individuals attacked by and the sum of row ($bk{\bullet}$) is the number of individuals attacking taxon k. Amount of biomass passing from taxon i to taxon k (assuming identical biomass of all species), and from taxon k to taxon i is represented as b_{ik} and b_{kj}, respectively.

Generality (G_q), the weighted average number of host genera per parasitoid (consumer) and vulnerability (V_q), the weighted average number of consumer genera per host were calculated as:

$$G_q = \sum_{k=1}^{S} \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{N,k} \qquad\qquad V_q = \sum_{k=1}^{S} \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{P,k}$$

Linkage density (LD_q) is number of links per species calculated as arithmetic mean of generality and vulnerability:

$$LD_q = \frac{1}{2}\left(\sum_{k=1}^{s} \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{P,k} + \sum_{k=1}^{s} \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{N,k} \right)$$

where *b*.. is the total number of attacked individuals and therefore represents averages of the equivalent numbers of prey and of consumers weighted by the genera total inflows and outflows.

Interaction Diversity (ID_q) was calculated as:

$$ID_q = -\sum p_i \log 2(p_i)$$

where p_i is the proportion of the interaction *i* between given genera to the total number of trophic interactions in a web. It uses Shannon's diversity index with links rather than species as a basic unit.

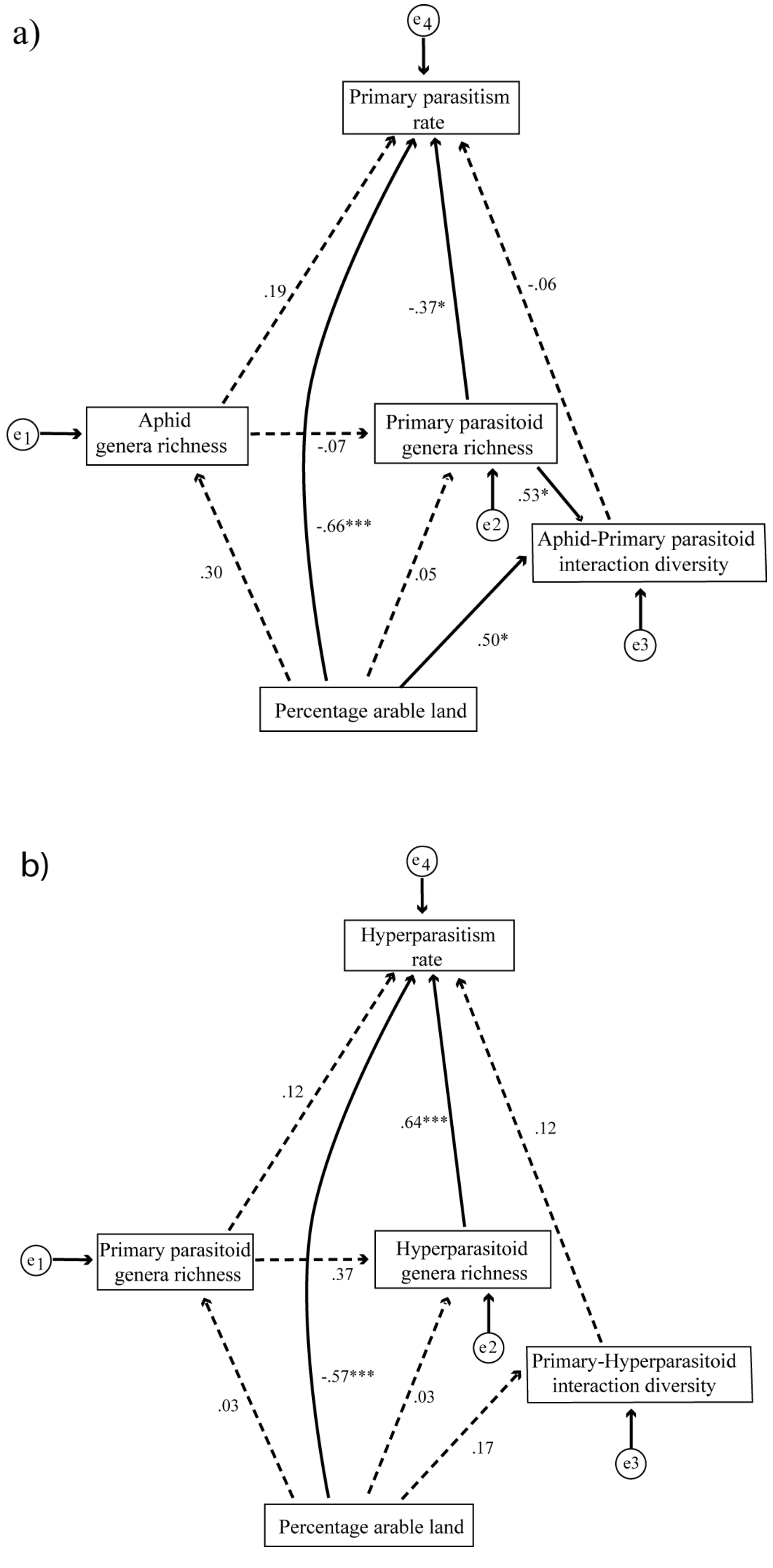
Supplementary Methods 2.2.

Path analysis

All variables used in path analyses were standardized (Legendre & Legendre 1998) by subtracting the mean and dividing by the standard deviation (see Grace 2006, p. 328 for justification). For every model, we started with a hypothesized structural relationship. We then used specification search (an exploratory technique) to find the most parsimonious model, given the full set of possible structural relations between the variables. Model fit was assessed using Chi^2 tests on the differences between the implied and observed covariance matrices, and by the root mean square error of approximation (RMSEA).

Supplementary Figure 2.1.

The most parsimonious biologically meaningful models for landscape complexity effect on: a) primary parasitism rates and b) hyperparasitism rates. Standardized path coefficients are given with the same significance codes as in the *Table 1*. Solid arrows indicate significant and dashed arrows non-significant path coefficients. ‘e_i’ denotes unexplained variance. Figures were created using AMOS 16.0 (Arbuckle 2007).



Supplementary Table 2.1.

Food web metrics and parasitism

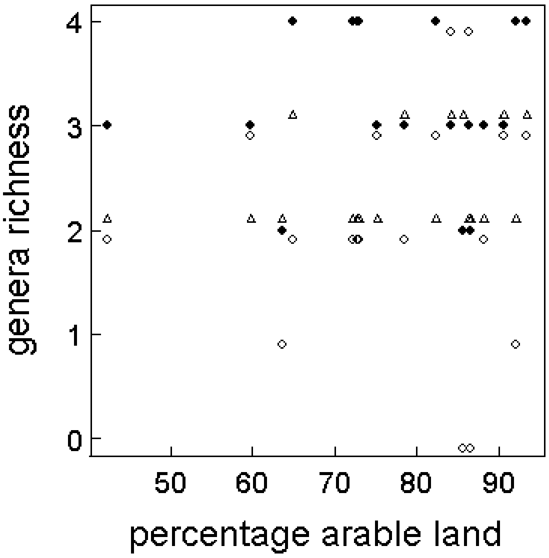
Arithmetic means ± standard errors, minimum and maximum values of food web metrics, parasitism and hyperparasitism.

	Food web metrics, parasitism, and hyperparasitism		
	mean ± SE	min	max
Aphid-primary parasitoid food webs			
Vulnerability	1.835 ± 0.122	1.221	3.025
Generality	1.72 ± 0.076	1.25	2.331
Linkage density	1.778 ± 0.044	1.438	2.138
Interaction diversity	1.168 ± 0.051	0.826	1.733
Parasitism	0.179 ± 0.025	0	0.367
Primary-hyperparasitoid food webs			
Vulnerability	1.87 ± 0.154	1	3.572
Generality	1.448 ± 0.143	1	2.636
Linkage density	1.659 ± 0.112	1	2.604
Interaction diversity	1.142 ±0.106	0.562	2.025
Hyperparasitism	0.182 ± 0.027	0	0.355

Supplementary Figure 2.2.

Genera richness

Genera richness of aphids (solid triangles), primary (filled diamonds) and hyperparasitoids (solid diamonds) across landscape complexity gradient.



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Chapter 3

Agricultural intensification and cereal aphid-parasitoid-hyperparasitoid food webs: network complexity, temporal variability and parasitism rates

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Abstract

Agricultural intensification (AI) is currently a major driver of biodiversity loss and related ecosystem functioning decline. However, spatio-temporal changes in community structure induced by AI, and their relation to ecosystem functioning, remain largely unexplored. Here, we analysed 16 quantitative cereal aphid-parasitoid and parasitoid-hyperparasitoid food webs replicated 4 times during the season, under contrasting AI regimes (organic farming in complex landscapes vs. conventional farming in simple landscapes). High AI increased food web complexity, but also temporal variability in aphid-parasitoid food webs and in the dominant parasitoid species identity. Enhanced complexity and variability appeared to be bottom-up controlled by changes in aphid dominance structure and evenness. Contrary to the common expectations of positive biodiversity-ecosystem functioning relationships, community complexity (food-web complexity, species richness and evenness) was negatively related to primary parasitism rates. However, this relationship was positive for secondary parasitoids. Despite differences in community structures among different trophic levels, ecosystem services (parasitism rates) and disservices (aphid abundances and hyperparasitism rates) were always higher in fields with low AI. Hence, community structure and ecosystem functioning appear to be differently influenced by AI and change differently over time and among trophic levels. In conclusion, intensified agriculture can support diverse, although highly variable parasitoid-host communities, but ecosystem functioning might not be easily predictable from observed changes in community structure and composition.

Keywords: community structure, biodiversity, biological control, agroecosystems

Introduction

Agricultural intensification (AI) on a local and a landscape scale is a major cause of biodiversity loss (Foley *et al.* 2005). Organic farming has been suggested to oppose such changes and to increase components of biodiversity such as species richness (Hole *et al.* 2005) and evenness (Crowder *et al.* 2010). Biodiversity may increase and stabilize overall ecosystem function (Tilman *et al.* 2006), but characteristics of particular species and food web structure are also important factors influencing the response of communities to human-induced habitat loss and alteration (Melian & Bascompte 2002; Sole & Montoya 2006; Brose *et al.* 2006; Laliberte & Tylianakis 2010). Even when species richness in a trophic guild remains constant, the frequency of their interactions can largely change owing to changes in habitat quality (Tylianakis *et al.* 2007). The effects of AI on interaction diversity in parasitoid-host food webs have so far been inconclusive, with both negative (Albrecht *et al.* 2007) or positive (Tylianakis *et al.* 2007) effects and unpredictable consequences for ecosystem functioning. Furthermore, most existing studies used pooled long-term samples or a single snap-shot in time, and there is still a low number of studies with spatio-temporal resolution in food web research across gradients of human impact (de Ruiter *et al*. 2005; Memmot *et al.* 2006; Rooney *et al.* 2008; but see Laliberte & Tylianakis 2010). We address these important questions by investigating the influence of AI on the temporal changes in structure and function of sixty-four aphid-parasitoid-hyperparasitoid food webs under contrasting levels of AI.

Parasitoids are one of the key controlling agents of agricultural pests (Schmidt *et al.* 2003; Thies *et al*. 2005), and together with their hosts and associated host plants comprise over half of all known species (Hawkins 1994). Hence, revealing mechanisms that structure host-parasitoid communities is an important task for both basic and applied ecology. Furthermore, the functional significance of the top consumers in this system, i.e. hyperparasitoids, and their spatio-temporal response to land use intensity, can be of particular importance, but remains unknown. It has been shown that higher trophic level organisms respond often stronger to AI (Kruess & Tscharntke 1994; Holt *et al*. 1999; Tscharntke *et al.* 2005), but which consequences this has for food web structure and ecosystem functioning remained largely unpredictable. Spatio-temporal multi-species and multi-trophic approaches may therefore contribute to understanding key ecosystem services such as pest control (Memmot *et al.* 2006).

Bottom-up control is important for parasitoid food webs (Hawkins 1992; Bukovinszky *et al.* 2008; Petermann *et al.* 2010; Scherber *et al.* 2010). Hence, changes in the host community can be expected to also affect food web interactions. Host communities may be influenced by a number of factors related to AI. Less intensified fields experience fewer disturbances by agricultural practices such as fertilizer and pesticide applications (Lampkin *et al.* 1999), and structurally complex landscapes allow for more host plants per unit area throughout the year. In addition, species-specific effects of nitrogen application on aphid performance (Honek 1991; Duffield 1997; Awmack & Leather 2002; Hambäck *et al.* 2007) might structure their trophic interactions in conventional and organic farms differently.

Here, we analysed aphid-parasitoid-hyperparsitoid community structure in winter wheat fields located in contrasting landscapes with low (organic fields embedded in structurally complex landscapes), versus high levels of AI (conventional fields embedded in structurally simple landscapes) in Germany. Our aim was to select fields that simultaneously vary in levels of AI on the local and landscape scale to maximize contrast in human-induced habitat changes and unravel its influence on ecologically and economically important parasitoid communities. Our study design reflects a situation commonly found in Central European farming systems: organic farms are often situated in areas containing large amounts of semi-natural vegetation; in contrast, conventional farms are mostly found on richer soils and in areas with less semi-natural vegetation (Gibson *et al.* 2007).

We collected time-series data on aphid-parasitoid and parasitoid-hyperparasitoid food webs, host abundances and parasitism rates, at weekly intervals from the period of aphid colonization to the period of aphid population breakdown (4 time periods). We calculated several measures of community complexity, namely food web complexity (quantitative weighted linkage density, interaction diversity, interaction evenness, generality and vulnerability), species richness and evenness. We tested the following hypotheses: (1) higher AI is related to higher variability of biodiversity and food web structure over time, because intensive agricultural practices cause higher disturbance of communities; (2) Higher AI allows lower food web complexity, owing to the lower species richness and evenness; (3) Higher community complexity leads to higher parasitism rates.

Material and methods

The organisms

In Germany, aphid communities (Hemiptera: Sternorrhyncha) in winter wheat fields are dominated by *Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker) and *Rhopalosiphum padi* (Linnaeus), which are attacked by hymenopteran parasitoids belonging to two groups, Aphidiinae (Braconidae, Ichneumonidea) and Aphelinidae (Chalcidoidea) (Adisu *et al.* 2002). Aphidiinae are primary solitary endoparasitoids of aphids with cosmopolitan distribution and represent the largest fraction of parasitoids infesting aphids (Starý 1988). Primary parasitoid larvae kill aphids by feeding internally in them and forming cocoons (referred to as "mummies"). Primary parasitoids are attacked by secondary parasitoids and this may disrupt their ability to control aphids (Rosenheim 1998). Secondary parasitoids form two groups, true hyperparasitoids (belonging to the Alloxystinae; Cynipoidea: Charipidae), which feed on a primary larval host in a living aphid, as well as mummy parasitoids (belonging to the Pteromalidae (Chalcidoidea) and Megaspilidae (Ceraphronoidea)), which attack their host in already mummified aphids (Sullivan & Völkl 1999). Since we are here not interested in host use differences of secondary parasitoids we will refer to both of these groups as hyperparasitoids. In addition, parasitoid-host dynamics in winter wheat fields may be influenced by predators and pathogens that attack parasitized or unparasitized aphids (Rosenheim 1998), but here it was unfeasible to simultaneously quantify these interactions and this study is therefore restricted to the parasitoid natural enemy guild (see also Müller *et al.* 1999).

Experimental design

The study was carried out in the year 2008 in eight winter wheat fields in the surroundings of Göttingen, Lower Saxony, Germany (Supplementary Map 1). We selected fields that simultaneously varied in levels of AI at local (field) and landscape scales (circle with 500m radius). Four organically managed fields (with no applications of mineral fertilizer and chemical pesticides), embedded in structurally complex landscapes (> 30 % of semi-natural habitats) were compared to four conventionally managed fields (with high applications of mineral fertilizer and chemical pesticides), embedded in structurally simple landscapes (> 90% of agricultural habitats). Thus, we had high vs. low AI at local and landscape scales (for further details see Thies *et al.* 2011). To avoid direct insect mortality, sampling was done on insecticide-free areas in all fields, a 60 m (along the field edge) by 12 m (into the fields) rectangle. Although our focal plots were not directly treated with insecticides, insecticide application in high AI fields may destabilise food webs owing to mobile foraging individuals moving in and out the treated area and due to possible effects of pesticide drift.

Species examination

Aphids and parasitized aphids ("mummies") were counted visually on 100 wheat shoots (5 randomly chosen subsamples with 20 shoots at each sampling occasion) per field on a weekly basis starting from wheat flowering in June (after the main period of aphid colonization of the fields), until wheat peak ripening in July (the period of aphid population breakdown). In addition, we randomly collected ~100 mummies per field at the same time intervals. Altogether, sampling took place over the course of four seven-day periods. All mummies were reared in the laboratory to identify primary and hyperparasitoid species. This allowed us to observe exact interaction frequencies between aphid and parasitoid species and between parasitoid genera and hyperparasitoid species (hence assuming no within-genus hyperparasitoid specialisation and no trophic loops, but allowing for fully resolved direct trophic links, see Müller *et al.* 1999). In primary parasitoid-hyperparasitoid networks, primary parasitoids were identified to the genus level based on mummy morphology (Powell 1982). Hence, species richness and evenness of primary parasitoids was calculated at the species level in aphid-primary parasitoid webs (using only parasitoids that hatched out of aphids) and at the genus level at primary-hyperparasitoid webs (using only genera of parasitoids that were hyperparasitized).

Network analysis

In total, we analysed sixty-four quantitative interaction networks, out of which thirty-two were aphid-primary parasitoid and another thirty-two were primary-hyperparasitoid networks. We calculated quantitative measures of food web complexity, namely linkage density, interaction diversity, generality, vulnerability and interaction evenness (for detailed formulae see *Bersier et al.* 2002; Tylianakis *et al.* 2007). Linkage density incorporates generality (the average number of host taxa per parasitoid) and vulnerability (the average number of parasitoid taxa per host), and represents the ratio of the number of trophic interactions to the number of species. Interaction diversity and interaction evenness are analogous to Shannon diversity and evenness, but with trophic interaction instead of species as the base unit.

Statistical analysis

Data were analyzed using the statistical software R 2.11.1 (R Development Core Team 2010). Our experimental design had a total of sample size of N=8 landscapes, each repeatedly observed over each N=4 time intervals (yielding a total N=32). This spatiotemporal structure was accounted for by fitting linear mixed effects models (nlme package, version 3.1-96, Pinheiro & Bates 2000). The fixed-effects part of the models included agricultural intensification ("AI", 2-level factor: low vs. high) and the sampling week ("Week", numeric, 1-4) as well as interactions between them. Abundances of aphids were not correlated to food web indices, but highly correlated to AI and Week, and therefore they were not included in models as a covariate. To account for non-linearity over time, we used polynomial terms for "Week", when necessary. Fields ("Field", 1-8) were considered random effects. In R notation, the corresponding model structure was y~AI*Week + I(Week)^2, random=~1|Field, where y is the response variable (parasitism rates, food web structure, species richness, evenness or relative abundances).

We tested for temporal pseudoreplication by inspecting the auto-correlation function (ACF) of the residuals, adjusted for missing values (Zuur 2006). A compound symmetry correlation structure (corCompSymm(form=~Week)) was used to account for correlations between observations taken at different time points; this assumes an equal correlation of within-group observations across all time points, and is particularly suitable for short time series (Pinheiro & Bates, 2000, p. 228). In addition, we used variance functions to model heteroscedasticity, when necessary. Models were fitted using restricted maximum likelihood and compared using AICc (Akaike´s information criterion, corrected for small sample sizes). We did not use Bonferroni or MANOVA approach to correct for multiple testing, because adjusting alpha values increases the likelihood of inflating Type II errors and MANOVA-type approaches have a decreased power when the number of tests increases (Moran 2003). This is particularly important for ecological studies which are often characterised by high variability, small number of replicates and consequently low statistical power (Moran 2003; Macfadyen *et al*. 2008).

As an estimate of the economic injury level, we calculated the number of aphids per 100 shoots (for a similar approach, see Larsson 2005). To estimate the potential for biological control, we used parasitism rates, and for biological control disruption, hyperparasitism rates. Parasitism rates were calculated as the proportion of parasitized hosts from all hosts, i.e. numbers of mummies per 100 shoots/aphid numbers per 100 shoots (including mummies) for primary parasitism rates, and number of hyperparasitoids emerged/all collected mummies (adjusted for densities per 100 shoots by calculating relation of hyperparasitoids to primary parasitoids in mummy collection data and applying this ratio to the count data) for hyperparasitism rates.

To test for additional effects of species richness and evenness on the food web metrics and (hyper-) parasitism rates, we developed series of alternative models that included different combinations of these explanatory variables and calculated their Akaike weights (Burnham & Anderson 2002, see Supplementary Table 4).

To assess the influence of community complexity (species richness, species evenness and food web structure) on (hyper) parasitism rates, we used principal component analysis (PCA). The first three axes of PCA explained 94 percent (PCA1 alone 54%) for aphid-parasitoid indices and 92 percent (PCA1 alone 51%) of cumulative variation for primary-hyperparasitoid indices. These PCA axes were then used as explanatory variables for the effect on primary and hyperparasitim rates in linear mixed-effects models (as above).

Results

Community composition

A total of 1269 aphid parasitoids emerged from the mummies collected and 2311 aphids were counted in the fields, of which 83% were *S. avenae*, 12% were *M. dirhodum*, and 5 % were *R. padi*. Aphid, primary and hyperparasitoid communities varied considerably between high and low AI fields as well as over time (Fig. 1, Supplementary Table 1). Over time, the proportions of parasitized *S. avenae* increased (“Week” $F_{1,21}$= 63.71, P< 0.0001), while those of *M. dirhodum* decreased ("Week" $F_{1,21}$= 30.89, P< 0.0001) in all fields. Proportions of parasitized *S. avenae* was higher in Low AI fields ("AI" $F_{1,6}$= 13.67, P= 0.01), and changed differently over time in fields with contrasting AI regimes (interaction "AI" x "Week^{2}" $F_{1,21}$= 5.38, P= 0.03) i.e. the response is non-linear with a peak at milk-ripening in fields with low AI, while it tends to be more linear and constantly increasing in fields with high AI. The most heavily parasitized aphid in fields with high AI was *M. dirhodum* ("AI" $F_{1,6}$= 5.42, P= 0.059), except for the last sampling period. Proportions of *M. dirhodum* and *S. avenae* in fields and in food webs are closely positively related ($F_{1,20}$= 12.25, P= 0.002; $F_{1,20}$= 32.81, P< 0.001, respectively).

Proportions of the primary parasitoid *Ephedrus plagiator* in food webs were higher in less intensified fields ("AI" $F_{1,6}$= 33.96, P= 0.001), increased during time ("Week" $F_{1,21}$= 15.37, P< 0.001), but increased faster in fields with high AI (interaction "AI" x "Week"; $F_{1,21}$= 9.11, P= 0.006). Proportions of the primary parasitoid *Aphidus rhopalosiphi* were higher in fields with high AI ("AI" $F_{1,6}$= 72.38, P= 0.0001) and decreased non-linearly over time ("Week^{2}" $F_{1,20}$= 5.41, P= 0.03), and faster in high AI fields (interaction "AI" x "Week"; $F_{1,20}$= 22.65, P= 0.0001). In the last sampling period (wheat peak ripening), *E. plagiator* dominated in all fields (Fig. 1, Supplementary Table 1). Proportions of the dominant parasitoids, *Aphidius, Ephedrus* and *Praon* in aphid-parasitoid and in parasitoid-hyperparasitoid webs are positively related.

The dominant hyperparasitoid species were *Dendrocerus carpenteri, Asaphes suspensus* and *A. vulgaris*. Proportions of *Dendrocerus carpenteri* were higher in fields with low AI ("AI" $F_{1,6}$= 7.71, P= 0.03). *A. suspensus* and *A. vulgaris* increased their proportions during time, but showed no response to AI.

Community complexity - Food web indices

In aphid-primary parasitoid webs, quantitative measures of interaction diversity, interaction evenness, linkage density, generality and vulnerability showed significant changes over time, forming hump-shaped curves with peaks at the time of wheat milk-ripening (Week 3) in high AI fields. We found significant interactions between levels of agricultural intensification and sampling week for these metrics (Fig. 1 and 2, Table1, for the mean ± SE see Supplementary Table 2).

In primary parasitoid-hyperparasitoid webs, quantitative values of interaction evenness, interaction diversity and generality changed significantly during time (Fig. 2, Table 1, and Supplementary Table 2). Generality increased faster over time in low AI fields and formed a hump-shaped curve at wheat milk-ripening. Interaction diversity increased over time, while interaction evenness decreased.

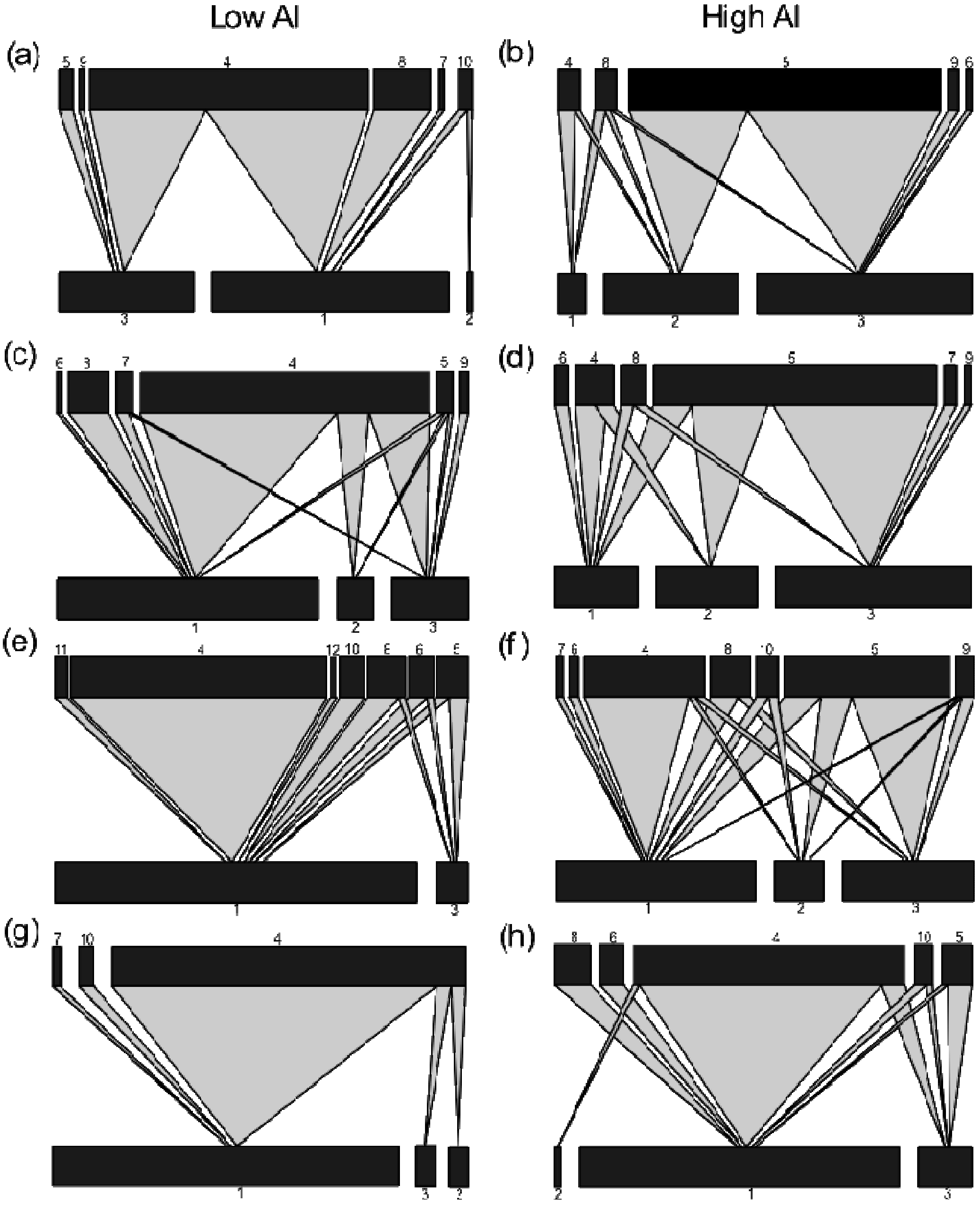

Figure 3.1. Aphid-parasitoid food webs calculated from pooled data for four fields with low (left) and four fields with high (right) levels of AI, and in four weekly time series, Week1 – (a) and (b), Week2 – (c) and (d), Week3 – (e) and (f), Week4 – (g) and (h). Black bars represent relative abundances of aphids (lower bars), primary parasitoids (upper bars) drawn at different scales. For host and parasitoid densities see Supplementary Table 1. The numbers are genera codes from Supplementary Table 1. Frequency of trophic interactions is indicated by the link width

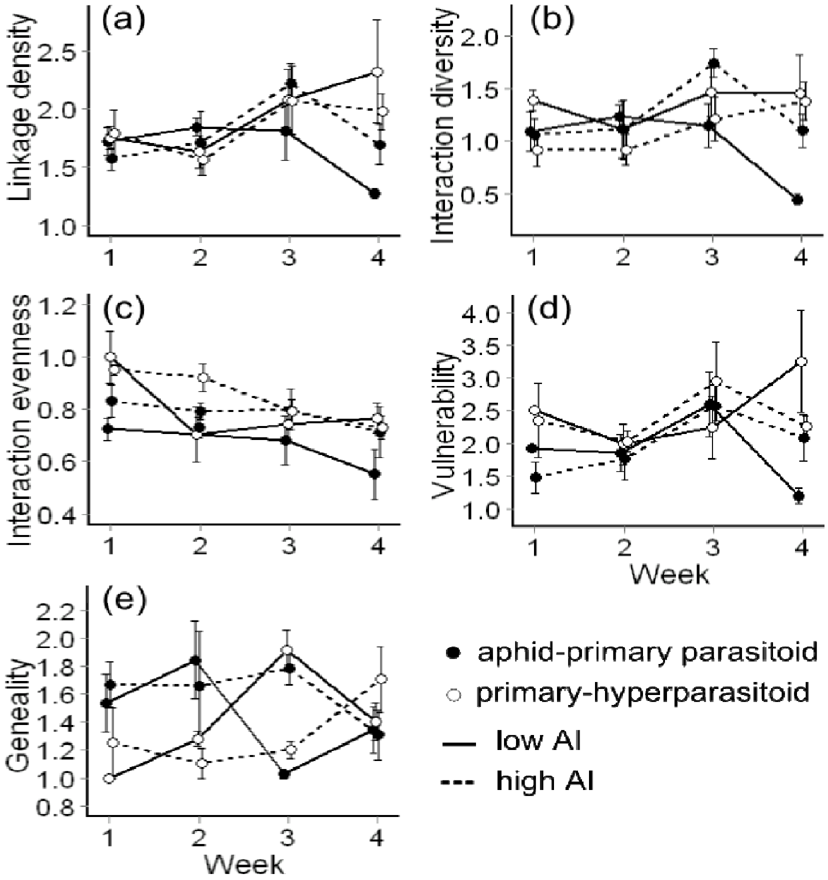

Figure 3.2. Illustration of aphid-primary parasitoid and primary-hyperparasitoid food web metrics (mean ± SE) across four sampling weeks for low and high AI fields.

Community complexity - Species richness and evenness

Species richness and evenness of different trophic level organisms changed differently over time and between low and high AI fields (Supplementary Fig. 1). Species richness of aphids increased faster in fields with low AI over time (interaction "AI" x "Week^3", $F_{1,17}$= 4.95, P= 0.039), while evenness of aphids changed in time ("Week" $F_{1,22}$=5.60, P=0.02), with a trend of higher evenness values in fields with high AI ("AI" $F_{1,6}$=4.89, P=0.06), and highest values at milk-ripening in these fields. Primary parasitoid species richness and evenness changed non-linearly over time ("Week^3" $F_{1,19}$= 9.78, P= 0.005; $F_{1,20}$= 9.16, P= 0.007, respectively), and were highest at wheat milk ripening in all fields, and remained high at the end of the sampling season only in fields with high AI levels (interaction "AI" x "Week", $F_{1,19}$= 8.25, P= 0.009; $F_{1,19}$= 8.90, P= 0.007, respectively).

In primary-hyperparasitoid webs, species richness and evenness of primary parasitoids and hyperparasitoids increased over time in all fields (“Week” $F_{1,18}$= 20.71, P< 0.001; $F_{1,19}$= 9.57, P= 0.006; $F_{1,20}$= 10.81, P= 0.004; $F_{1,22}$= 4.15, P= 0.054, respectively) and hyperparasitoid species richness had (with marginal significance) higher values in fields with low AI (“AI” $F_{1,6}$= 4.35, P=0.08). Richness and evenness of primary parasitoids in primary-hyperparasitoid webs reached a maximum at milk-ripening, but only in low AI fields (interaction: AI × Week^2, $F_{1,19}$= 11.52, P= 0.003; $F_{1,19}$= 8.68, P= 0.008).

Ecosystem function: aphid abundances, parasitism and hyperparasitism rates

Aphid abundances formed hump-shaped curves with highest peak in the second sampling period in low AI fields. Primary and hyperparasitism rates increased over time, and increased faster in fields with low level of AI (Table 1, Fig. 3, for the mean ± SE see Supplementary Table 2).

Table 3.1. F-values and levels of significance from linear mixed-effects models relating food web metrics (linkage density, interaction diversity, interaction evenness, vulnerability and generality), (hyper-) parasitism rates and aphid density, for aphid-primary parasitoid webs and primary-hyperparasitoid webs to two predictive factors: (1) agricultural intensification and (2) sampling week (including polynomial terms for “Week”). A strict interpretation (corrected for multiple testing) would render only P values <0.003 significant (but see Method section for arguments against correcting for multiple testing).

	AI	*Week*	*Week*^{2}	*Week*^{3}	*AI:Week*	*AI: Week*^{p}
Aphid-primary parasitoid						
Linkage density	n.s	23.42 ***	14.20**	n.s	6.52 *	n.s
Interaction diversity	10.38*	32.05 ***	18.19**	n.s	7.52*	n.s
Interaction evenness	n.s	4.35*	n.s	n.s	n.s	n.s
Vulnerability	n.s	n.s	8.88***	6.48*	7.86 **	n.s
Generality	n.s	4.49*	n.s	n.s	n.s	5.31*
Primary parasitism rate	n.s	9.82**	n.s	n.s	5.88*	n.s
Primary-hyperparasitoid						
Linkage density	n.s	n.s	n.s	n.s	n.s	n.s
Interaction diversity	n.s	7.17 *	n.s	n.s	n.s	n.s
Interaction evenness	n.s	45.76 ***	n.s	n.s	n.s	n.s
Vulnerability	n.s	n.s	n.s	n.s	n.s	n.s
Generality	n.s	8.69**	n.s	n.s	n.s	13.63**
Hyperparasitism rate	n.s	53.82***	n.s	n.s	4.60*	n.s
Aphid density	n.s	n.s	n.s	5.41*	5.67*	n.s

Signif. codes: p<0.001‘***’, p< 0.01 ‘**’, p<0.05 ‘*’ , p>0.05 'n.s' ; “ ^{p}“-polynomial, i.e. 2 or 3

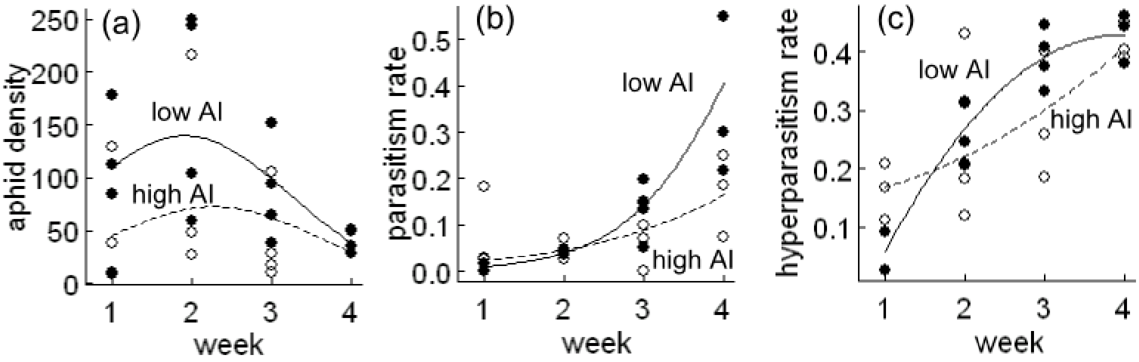

Figure 3.3. Primary parasitism rates (a), hyperparasitism rates (b), and aphid density (c), across four weeks in low AI fields (filled line) and high AI fields (dashed line)

Biodiversity-ecosystem functioning relationship

Primary parasitism rate was negatively related to the first two PCA axes (PCA1, $F_{1,18}$= 5.53, P=0.03; PCA2, $F_{1,18}$= 6.61, P= 0.01, see Supplementary Table 3 for the description of PCAs). Hyperparasitism rate was positively related to the first axis (PCA1, $F_{1,14}$= 75.36, P< 0.001) and negatively related to the second and third axes (PCA2, $F_{1,14}$= 29.18, P< 0.001; PCA3, $F_{1,14}$= 37.69, P< 0.001). All community complexity variables (i.e. food web indices and species richness and evenness) were positively related to PCA1. Hence, our results indicate an overall negative relation between primary parasitism rates and community complexity, but an overall positive relation between hyperparasitism rates and community complexity.

Discussion

In this study we found distinct differences in aphid, parasitoid and hyperparasitoid communities between fields with low and high AI and over time. Aphid-parasitoid diversity and food web structure showed greater changes over time in fields with high AI, higher food web complexity, but lower parasitism rates. Highly intensified fields were mainly colonised by leaf-colonizing aphids (*M. dirhodum, R. padi*), which may have benefited from higher nitrogen levels (Honek 1991; Hasken & Poehling 1995), coming from high amounts of inorganic fertilizers applied in conventionally managed fields. This may be owing to the greater amounts of amino acids in the phloem sap of treated plants, increased leaf area, leaf chlorophyll content and/or the number of shoots per plant of treated compared to untreated plants (Honek 1991; Riedell & Kieckhefer 1993; Hasken & Poehling 1995; Duffield *et al.* 1997). On the other hand, the dominant aphid species in fields with low AI, *S. avenae,* has been shown to be less influenced by nitrogen (Honek 1991; Hasken & Poehling 1995). It benefits from higher percentage of grassland in structurally complex landscapes (Schmidt *et al.* 2004; Purtauf *et al.* 2005), which serve as hibernating sites (Leather 1993; Thies *et al.* 2005). These differences in aphid community appeared to have induced bottom-up effects of changes in primary and hyperparasitoid community composition and food web structure. The identity of the dominant primary parasitoid species differed between fields with high (*A. rhopalosiphi,* commonly associated with *M. dirhodum* and *R. padi*) and low AI (*E. plagiator,* commonly associated with *S. avenae*) at the time of aphid colonization. This should have large implications for biological control (given differences in the dominant parasitoid species identity between fields with contrasting AI regimes, but similar total parasitism rates at wheat flowering), because parasitoids that are active early in the year are important to maintain aphid densities at low levels (Langer *et al.* 1997). The identity of the dominant parasitoid species also changed over time within fields with high AI, as leaf nutritional quality decreased and proportions of ear-colonising aphid *S. avenae* increased, with possible influence on the parasitoid species pool in the next year. In addition, the dominant hyperparasitoid species in low AI fields, *D. carpenteri,* increased as *E. plagiator* and *S. avenae* proportions increased, whereas in fields with high AI, *A. suspensus* and *A. vulgaris* dominated. These results emphasise the changing identity of one or few species dominating communities and ecosystem processes. Changes in the dominance structure under influence of AI suggest that management strategies should be adapted to different key species and AI levels, such as for example, favouring specific alternative host species that would support different parasitoids in different landscapes. However, dominance structure might change among years and regions and long-term studies are needed before recommendations of adjusted management strategies are possible.

Changes in aphid-parasitoid network complexity (linkage density, interaction diversity, generality and vulnerability) under different AI regimes, with more distinct nonlinear changes in fields with high AI over time, were best explained by models that included evenness of both trophic levels. Evenness of aphids, showed similar changes to those in food web metrics, increased faster over time in fields with high AI and formed humped-shaped curves, reaching their peaks at the milk-ripening period (the period of aphid reproduction in fields). Primary parasitoid species richness and evenness in aphid-parasitoid webs were highest at the milk ripening period in all fields and remained high in fields with high AI. This is contrary to findings by Crowder *et al.* (2010), who found organic farming to promote predator evenness. Nonlinearity in food web descriptors and higher aphid-parasitoid network complexity in our study did not simply result from higher aphid and parasitoid abundance as they increased faster over time in fields with low levels of AI. However, complexity of biotic interactions can also decrease as species abundances decrease (Albrecht *et al.* 2007; Tylianakis *et al.* 2007). Our results support findings by Gagic *et al*. (2011) who found aphid-parasitoid food web complexity to increase with landscape structural simplification. However, their study was a snap-shot in time, conducted at wheat milk-ripening, and missed temporal changes of food web structure. In primary-hyperparasitoid webs, generality was higher in fields with low AI, reaching a peak at wheat milk-ripening, and the best model for generality included evenness of the lower trophic level that followed the same pattern.

Parasitism and hyperparasitism rates were higher in fields with low intensity agriculture, presumably owing to the higher availability of alternative resources in structurally complex landscapes. There is evidence that organic farming has no or only little influence on parasitoid abundances (Roschewitz *et al.* 2005; Mcfadyen *et al*. 2009), whereas landscape simplification can decrease parasitoid abundances (Thies *et al*. 2005; Roschewitz *et al.* 2005), resulting in lower biological control. Increases in parasitism rates over time appeared to be due to increases in parasitoid total abundances, rather than to changes in species identity (indicating a certain extent of functional redundancy or temporal complementarity among these species), given greater increases in parasitism rates, but smaller changes in parasitoid dominance structure over time in fields with low AI, compared to fields with high AI. Moreover, we are not aware of any published evidence that species dominant later in the season in all fields (*E. plagiator)* are more efficient compared to other parasitoids, while in contrast, *A. rhopalosiphi* is often reported as one of the most efficient parasitoids of cereal aphids (Farrell & Stufkens 1990; Levie *et al.* 2000; Adisu *et al.* 2002). Hyperparasitism rates were better explained by models including species richness than species evenness. However, when analysing this together with food web metrics in multivariate analysis, there was no single best predictor of (hyper -) parasitism rates. More generally, parasitism rates were negatively related to the community complexity indices, supporting findings that parasitoids function better in simplified food webs dominated by a single link (Hawkins 1999; Montoya *et al.* 2003; Finke & Denno 2004; Tylianakis *et al.* 2007). In contrast, hyperparasitism rates were positively related to overall community complexity in our study, supporting the traditional view of positive biodiversity-ecosystem functioning relationship.

In conclusion, aphid-parasitoid-hyperparasitoid community structure markedly changed under different AI regimes. Over time, changes in the identity of dominant species and the increase in community variability (nonlinear increases in aphid-parasitoid food web complexity) in high AI fields were presumably due to the bottom-up effect of plant nutritional quality, more specifically nitrogen availability. Despite similar food web structure and species richness at the time of aphid colonisation, identity of the dominant parasitoid species differed between fields with high and low AI, indicating importance of focusing on both the species and community level analysis to understand ecosystem functioning. Aphid-parasitoid community complexity was negatively related to parasitism rates, thus contradicting common expectations of positive biodiversity-ecosystem functioning relationship. Thus, intensified agricultural fields may support diverse, but highly variable parasitoid-host community, however, ecosystem functioning might not be easily predictable from observed changes in community structure and composition.

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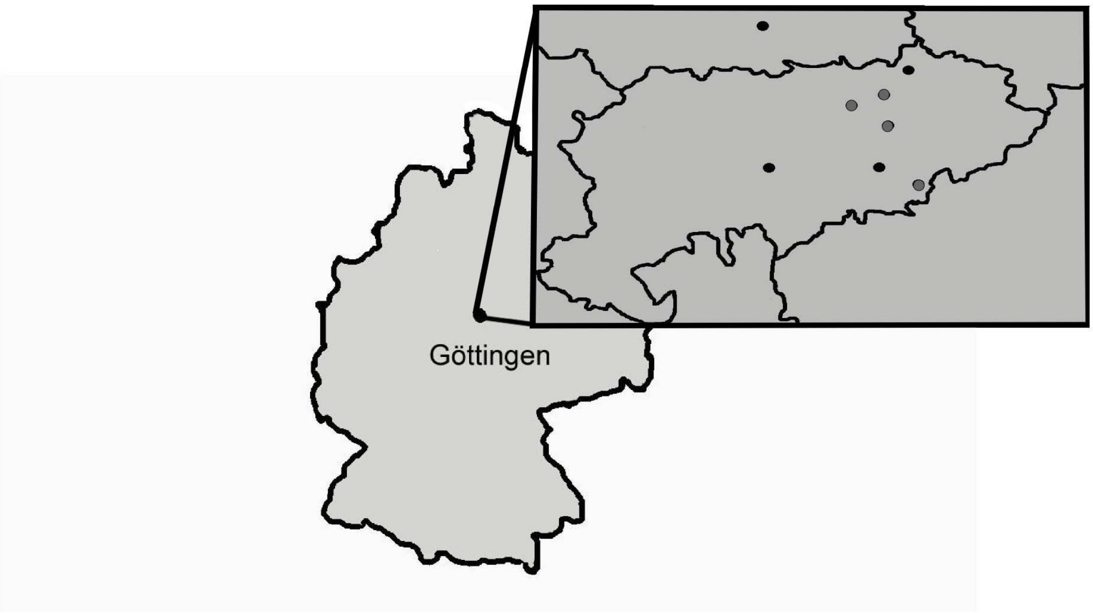
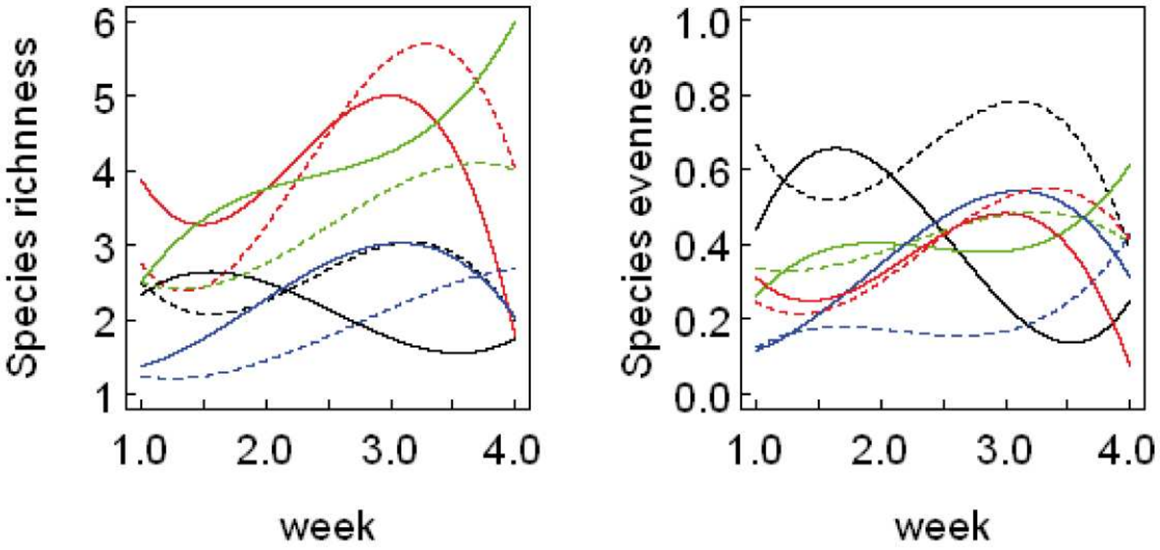
Supplementary material

Supplementary Map 3.1. Map showing the location of study sites. Organically managed fields are shown in dark gray and conventionally managed fields in black



Supplementary Figure 3.1. Species richness and evenness across four weeks for aphids (black) and primary parasitoids (red) in aphid-parasitoid webs, and primary parasitoids (blue) and hyperparasitoids (green) in primary-hyperparasitoid webs, for low AI fields (filled lines) and high AI fields (dashed lines) Lines show model predictions (based on polynomial fits).



Supplementary Table 3.1. Arithmetic means ± standard errors of abundances of aphids, primary and hyperparasitoid species per 100 shoots in high and low AI fields and across four weeks

	High AI				Low AI			
Taxa code	1	2	3	4	1	2	3	4
Aphids								
1 S. avenae	27.50±23.8	57.00±36.8	24.75±16.5	32.33±5.36	86.75±34.8	152.25± 44.52	79.2±21.2	37.67±6.12
2 R. padi	2.25±1.31	5.50±2.72	3.50± 2.60	3.33±2.85	3.00±1.58	4.50±3.84	4.25±1.44	0.00±0.00
3 M. dirhodum	17.25±8.10	17.00±6.42	12.25±4.00	10.00±9.02	6.75±3.09	7.50±3.52	3.75±3.09	0.00±0.00
Primary parasitoids								
4 E. plagiator	0.23±0.23	0.27± 0.23	0.92± 0.34	6.42± 2.18	1.27±0.64	5.15±1.30	6.32±1.58	26.63±16.6
5 A. rhopalosiphi	1.39±0.64	2.32±0.64	1.96±1.23	0.76±0.21	0.02±0.02	0.36±0.18	1.31±0.62	0.00±0.00
6 A. ervi	0.00±0.00	0.15±0.09	0.10±0.08	1.01±0.46	0.03±0.03	0.06±0.06	1.25±0.65	0.00±0.00
7 A. uzbekistanicus	0.00±0.00	0.13±0.08	0.01±0.01	0.00±0.00	0.02±0.02	0.36±0.21	0.00±0.00	0.13±0.13
8 A. avenae	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.42±0.42	0.00±0.00
9 P. volucrae	0.04±0.04	0.15±0.09	0.58±0.34	1.71±1.29	0.38±0.35	0.97±0.55	3.48±2.71	0.00±0.00
10 P. gallicum	0.08±0.08	0.08±0.08	0.14±0.14	0.00±0.00	0.00±0.00	0.14±0.10	0.00±0.00	0.00±0.00
11 P. abjectum	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.72±0.72	0.00±0.00	0.00±0.00
12 A. abdominalis	0.00±0.00	0.00±0.00	0.29±0.15	0.41±0.33	0.07± 0.08	0.00±0.00	0.95±0.66	0.57±0.40
Hyperparasitoids								
13 D. carpenteri	0.12±0.12	0.10±0.11	0.27±0.17	0.77±0.62	0.04±0.02	2.04±0.91	6.60±2.96	7.01±2.31
14 P. villosa	0.00±0.00	0.08±0.05	0.00±0.00	0.30±0.30	0.00±0.00	0.00±0.00	0.12±0.07	0.66±0.27
15 P. muscarum	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.07±0.07	0.79±0.64
16 P. aphidis	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.34±0.34
17 C. clavata	0.00±0.00	0.00±0.00	0.03±0.03	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.43±0.31
18 A. brevis	0.00±0.00	0.02±0.02	0.03±0.03	0.00±0.00	0.02±0.02	0.23±0.10	0.29±0.08	1.56±1.30
19 A. victrix	0.09±0.06	0.27±0.10	0.25±0.15	0.21±0.10	0.02±0.02	0.07±0.04	0.25±0.25	0.52±0.30
20 A. suspensus	0.05±0.03	0.40±0.25	0.45±0.30	2.19±0.94	0.02±0.02	0.15±0.08	0.99±0.61	5.05±4.20
21 A. vulgaris	0.03±0.03	0.07±0.07	0.62±0.40	2.92±2.24	0.00±0.00	0.15±0.08	0.99±0.68	6.13±5.21

Supplementary Table 3.2. Arithmetic means ± standard errors of quantitative measures of interaction diversity, linkage density, interaction evenness, generality, vulnerability, primary and hyperparasitism rates and aphid density in high and low AI fields and across four weeks.

		Week			
		1	2	3	4
Aphid-primary parasitoid food-webs					
Interaction diversity	HighAI	1.06±0.15	1.11±0.28	1.75±0.13	1.10± 0.16
	LowAI	1.09±0.19	1.24±0.10	1.15±0.21	0.44±0.05
Linkage density	HighAI	1.57±0.09	1.71±0.29	2.22±0.17	1.69±0.17
	LowAI	1.73±0.12	1.85±0.07	1.81±0.24	1.27±0.04
Interaction evenness	HighAI	0.83±0.06	0.79±0.03	0.80±0.08	0.71±0.10
	LowAI	0.72±0.04	0.73±0.04	0.68±0.09	0.55±0.09
Generality	HighAI	1.67±0.16	1.66±0.39	1.79±0.12	1.31±0.18
	LowAI	1.54±0.21	1.85±0.28	1.03±0.26	1.35±0.16
Vulnerability	HighAI	1.47±0.23	1.76±0.32	2.57±0.32	2.08±0.35
	LowAI	1.92±0.03	1.85±0.28	2.60±0.49	1.20±0.12
Parasitism rate	HighAI	0.06±0.04	0.05±0.01	0.08±0.03	0.17±0.05
	LowAI	0.01±0.01	0.04±0.003	0.13±0.03	0.36±0.10
Primary-hyperparasitoid food webs					
Interaction diversity	HighAI	0.92±0.15	0.92±0.15	1.22±0.21	1.38±0.18
	LowAI	1.39±0.10	1.11±0.27	1.47±0.24	1.46±0.36
Linkage density	HighAI	1.80±0.20	1.56±0.13	2.07±0.30	1.98±0.15
	LowAI	1.75±0.10	1.63±0.14	2.08±0.27	2.32±0.44
Interaction evenness	HighAI	0.95±0.02	0.92±0.05	0.79±0.04	0.73±0.05
	LowAI	1.00±0.01	0.70±0.10	0.74±0.07	0.77±0.06
Generality	HighAI	1.25±0.25	1.10±0.10	1.20±0.06	1.71±0.24
	LowAI	1.00±0.10	1.28±0.06	1.92±0.15	1.41± 0.13
Vulnerability	HighAI	2.34±0.57	2.02±0.16	2.95± 0.60	2.25± 0.17
	LowAI	2.50±0.01	1.98±0.30	2.24±0.48	3.24±0.78
Hyperparasitism rate	HighAI	0.16±0.03	0.23±0.07	0.28±0.06	0.42±0.02
	LowAI	0.06±0.03	0.27±0.03	0.39±0.02	0.43±0.02
Aphid density	HighAI	47.0±28.2	79.5±45.8	40.5±21.8	45.7±5.33
	LowAI	96.5±34.6	164.5±48.5	87.2±24.0	37.7±6.12

Supplementary Table 3.3. Principal component analysis

Correlation table for the first three principal component axes with (a) aphid-primary parasitoid and (b) primary-hyperparasitoid community complexity indices.

(a)

Aphid-primary parasitoid webs	PC1	PC2	PC3
Generality	0.249009	0.46927	-0.05197
Linkage density	0.415581	-0.11161	-0.15655
Interaction evenness	0.301532	0.13611	-0.71458
Interaction diversity	0.446175	-0.01574	0.03911
Vulnerability	0.294561	-0.43702	-0.17884
Higher trophic level evenness	0.332730	-0.37260	0.06305
Lower trophic level evenness	0.306636	0.42865	0.10673
Higher trophic level richness	0.319295	-0.29329	0.50635
Lower trophic level richness	0.286082	0.38597	0.39610

(b)

Primary-hyperparasitoid webs	PC1	PC2	PC3
Generality	0.201399	-0.50710	0.06862
Linkage density	0.425232	0.10889	-0.08592
Interaction evenness	0.077185	0.24275	0.90233
Interaction diversity	0.452479	-0.00861	0.07450
Vulnerability	0.375503	0.32793	-0.12122
Higher trophic level evenness	0.352128	0.30731	0.03931
Lower trophic level evenness	0.265323	-0.45148	0.27178
Higher trophic level richness	0.416592	0.12272	-0.27863
Lower trophic level richness	0.242857	-0.50111	-0.02059

Supplementary Table 3.4. We used Akaike weights to test for for additional effects of species richness and evenness on the food web metrics. The series of alternative linear mixed-effects models were developed in the same manner, as in the main analysis (see Material and methods section in the main document). Since “AI” and “Week” are design-based variables and there was good evidence that they were important for the explanation of variation in our response variables (see results), we included them in all models (for justification see Zuur et al. 2009 Mixed effects models and extensions in ecology with R. Statistics for biology and health. Springer, New York, pp. 483-485). These models can be thought of as different ‘hypotheses’ about the relationships between response and explanatory variables. We fitted models without interactions and used variance-inflation factors (VIF) to assess the extent of collinearity. The collinearity was low, and in all cases VIFs were well below 10 (cf. Zuur et al. 2009). We then calculated the relative probability of each model being the best model by calculating their Akaike weights, using AICc (Burnham & Anderson 2002 Model selection and multimodel inference: a practical information-theoretic approach. 2nd edn. Springer-Verlag, New York). The model rankings and Akaike weights (*wi*) for the best three models relating food web metrics and (hyper-) parasitism rates to (1) Agricultural intensification, “1”, (2) Sampling Week “2”, (3) lower trophic level evenness “3”, (4) higher trophic level evenness “4”, (5) higher trophic level richness “5”, (6) lower trophic level richness “6” are presented in the table. In aphid-primary parasitoid webs, models that included evenness of aphids and parasitoids had the highest relative probability of being the best models (except for interaction evenness, which included also aphid species richness). In primary-hyperparasitoid webs, the best models for the explanation of interaction diversity and vulnerability included evenness of both trophic levels and richness of hyperparasitoids, and for interaction evenness, evenness of both trophic levels and the richness of primary parasitoids. The best models for the explanation of linkage density and generality included hyperparasitoid richness and primary parasitoid evenness, respectively.

	Model 1 (*wi*)	Model 2 (*wi*)	Model 3 (*wi*)
Aphid-primary parasitoid			
Linkage density	3+4 (0.63)	4 (0.20)	4+6 (0.06)
Interaction diversity	3+4 (0.92)	3+4+6(0.04)	4 (0.02)
Interaction evenness	3+6 (0.48)	3+4+6 (0.25)	3 (0.09)
Vulnerability	4 (0.60)	3+4 (0.21)	4+6 (0.14)
Generality	3+4 (0.56)	3 (0.33)	3+6 (0.05)
Primary-hyperparasitoid			
Linkage density	5 (0.74)	4+5 (0.13)	3+5 (0.08)
Interaction diversity	3+5 (0.43)	3+4+5 (0.43)	5+6 (0.05)
Interaction evenness	4 (0.42)	3+4+6 (0.35)	3+4 (0.20)
Vulnerability	3+5 (0.40)	3+4+5 (0.32)	4+5 (0.11)
Generality	3 (0.80)	3+4 (0.12)	3+6 (0.04)

Chapter 4

Community variability of aphid parasitoids vs. predators in response to agricultural intensification

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Abstract

Agricultural intensification (AI) often causes shifts in community composition in space and time. However, the effects of AI on community variability have rarely been studied, despite their importance for understanding the ways communities are structured and how they respond to disturbances. Depending on species traits, such as dispersal ability and habitat specialisation, within-group variability can be hypothesized to increase or decrease due to AI, with or without shifts in communities' mean state. In this study, we focused on cereal aphid natural enemies in winter wheat fields with contrasting AI regimes (organic fields in structurally complex landscapes vs. conventional fields in structurally simple landscapes). We found that within-group variability of more specialized, low-dispersing primary and secondary parasitoids was increased in fields with high AI, probably due to the disruption of the exchanges between local populations in structurally simple landscapes. In contrast, within-group variability of less specialized, highly-dispersing carabid beetles and hoverflies was decreased in fields with high AI, where they were characterized by the dominance of vagile species adapted to high land-use. Furthermore, spatial shifts in communities' mean state due to AI were significant in all groups, while temporal community shifts were only pronounced in primary parasitoids and hoverflies, with primary parasitoids showing greater temporal changes in fields with high AI. Collectively, our results illustrate that environmental homogenization due to AI does not necessarily induce spatio-temporal homogenization of communities, but rather can have contrasting effects on the community variability of specialist and low-dispersive parasitoids vs. generalist and high-dispersive predators, thereby demonstrating great differences in the manner these communities are structured and in predictability of their responses to AI.

Keywords: community composition, biotic homogenisation, spatio-temporal changes

Introduction

Agricultural intensification (AI) is currently the greatest threat to biodiversity (Sala *et al.* 2000, Foley *et al.* 2005). It promotes habitat homogeneity, thereby causing shifts in community composition (Lockwood and McKinney 2001). While community shifts in both space and time are commonly expected consequences of land-use, changes in within-group variability (variability among replicates) have rarely been studied but are of interest for several reasons. Within-group variability can be an important indicator of environmental stress and ecological transition (Warwick & Clarke, 1993, Carpenter &Brock 2006). It has important implications for regional biodiversity planning (Champan *et al.* 1995) and for assessing the predictability of community responses to various types of perturbations (Houseman *et al.* 2008). Furthermore, increased similarity in community composition among local communities may decrease variability in ecosystem processes and increase ecosystem reliability (Fukami *et al.* 2001).

A number of factors associated with high levels of AI at local, field scale (such as increased input of fertilisers, pesticides, increased productivity and disturbances by agricultural practices), and at the landscape scale (such as habitat loss, increased fragmentation, decreased habitat connectivity and size etc.) may influence changes within and among communities (Dormann *et al.* 2007, Houseman *et al.* 2008, Ekroos *et al.* 2010, Zurita and Bellocq 2010). In contrast, low levels of AI (such as organic agriculture and higher landscape structural complexity) have been suggested to reverse these changes by providing overwintering sites, refuges from disturbances by agricultural practices and alternative resources (Hole *et al.* 2005, Bengtsson *et al.* 2005, Bianchi *et al.* 2006). In hypothetical scenarios, AI may cause shifts in communities' mean state (group centroid in multivariate space) and increases (Figure 4.1.a), decreases (Figure 4.1.b) or no change (Figure 4.1.c) in within-group community variability (dispersion of replicates around the group centroid). Alternatively, within-group variability could increase (Figure 4.1.d), decrease (Figure 4.1.e) or stay unchanged (Figure 4.1.f) without changes in communities' mean state. Increased land-use intensity commonly homogenises landscapes that are then dominated by monocultures, consequently leading to homogenisation of communities (by decreasing community dissimilarity, see Lockwood and McKinney 2001). For example, within-group variability should decrease, if AI favours species that are dominant and evenly distributed among replicates (Housemann *et al.*2008).

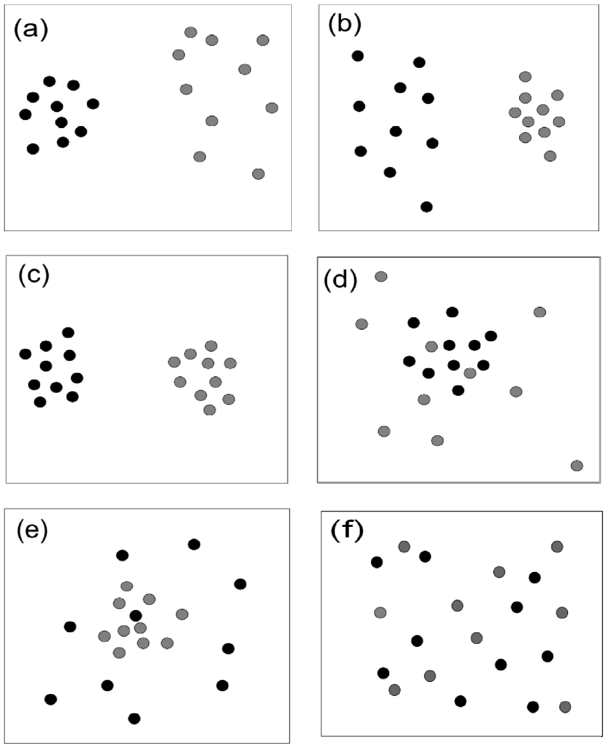

Figure 4.1. Diagram showing hypothetical differences in location and dispersion of points in a multivariate space (two dimensions shown). Given the set of fields with low AI (black circles) and fields with high AI (gray circles), six patterns are possible (see Introduction section for detailed explanation).

On the other hand, intensive agricultural practices and temporally unsynchronised, common disturbances in agricultural landscapes may introduce spatial and temporal habitat heterogeneity among replicates. This may reduce the skewness of species abundance towards dominant species, thereby increasing within-group variability. If in addition, habitats with different land-use intensities favour different species, the communities' mean states will also differ.

Differences in within-group variability may be caused by changes in the total number of individuals or species, or by changes in the abundance and presence of a particular species (Warwick & Clarke 1993). These changes depend on both environmental characteristics (extrinsic factors) and on the characteristics of species within communities (intrinsic factors, Soininen 2010). Communities may respond differently to AI due to differences in species' dispersal behaviour, degree of specialization, population sizes, and variability and body sizes (Tscharntke *et al.* 2002). Species with high-dispersal abilities are less vulnerable to factors related to AI (King and With 2002, Tscharntke *et al.* 2002). A number of studies have shown the homogenizing effect of high dispersal rates on species turnover (Loreau 2000, Mouquet & Loreau 2003, Soininen *et al.* 2007). In contrast, highly intensified land-use systems can be particularly detrimental for rare, specialized, low-dispersing species (Steffan-Dewenter & Tscharntke 2002, Tscharntke *et al.* 2002). Dormann *et al.* (2007) argued that how two major features of species, dispersal and degree of specialisation, interact with each other determines how community similarity relates to land-use.

Changes in community composition have rarely been studied simultaneously in space and time (Soininen 2010). Here, we examine spatio-temporal changes in both the mean state and in multivariate dispersion (variability) in the community composition of four groups of organisms. We sampled eight winter wheat fields, four times across the season, for aphids, hoverflies, carabid beetles, and aphid primary and secondary parasitoids. The fields were managed under contrasting AI regimes (high vs. low AI). The main focus of the study was to reveal whether AI influences within- and between-group changes, and, if so, which organism groups are most affected. The focus here is on the turnover of species as affected by AI, and not on local field diversity (alpha diversity) and total abundances, which were analysed elsewhere (Gagic *et al.* in prep; Hänke *et al.* in prep). We used multivariate approaches, developed by Anderson *et al.* (2001, 2006) which allowed us to detect changes in the communities' mean state and variability due to changes in species composition and relative abundances, using a community dissimilarity measure. Specifically, we addressed the following questions: (i) Does AI cause changes in communities' variability? (ii) Does AI induce changes in the communities' mean state? (iii) How do communities of different feeding guilds change over time? Following Dormann *et al.* (2007), the results were expected to be related to the organisms' dispersal rates and degree of specialisation.

Material and methods

Experimental design

Sampling was carried out in the year 2008, in eight winter wheat fields in the surroundings of Göttingen, Lower Saxony, Germany (for details see Thies *et al.* 2011). Four low-intensity land-use fields, embedded in structurally complex landscapes (> 30 % of semi-natural habitats), were organically managed (no applications of mineral fertilizer and chemical pesticides), and four high-intensity land-use fields, embedded in structurally simple landscapes (> 90% of arable land), were conventionally managed (high applications of mineral fertilizer and chemical pesticides). Hence, the fields were managed under contrasting AI regimes, by simultaneously varying AI at both local and landscape scales, thereby reflecting a situation commonly found in European farming systems (Gibson *et al.* 2007). Fields with high-intensity land-use were insecticide-free in the area of sampling (60 x 12 m). Landscape complexity was analyzed in a circle of 500m radius.

Study system

Aphids (Homoptera, Aphididae) are the economically most important pest species in winter wheat in Germany. Enemy guilds contributing to biological control of aphids consist of more specialized, primary parasitoids (Hymenoptera, Parasitica), and of less specialized predators, such as hoverflies (Syrphidae) and carabid beetles (Carabidae). From predators, we analyzed only aphidophagous hoverflies whose larvae feed on aphids (hereafter "hoverflies") and carnivorous beetles (hereafter "carabid beetles"), as we were interested only in groups which contribute to aphid biological control. In addition, we analyzed secondary parasitoids that are less specialized compared to primary parasitoids and may disrupt ability of primary parasitoids to control aphids (Rosenheim 1998). Hence, we observed a gradient in specialization from primary parasitoids, to secondary parasitoids, hoverflies and carabid beetles. With regard to dispersal abilities, we roughly classified communities into poor dispersers (parasitoids) and good dispersers (predators). Parasitoids have low dispersal rates in agricultural landscapes (0.5-2km, Thies *et al.* 2005), while hoverflies and carabid beetles are less spatially restricted (Gutiérrez & Menéndez 2003, Jauker et al 2009). All carabid beetles analyzed here were macropterous.

Species examination

All samples, except for carabid beetles, were taken over the course of four seven-day periods, starting from the wheat flowering period (after the main period of aphid colonization of the fields), until wheat peak ripening (the period of aphid population breakdown). Aphids were counted visually on 100 wheat shoots (5 randomly chosen subsamples with 20 shoots) per field in each sampling period. At each sampling occasion, we collected approximately 100 parasitised aphids ("mummies"), which were subsequently reared in laboratory and identified to primary and secondary parasitoid species. To sample hoverflies, we used six colored pan-traps per field (two of each color, yellow, white and blue). Pan-traps were filled with 500ml of a 1:4 mixture of water and ethylene glycol and a bit of detergent (to reduce surface tension), and then attached to wooden sticks at the height of the cereal plants. They were placed along a 60m transect (at 10m distance from each other) and ~10m into the fields parallel to the edge. Five pitfall traps per field were used to collect carabid beetles over the course of two seven-day periods during the wheat flowering and the wheat milk-ripening. Pitfall traps were made of polypropylene beakers (height 154.5mm, diameter 95mm) and filled with a mixture of water and glycol as described above, and covered by a 10 cm high roof to protect them from the rain. Pan-traps and pitfalls were exposed for one week in the fields before collecting samples.

Statistical analysis

To measure changes in community composition, we used the Morisita-Horn dissimilarity index. We chose this index because it has a low sensitivity to sample size and species richness (Magurran 1988, Chao *et al.* 2006) which may be affected by AI, but were not the focus of this study.

Comparisons of dissimilarities between fields with high and low AI were performed separately for each arthropod group using PERMANOVA, an analysis of variance procedure for the distance matrices. Unrestricted permutations of the raw data (9999 permutations) with pseudo-F ratios were used to perform significance tests. This method is directly analogous to MANOVA (multivariate analysis of variance) and referred to as “non-parametric manova” by Anderson (2001). We analyzed the main effects of two factors, “AI” (fixed with two levels, high and low) and “Time” (fixed with 4 levels), and their interaction, while “Field” was included as a random factor (nested in AI, 1:8). Time was considered to be a fixed factor because time points were not chosen at random, but represented the interval we were interested in, i.e. from colonization of fields by arthropods to the near-harvest period. The PERMANOVA test has no assumption of normality, but it is sensitive to differences in the multivariate dispersion and to the non-independence of points (Anderson 2001, Anderson *et al.* 2008).

To test for multivariate dispersion (within-group variability), we used the PERMDISP function, which is a multivariate analogue of Levin’s test for the homogeneity of variances (Anderson 2006). This test uses ANOVA F-statistics to compare distances to centroids (Anderson 2006), and P-values are obtained by using 9999 permutations of residuals. In addition, this test helps us to decide whether significant results detected by PERMANOVA are due to the differences in location or dispersion in multivariate space. We performed tests for the homogeneity of dispersions for each of the main effects separately.

Following recommendations by Anderson *et al.* (2008), we tested for the non-independence of samples over time by performing tests analogous to testing for sphericity (Quinn & Keough 2002). This was done by calculating the dissimilarities between time points for each field. The dissimilarities represent differences among time points which are usually examined in a univariate analysis (see Anderson *et al.* 2008). The estimated variances in these dissimilarities were compared among six paired groups using Levin's test for the homogeneity of variances (using medians). The test was done for all groups except for carabid beetles, since in that case there was only one paired group (T1, T2). Levin's test was in all cases non-significant.

To visualize patterns in the data we used non-metric multidimensional (NMDS) scaling. Mantel's test (9999 permutations) was used to analyze Spearman's rank correlation among aphids on one side and consumer guilds on the other side. We used similarity percentage analysis (SIMPER) to reveal which species is responsible for differences in composition. Statistical analysis was done in R (R Development Core Team (2011)), using the "vegan" package (Oksanen *et al.* 2011) and in PRIMER 6 (Clarke & Gorley 2006) with the PERMANOVA add on (Anderson *et al.* 2008).

Results

Primary parasitoids

Primary parasitoids showed significant community shifts due to AI ($F_{1,23}$= 113.27, p = 0.0001) and over time ($F_{3,23}$= 16.59, p = 0.0001) with greater changes over time in fields with high AI (AI×Time $F_{3,23}$= 10.89, p = 0.0002). There were significant differences in dispersion for the main effects of "AI" ($F_{1,29}$= 12.68, p = 0.0059) and "Time" ($F_{3,27}$= 31.281, p = 0.0001), but NMDS plots (stress= 0.024) revealed that the results for multivariate dispersion may be partly confounded by a significant AI×Time interaction in PERMANOVA;
i.e. significant results found in PERMDISP may not only be caused by differences in dispersion *per se*, but also by the fact that "AI" interacts with "Time" (Figure 4.2.). However, separate NMDS plots for each date showed higher multivariate dispersion in fields with high AI, particularly in the last sampling period. Furthermore, NMDS plots revealed that the main effect of "Time" was mostly due to the difference between the final and previous sampling periods, and the effects of AI were significant throughout the season. Based on SIMPER analysis, *Ephedrus plagiator*, *Aphidius rhopalosiphi* and *Praon volucre* contributed most to community shifts under contrasting AI regimes, with average abundance in fields with high and low AI of 6.13, 10.50, 1.88, and 14.25, 0.81, 2.20, respectively (Figure 4.3.).

Secondary parasitoids

Secondary parasitoids showed significant differences in location and weak dispersion in multivariate space due to AI ($F_{1,23}$= 8.91, p = 0.0045; $F_{1,29}$= 4.72, p = 0.044, respectively). The pattern in the NMDS plots (stress= 0.10) indicates a slightly greater dispersion of points for fields with high AI, compared to fields with low AI (Figure 4.2.). *Dendrocerus carpenteri*, *Asaphes suspensus* and *Asaphes vulgaris* contributed most to community shifts under contrasting AI regimes, with average abundance in fields with high and low AI of 3.88, 7.44,

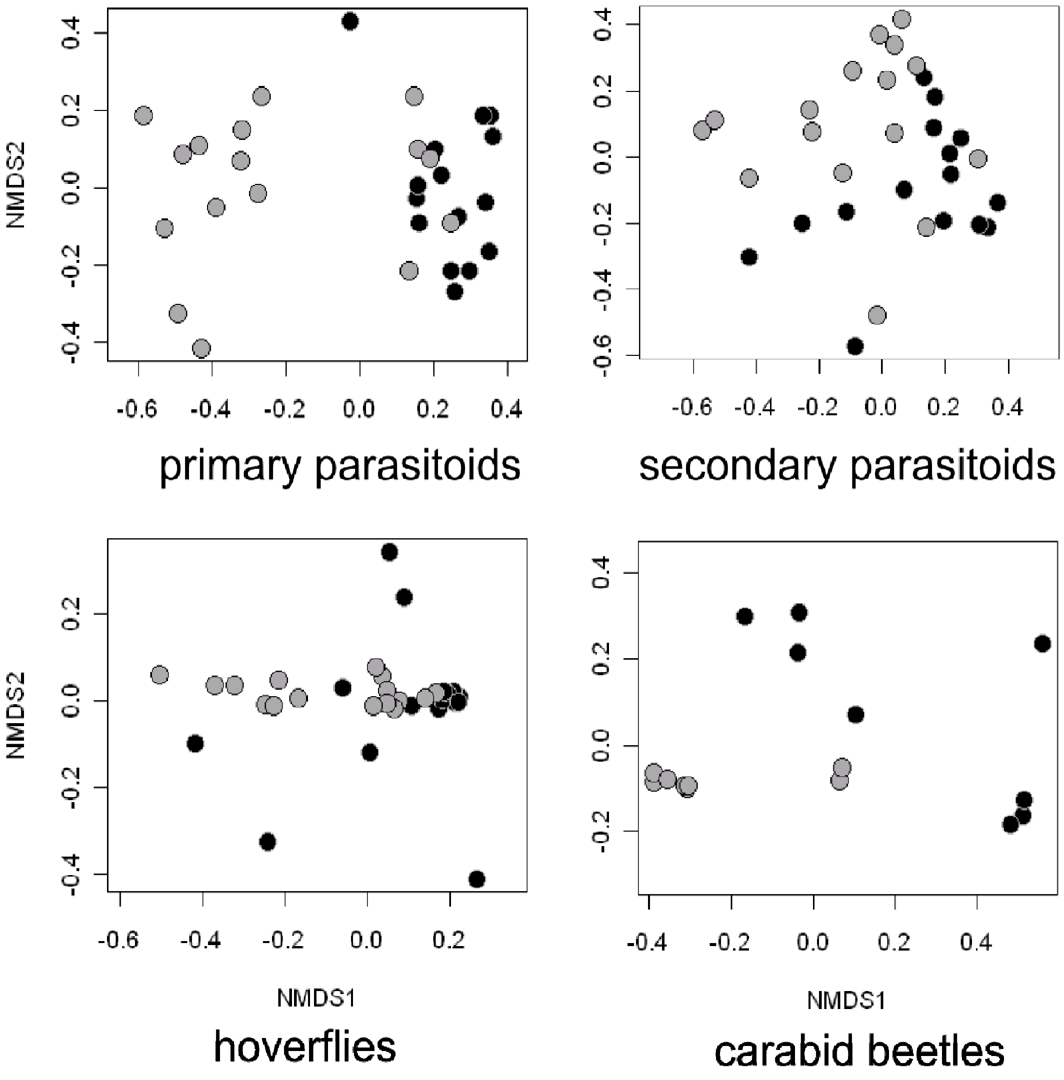

Figure 4.2. NMDS graphs using Morisita-Horn index, for primary paraitoids, secondary parasitoids, hoverflies and carabid beetles.

6.75, and 12.31, 3.7, 3.37, respectively (Figure 4.3.).

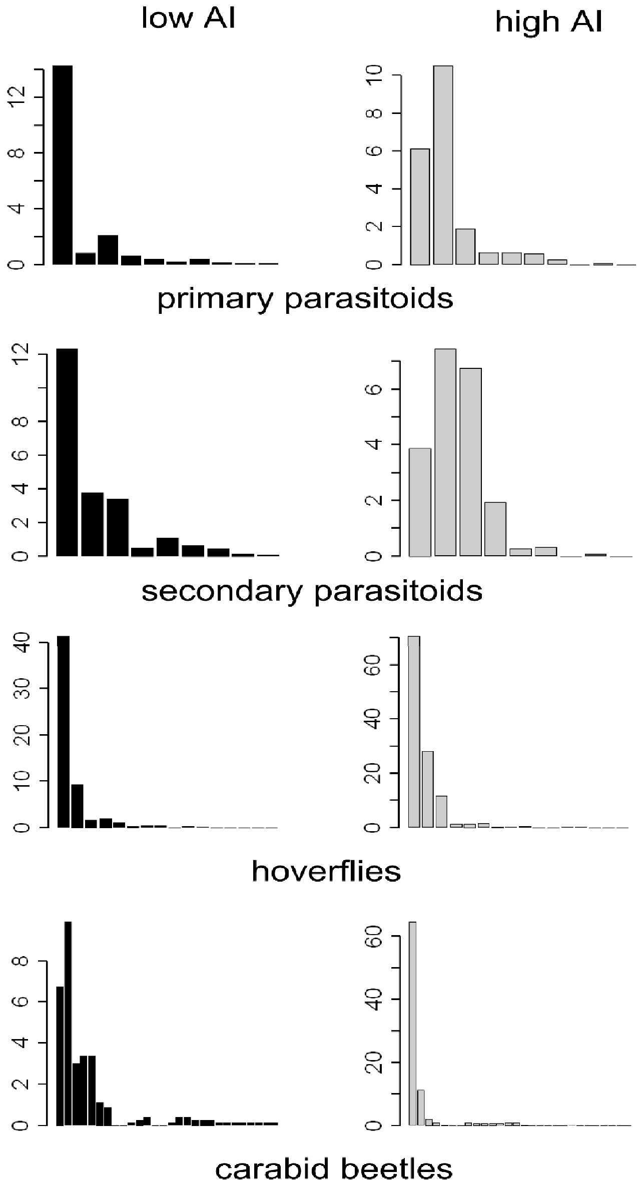

Figure 4.3 Average abundances of species, ranked and ordered by their contribution to between-group differences (low AI-black bars; high AI-gray bars), for each consumer guild separately. Note differences in the scale of y-axes. Names of the dominant species with exact values for their average abundances are given in the Results section in the same order as they appear in the figure.

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Hoverflies

Aphidophagous hoverflies showed significant community shifts due to “AI” ($F_{1,24}$= 9.65, p = 0.004) and “Time” ($F_{3,24}$= 7.02, p = 0.0003). There were no significant differences in dispersion for any investigated factor, but inspection of NMDS graphs (stress=0.06) indicates higher dispersion of points in fields with low AI at the time of colonization (Figure 4.2.) and that the significant effects of time in PERMANOVA were due to the most pronounced difference between the colonization period and later time periods. After the first sampling occasion, communities in fields with low AI converged over time, leading to similar multivariate dispersions between fields with high and low AI. SIMPER analysis revealed that three species, *Episyrphus balteatus, Eupeodes corollae* and *Sphaerophoria scripta* contributed most to community shifts under contrasting AI regimes, with average abundance in fields with high and low AI of 70.56, 28, 11.56 and 41.25, 9.31, 1.69, respectively (Figure 4.3.).

Carabid beetles

Carnivorous carabid beetles showed significant community shifts due to “AI” ($F_{1,12}$= 13.08, p = 0.004). There were significant differences in dispersion for the main effect of “AI” ($F_{1,14}$= 22.95, p = 0.001). Inspection of NMDS graph (stress=0.095) shows that the differences between fields with contrasting AI regimes are due to both location and dispersion in multivariate space (Figure 4.2.). SIMPER analysis revealed that carabid species *Pterostichus melanarius* contributed most to between-group differences (average contribution 48.46) with average abundance in fields with a high AI of 64.37, and in fields with a low AI of 6.75 (see Figure 4.3.).

Correlation of aphids and consumer communities

Correlation of aphids with consumer communities decreased with decreasing degree of specialization of the feeding guilds, i.e. from primary parasitoids to secondary parasitoids, hoverflies and carabid beetles (Mantel test, r = 0.32, p = 0.0011; r = 0.26, p = 0.005; r = 0.19, p = 0.03; r = 0.14, p > 0.1, respectively).

Discussion

Does AI cause changes in communities’ variability?

Our study suggests that AI has contrasting effects on variability of different arthropod communities. AI increased within-group variability in more specialized, low-dispersing primary and secondary parasitoids, and decreased within-group variability in less specialized, high-dispersing hoverflies and carabid beetles. Dormann *et al.* (2007) hypothesized that community dissimilarity will increase with land-use intensification when dispersal limitation is more important than resource specialization, and vice versa. Low niche differentiation in communities such as cereal aphid parasitoids may hinder selection of a robust species that can become dominant in fields with high land-use. Furthermore, low-dispersing specialists may be more affected by land-use than vagile generalist, which perceive fragmented landscapes as sufficiently connected (Steffan-Dewenter & Tscharntke 2002, King & With 2002). Increases in within-group variability of parasitoids in fields with high AI in our study thus may be due to the disruption of the exchange of species among local communities which promotes their differentiation in structurally simple landscapes (see also Dormann *et al.* 2007). The less pronounced response of secondary parasitoids compared to primary parasitoids is likely due to their higher trophic level and lower specialization (Rand *et al.* 2011). However, here we cannot sufficiently test directly for the direct influence of dispersal and/or specialization on different arthropod groups, given differences in evolutionary history, dispersal modes and the low number of feeding guilds.

Contrary to parasitoids, within-group variability of carabid beetle communities and, to a lesser extent, hoverfly communities, decreased in fields with high AI where they were reduced to robust species adapted to high land-use conditions. These results are in line with findings of increased community similarity in high land-use systems for hoverflies and carabid beetles (Dorman *et al.* 2007). AI often favours vagile generalist species that are robust to high intensity land-use conditions and disfavours rare and specialized ones (Warren *et al.* 2001, Kotze *et al.* 2003, Cadotte *et al.* 2006, Ekroors *et al.* 2010). This can lead to homogenized (more similar) communities when the dominant species that can survive these conditions is the same among local communities (McKinney & Lockwood 1999, Housemann *et al.* 2008, Fried *et al.* 2010). Mouquet & Loreau (2003) have shown that communities containing species with high dispersal abilities tend to homogenize, making the species' rank abundance relationship steeper.

Does AI induce changes in communities' mean state?

Community shifts under contrasting AI regimes were significant in all groups, but most pronounced in carabid beetles. Carabid beetles had highly skewed abundances towards the dominant species, *Pterostichus melanarius*, in fields with high AI, and much lower numbers of this species and more even species distribution in fields with low AI. This species distribution, combined with a number of species being present only in fields with low AI, might have caused pronounced shifts in community composition between fields with contrasting AI regimes. *P. melanarius* is a common species in high-intensity land-use, probably because it overwinters within arable fields, and seems to be able to compensate for high losses due to tillage systems through its high dispersal ability (Nordhuis *et al.* 2000, Irmler 2003). Furthermore, the pitfall-trap catches of this species may increase after insecticide (Chiverton 1984, Dixon & McKinlay 1992), and herbicide application (Powell *et al.* 1985), and with increasing distance from hedges (Fournier & Loreau 1999).

Shifts in hoverfly communities were most pronounced at the time of crop colonization, due to the dominance of *E. balteatus* in fields with high AI, probably owing to its high dispersal ability which may allow for its early colonization of more isolated fields (Sutherland *et al.* 2001, Hondelmann *et al.* 2005). In primary and secondary parasitoids, different species have been favored in different AI regimes, which caused community shifts, likely due to changes at the bottom of the food web. Correlations among aphid communities on the one hand and primary parasitoid communities on the other were high in our study, with decreasing strength of correlation towards less specialized guilds.

How do communities of different feeding guilds change over time?

Primary parasitoids and hoverflies showed community shifts over time. While hoverflies had similar patterns in fields with contrasting AI regimes, primary parasitoids showed greater changes in fields with high AI. Temporal changes in hoverfly are likely to be associated with changes in aphid communities (Hänke *et al.* 2009). In our study abundances of the common species were mainly accompanied with highest aphid abundances in fields. However, changes in hoverfly communities should be related to habitat and resource requirements of both adults and larvae (Meyer *et al.* 2009). In primary parasitoids, community shifts under contrasting AI regimes were pronounced until the end of the season, when large community changes in fields with high AI decreased between-group dissimilarity. Pre-analyses of the same data (Gagic *et al.*, unpublished data) revealed a high variability in aphid-parasitoid food web interactions over time in fields with high AI, presumably owing to the bottom-up effect of changes in aphid communities. Hence, local species interactions may be important for determining changes in community compositons of primary parasitoids, due to dispersal limitation and high resource specialisation. However, an increase in community variability in parasitoids may have been affected by their lower species richness compared to predators, as less diverse communities tend to be more variable (Cottingham *et al.* 2001).

In conclusion, environmental homogenization due to AI does not necessarily induce spatio-temporal homogenization of communities, whose responses may depend on species traits. We have shown that AI can have contrasting effects on the community variability of specialist and low-dispersive parasitoids vs. generalist and high-dispersive predators, thereby demonstrating great differences in the predictability of species group responses to AI.

Furthermore, high turnover of primary parasitoids, especially in fields with high land-use intensity might have implications for ecological landscape management and regional biodiversity planning, given that their local species richness doesn't seem to be influenced by AI (Marino & Landis 1996, Mennalend *et al.* 1999, Vollhardt *et al.* 2008, Gagic *et al.* 2011). Also, our study reveals possible pitfalls in the common practice of assessing changes in community response as a snap-shot in time, because initial differences in community composition in fields with contrasting AI regimes may decrease over time, as shown here for primary parasitoids. Future studies should, therefore, consider the spatio-temporal changes in community mean response and variability to understanding key processes that structure natural enemy communities in different land-use systems.

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Summary

Agricultural intensification (AI) is a major driver of losses in agrobiodiversity and associated ecosystem functions such as biological control, thereby indirectly affecting agricultural production. AI may influence community structure, composition and variability in both space and time, by differently affecting species with different traits. Species at higher trophic levels, with higher specialization and lower dispersal abilities, are expected to be more vulnerable to AI and have high spatio-temporal population and food-web dynamic. Hence, understanding patterns of agrobiodiversity and their associated trophic interactions, as well as species turnover due to AI, requires a focus on the spatio-temporal changes in communities belonging to different feeding guilds and trophic levels. The aim of my study is to address these patterns in agrobiodiversity and to investigate their relation to biological-control functioning in different land-use systems. My work is part of the AGRIPOPES project (http://agripopes.net) and comprises three field studies, carried out in the surroundings of Göttingen, Lower Saxony, Germany.

(1) In the first study, we analysed food webs of cereal aphids, their primary parasitoids and hyperparasitoids in 18 agricultural landscapes differing in structural complexity (42–93% arable land). Despite little variation in the richness of each trophic group, we found considerable changes in trophic link properties across the landscape complexity gradient. In contrast to our expectations, aphid–parasitoid food webs exhibited a lower complexity (lower linkage density, interaction diversity and generality) in structurally complex landscapes, presumably owing to the dominance of one (of the mainly three) aphid species in complex landscapes. Nevertheless, primary parasitism, as well as hyperparasitism, was higher in complex landscapes, with primary parasitism reaching levels of potentially successful biological control.

(2) In the second and the third study, we varied AI simultaneously at local (field) and landscape scales, with four fields being organically managed (no application of mineral fertilizers and chemical pesticides) and embedded in structurally complex landscapes (>30% of semi-natural habitats) and four fields being conventionally managed (high application of mineral fertilizers and chemical pesticides) and embedded in structurally simple landscapes (>90% of agricultural habitats). We analysed the spatio-temporal variability of 64 quantitative aphid-parasitoid and parasitoid-hyperparasitoid food webs. Surprisingly, high AI raised food web

complexity and temporal variability in aphid-parasitoid, but not in parasitoid-hyperparasitoid food webs. The enhanced complexity of aphid-parasitoid webs was independent of aphid abundances and parasitism rates, which increased during the season, faster in fields with low AI. Furthermore, dominant parasitoid species differed between high and low AI fields, and within high AI fields over time. Principal component analysis showed that biodiversity (as measured by species richness, evenness and food web indices) is negatively related to primary parasitism rates and positively to hyperparasitim rates.

(3) In the third study, we analysed the influence of AI on within- and between-group changes in species abundance data (using the Morisita-Horn dissimilarity index), by comparing different aphid natural enemy guilds: carabid beetles, hoverflies, and primary and secondary parasitoids. AI increased within-group community variability in more specialized, low-dispersing primary and hyperparasitoids, probably due to the disruption of the exchange of species between local communities. On the contrary, within-group community variability of less specialized, highly-dispersing hoverflies and carabid beetles, decreased in fields with high AI, presumably owing to the skewed abundance of dominant robust species adapted to high-AI conditions. In addition, between-group dissimilarity under contrasting AI regimes decreased over time in primary parasitoids, due to greater changes in fields with high AI.

In conclusion, landscape complexity may foster higher parasitism rates, but simpler food webs, thereby casting doubt on the general importance of food web complexity for ecosystem functioning. Homogenized landscapes due to AI can support diverse, although highly variable parasitoid communities, but ecosystem functioning might not be easily predictable from observed changes in community structure and composition. Community structure and ecosystem functioning appear to be differently influenced by AI, changing differently over time and among trophic levels. Furthermore, AI can have contrasting effects on the community variability of specialist and low-dispersive parasitoids vs. generalist and high-dispersive predators, which may demonstrate their different vulnerability to changing environments. Hence, landscape homogenization due to AI does not necessarily homogenize communities, whose response may depend on species traits. We suggest that effects of AI on agrobiodiversity and biological control should be assessed with a multi-species, multi-trophic and multi-scale approach, while taking into account different biodiversity measures.

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