

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

Vesna Gagic^{1,*}, Teja Tscharnke¹, Carsten F. Dormann³,
Bernd Gruber^{3,4}, Anne Wilstermann^{1,2} and Carsten Thies¹

¹Department of Crop Science, Agroecology, and ²Department of Crop Science, Agricultural Entomology, Georg-August-University, Grisebachstrasse 6, 37077 Göttingen, Germany

³Department of Computational Landscape Ecology, Helmholtz Centre for Environmental Research-UFZ, Permoserstrasse 15, 04318 Leipzig, Germany

⁴Institute of Applied Ecology, University of Canberra, 2601 Bruce, Canberra, Australia

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

1. 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 [1–5], but can also promote species groups via higher productivity or specific resources provided by agriculture [5,6]. 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 [7,8]. Furthermore, even when species richness is unaffected by agricultural intensification, the structure of the food web interactions may change [9], 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 [10,11]. There is experimental evidence for pest suppression in agricultural systems by diverse enemy communities [12–15], but this is also documented in simplified habitats and by less species-rich enemy

communities [16–18]. For example, Rodriguez & Hawkins [19] 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 [20], but such relationships may not be causal as the dynamics of systems are often driven by one or few species [21].

Biological control of aphids is an important ecosystem service as aphids are one of the major pests in cereal fields in Europe [22–24]. Naturally occurring parasitoids have been shown to be important in suppressing aphid abundances [14,23]. 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 [23,25,26]. However, hyperparasitoids may disrupt biological control of aphids mediated by primary parasitoids [27], 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 [11,13], 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

* Author for correspondence (vgagic@gwdg.de).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2010.2645> or via <http://rspb.royalsocietypublishing.org>.

recently developed quantitative, weighted descriptors of food web complexity [28] that are more accurate, more robust to differences in sampling effort and less sensitive to among system differences, compared with their qualitative counterparts [29,30]. 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* [9,31–34]. Here, we analysed four of these quantitative metrics (generality, vulnerability, interaction diversity, 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.

2. METHODS

(a) *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 [35], 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) [36]. For simplicity, we will refer to both true hyperparasitoids and mummy parasitoids as hyperparasitoids in this paper.

(b) *Study design*

We analysed a dataset partly used and described in detail by Thies *et al.* [23], 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 [2,37,38]. 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 [23]. 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 [23]). 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 m², 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 [35]. 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 [39].

Quantitatively weighted food web metrics (linkage density, generality, vulnerability, interaction diversity) were calculated following Bersier *et al.* [28] (for details refer to the electronic supplementary material, methods S1). 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 [30,40,41]. 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).

(c) *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.* [9]. 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

Table 1. Arithmetic means \pm s.e., minimum and maximum values ($n = 18$) of cereal aphid, their primary and hyperparasitoid densities (individuals per 100 shoots).

taxa code	individuals per 100 shoots		
	mean \pm s.e.	min	max
aphids			
1. <i>S. avenae</i>	31.74 \pm 6.19	6.25	101.25
2. <i>M. dirhodum</i>	13.89 \pm 2.93	0	46.25
3. <i>R. padi</i>	1.32 \pm 0.29	0	3.75
primary parasitoids			
4. <i>Aphidius</i> sp.	6.94 \pm 1.26	0	19.09
5. <i>Ephedrus</i> sp.	1.10 \pm 0.39	0	5.68
6. <i>Praon</i> sp.	0.63 \pm 0.15	0	2.05
7. <i>Aphelinus</i> sp.	0.15 \pm 0.08	0	1.17
8. <i>Diaeretiella</i> sp. ^a	<0.01		
9. <i>Toxares</i> sp.	0.68 \pm 0.00	0	0.68
hyperparasitoids			
10. <i>Alloxysta</i> sp.	0.06 \pm 0.03	0	0.42
11. <i>Phaenoglyphis</i> sp.	0.07 \pm 0.05	0	0.88
12. <i>Dendrocerus</i> sp.	1.33 \pm 0.38	0	5.88
13. <i>Asaphes</i> sp.	1.10 \pm 0.34	0	4.81
14. <i>Coruma</i> sp.	0.02 \pm 0.01	0	0.23

^aOnly one individual of *Diaeretiella* sp. was found (mummy collection data).

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.

We used path analysis (a form of structural equation modeling (SEM)) to evaluate pathways of direct and indirect effects of landscape structural complexity on parasitism and hyperparasitism rates (see the electronic supplementary material, methods S2). 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 [42].

Statistical analyses were performed using the statistical software R V. 2.8.0 [43], and the packages 'bipartite' (for food web analysis, [44,45]) and 'SEM' [46].

3. RESULTS

Genera abundance and food web metrics varied considerably across the landscape complexity gradient (for an overview, see table 1 and electronic supplementary material, table S1). 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 1). 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

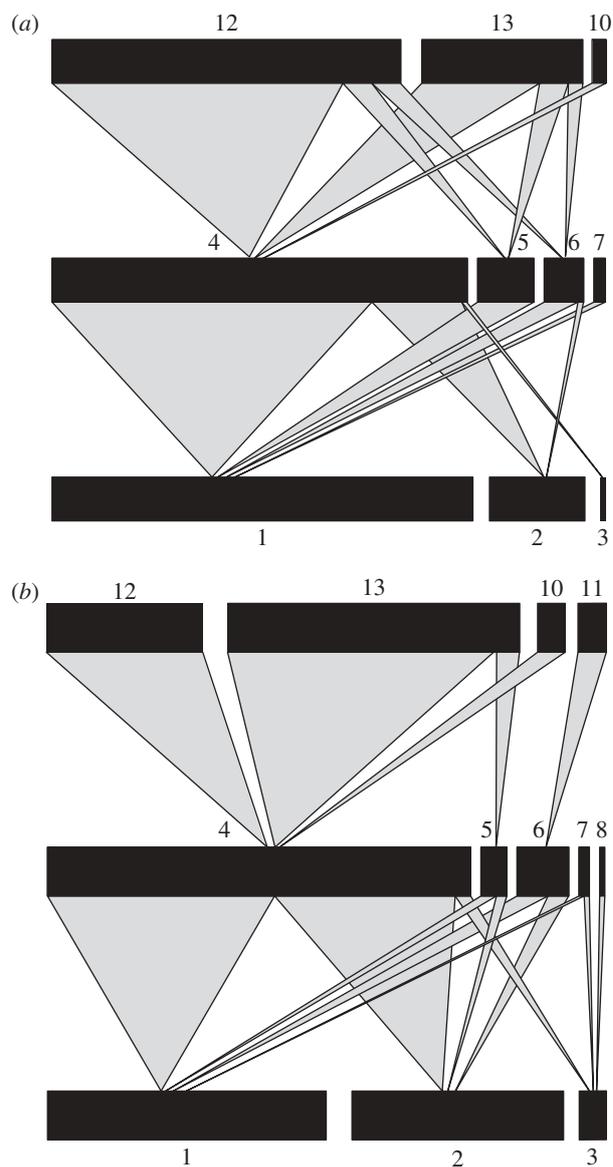


Figure 1. Parasitoid food webs calculated from pooled data for (a) four landscapes with the lowest ($57.6 \pm 5.22\%$; mean \pm s.e.) and (b) four landscapes with the highest ($90.16 \pm 1.23\%$; mean \pm s.e.) percentage arable land. Black bars represent relative abundances of aphids (lower bars), primary 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.

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* ($r_s = -0.658$, $p = 0.006$).

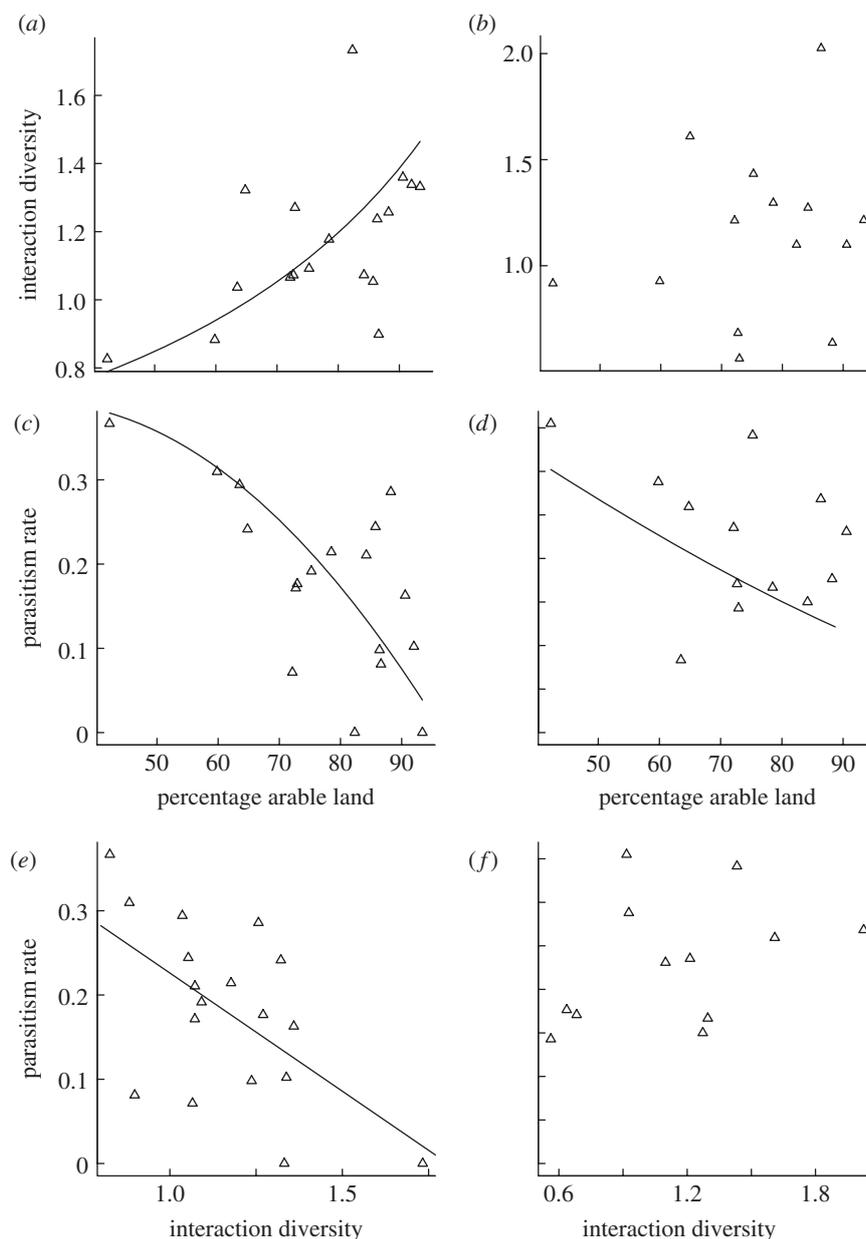


Figure 2. Interaction diversity and parasitism rates across a landscape complexity gradient and relation of parasitism rate to interaction diversity for (a,c,e) primary and (b,d,f) hyperparasitoid webs.

We found significant differences in the food web structure across the landscape complexity gradient (figures 1 and 2 and table 2). In aphid–primary parasitoid food webs, linkage density, generality and interaction diversity (figure 2a) increased as the percentage of arable land increased, while vulnerability did not change across the landscape gradient (table 2). Linkage density, interaction diversity and vulnerability were positively influenced by consumer (primary parasitoid) richness, while generality and linkage density were 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 2b 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 $r_s = 0.078$, $p = 0.76$; electronic supplementary material, figure S2).

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 2c,d and table 2). In aphid–parasitoid food webs, parasitism correlated negatively with interaction diversity ($F_{1,16} = 8.14$, $p = 0.01$; figure 2e) and linkage density ($F_{1,16} = 5.77$, $p = 0.03$).

Table 2. *F*-values and levels of significance from general linear models relating parasitism rates and food web metrics (linkage density, interaction diversity, vulnerability and generality) for aphid–primary parasitoid webs and primary–hyperparasitoid webs to three predictive factors: (i) percentage of arable land, (ii) aphid species richness, (iii) parasitoid (or hyperparasitoid) genera richness. (Significant codes: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; $p > 0.05$ n.s.)

	<i>F</i> -value
<i>aphid–primary parasitoid food webs</i>	
linkage density	
no. of aphid species	4.74*
no. of primary parasitoid genera	10.38**
arable land	5.77*
interaction diversity	
no. of aphid species	n.s.
no. of primary parasitoid genera	11.81**
arable land	13.89**
vulnerability	
no. of aphid species	n.s.
no. of primary parasitoid genera	9.47**
arable land	n.s.
generality	
no. of aphid species	7.26*
no. of primary parasitoid genera	n.s.
arable land	7.41*
primary parasitism rate	
no. of aphid species	n.s.
no. of primary parasitoid genera	8.32*
arable land	17.44**
<i>primary–hyperparasitoid food webs</i>	
linkage density	
no. of primary parasitoid genera	12.84**
no. of hyperparasitoid genera	12.37**
arable land	n.s.
interaction diversity	
no. of primary parasitoid genera	21.37**
no. of hyperparasitoid genera	13.75**
no. of hyperparasitoid genera	5.41*
arable land	n.s.
vulnerability	
no. of primary parasitoid genera	n.s.
no. of hyperparasitoid genera	24.93***
arable land	n.s.
generality	
no. of primary parasitoid genera	49.09***
no. of hyperparasitoid genera	n.s.
arable land	n.s.
hyperparasitism rate	
no. of primary parasitoid genera	53.18***
no. of hyperparasitoid genera	14.75**
arable land	8.01*

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*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 the electronic supplementary material,

figure S1). 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.

4. 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.

(a) *Species richness*

Ecological theory predicts that insect diversity will increase with increasing vegetation diversity and structural complexity [47–49], which may then spill over to adjacent habitats [50]. 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 [51–53], 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 [21]. 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.

(b) *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 [37,54]), and habitats such as grassland may provide a good source for colonization of cereals by grass-hibernating aphid species *S. avenae* [23,55]. 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 [56], who argues that parasitoid communities are likely to be bottom-up controlled (see also Scherber *et al.* [57]).

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.

(c) 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 [23,58]. These findings are consistent with the studies showing that top-down control is often stronger in simplified food webs dominated by a single link [9,16–18]. 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 [23,26]), 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* [59]. 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*, [22,24]) and the main parasitoid and hyperparasitoid genera, *Aphidius* and *Dendrocerus* [60]. 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.

5. 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 [23,61], implying dynamic changes in food web structures among years and regions. Our results represent a snapshot 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.

We thank C. Scherber, C. Dennis and two anonymous reviewers for helping in statistical analysis and/or insightful comments on the manuscript. This research was funded by the German Ministry of Research and Education (BMBF). C.F.D. acknowledges funding by the Helmholtz Association (VH-NG 247).

REFERENCES

- 1 Robinson, R. A. & Sutherland, W. J. 2002 Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* **39**, 157–176. (doi:10.1046/j.1365-2664.2002.00695.x)
- 2 Thies, C. & Tschardtke, T. 1999 Landscape structure and biological control in agroecosystems. *Science* **285**, 893–895. (doi:10.1126/science.285.5429.893)
- 3 Benton, T. G., Vickery, J. A. & Wilson, J. D. 2003 Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**, 182–188. (doi:10.1016/S0169-5347(03)00011-9)
- 4 Bianchi, F. J. J. A., Booij, C. J. H. & Tschardtke, T. 2006 Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. B* **273**, 1715–1727. (doi:10.1098/rspb.2006.3530)
- 5 Tschardtke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. 2005 Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecol. Lett.* **8**, 857–874. (doi:10.1111/j.1461-0248.2005.00782.x)
- 6 Rand, T. A., Tyljanakis, J. M. & Tschardtke, T. 2006 Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* **9**, 603–614. (doi:10.1111/j.1461-0248.2006.00911.x)
- 7 Holt, R. D., Lawton, J. H., Polis, G. A. & Martinez, N. D. 1999 Trophic rank and the species–area relationship. *Ecology* **80**, 1495–1504. (doi:10.1890/0012-9658(1999)080[1495:TRATSA]2.0.CO;2)
- 8 Kruess, A. & Tschardtke, T. 1994 Habitat fragmentation, species loss, and biological control. *Science* **264**, 1581–1584. (doi:10.1126/science.264.5165.1581)
- 9 Tyljanakis, J. M., Tschardtke, T. & Lewis, O. T. 2007 Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* **445**, 202–205. (doi:10.1038/nature05429)
- 10 Loreau, M. *et al.* 2001 Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808. (doi:10.1126/science.1064088)
- 11 Memmott, J., Alonso, D., Berlow, E., Dobson, A. P., Dunne, J. A., Sole, R. & Weitz, J. S. 2006 Biodiversity

- loss and ecological network structure. In *Ecological networks: linking structure to dynamics in food webs* (eds M. Pascual & J. A. Dunne), pp. 325–347. New York, NY: Oxford University Press.
- 12 Cardinale, B. J., Harvey, C. T., Gross, K. & Ives, A. R. 2003 Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecol. Lett.* **6**, 857–865. (doi:10.1046/j.1461-0248.2003.00508.x)
 - 13 Letourneau, D. K., Jedlicka, J. A., Bothwell, S. G. & Moreno, C. R. 2009 Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **40**, 573–592. (doi:10.1146/annurev.ecolsys.110308.120320)
 - 14 Schmidt, M. H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. & Tscharnkte, T. 2003 Relative importance of predators and parasitoids for cereal aphid control. *Proc. R. Soc. Lond. B* **270**, 1905–1909. (doi:10.1098/rspb.2003.2469)
 - 15 Snyder, W. E. & Ives, A. R. 2003 Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* **84**, 91–107. (doi:10.1890/0012-9658(2003)084[0091:IBSAGN]2.0.CO;2)
 - 16 Finke, D. L. & Denno, R. F. 2004 Predator diversity dampens trophic cascades. *Nature* **429**, 407–410. (doi:10.1038/nature02554)
 - 17 Hawkins, B. A., Mills, N. J., Jervis, M. A. & Price, P. W. 1999 Is the biological control of insects a natural phenomenon? *Oikos* **86**, 493–506. (doi:10.2307/3546654)
 - 18 Montoya, J. M., Rodriguez, M. A. & Hawkins, B. A. 2003 Food web complexity and higher-level ecosystem services. *Ecol. Lett.* **6**, 587–593. (doi:10.1046/j.1461-0248.2003.00469.x)
 - 19 Rodriguez, M. A. & Hawkins, B. A. 2000 Diversity, function and stability in parasitoid communities. *Ecol. Lett.* **3**, 35–40. (doi:10.1046/j.1461-0248.2000.00115.x)
 - 20 Hawkins, B. A. & Gagné, R. J. 1989 Determinants of assemblage size for the parasitoids of Cecidomyiidae (Diptera). *Oecologia* **81**, 75–88. (doi:10.1007/BF00377013)
 - 21 Hawkins, B. A. 1994 *Pattern and process in host–parasitoid interactions*. London, UK: Cambridge University Press.
 - 22 Ankersmit, G. W. & Carter, N. 1981 Comparison of the epidemiology of *Methopolophium dirhodum* and *Sitobion avenae* on winter wheat. *Neth. J. Plant Pathol.* **87**, 71–81. (doi:10.1007/BF01976641)
 - 23 Thies, C., Roschewitz, I. & Tscharnkte, T. 2005 The landscape context of cereal aphid–parasitoid interactions. *Proc. R. Soc. B* **272**, 203–210. (doi:10.1098/rspb.2004.2902)
 - 24 Vickerman, G. P. & Wratten, S. D. 1979 The biology and pest status of cereal aphids (Hemiptera: Aphididae) in Europe: a review. *B. Entomol. Res.* **69**, 1–32. (doi:10.1017/S0007485300017855)
 - 25 Landis, D. A., Wratten, S. D. & Gurr, G. M. 2000 Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* **45**, 175–201. (doi:10.1146/annurev.ento.45.1.175)
 - 26 Roschewitz, I., Hücker, M., Tscharnkte, T. & Thies, C. 2005 The influence of landscape context and farming practices of cereal aphids. *Agricult. Ecosyst. Environ.* **108**, 218–227. (doi:10.1016/j.agee.2005.02.005)
 - 27 Rosenheim, J. A. 1998 Higher-order predators and the regulation of insect herbivore populations. *A. Rev. Entomol.* **43**, 421–447. (doi:10.1146/annurev.ento.43.1.421)
 - 28 Bersier, L. F., Banašek-Richter, C. & Cattin, M. F. 2002 Quantitative descriptors of food-web matrices. *Ecology* **83**, 2394–2407. (doi:10.1890/0012-9658(2002)083[2394:QDOFWM]2.0.CO;2)
 - 29 Banašek-Richter, C., Cattin, M. F. & Bersier, L. F. 2004 Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *J. Theor. Biol.* **226**, 23–32. (doi:10.1016/S0022-5193(03)00305-9)
 - 30 Banašek-Richter, C. *et al.* 2009 Complexity in quantitative food webs. *Ecology* **90**, 1470–1477. (doi:10.1890/08-2207.1)
 - 31 Albrecht, M., Duelli, P., Schmid, B. & Müller, C. B. 2007 Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *J. Anim. Ecol.* **76**, 1015–1025. (doi:10.1111/j.1365-2656.2007.01264.x)
 - 32 Bukovinszky, T., Van Veen, F. J. F., Jongema, Y. & Dicke, M. 2008 Direct and indirect effects of resource quality on food web structure. *Science* **319**, 804–807. (doi:10.1126/science.1148310)
 - 33 Murakami, M., Hirao, T. & Kasei, A. 2008 Effects of habitat configuration on host–parasitoid food web structure. *Ecol. Res.* **23**, 1039–1049. (doi:10.1007/s11284-008-0478-0)
 - 34 Van Veen, F. J. F., Müller, C. B., Pell, J. K. & Godfray, H. C. J. 2008 Food web structure of three guilds of natural enemies: predators, parasitoids and pathogens of aphids. *J. Anim. Ecol.* **77**, 91–200. (doi:10.1111/j.1365-2656.2007.01325.x)
 - 35 Powell, W. 1982 The identification of hymenopterous parasitoids attacking cereal aphids in Britain. *Syst. Entomol.* **7**, 465–473. (doi:10.1111/j.1365-3113.1982.tb00457.x)
 - 36 Sullivan, D. J. 1988 Hyperparasites. In *Aphids, their biology, natural enemies and control*, vol. B (eds A. K. Minks & P. Harrewijn), pp. 189–203. Amsterdam, The Netherlands: Elsevier.
 - 37 Schmidt, M. H., Thies, C. & Tscharnkte, T. 2004 Landscape context of arthropod biological control. In *Ecological engineering for pest management: advances in habitat manipulation for arthropods* (eds G. M. Gurr, S. D. Wratten & M. A. Altieri), pp. 55–63. Melbourne, Australia: CSIRO Publications.
 - 38 Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharnkte, T. 2002 Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**, 1421–1432. (doi:10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2)
 - 39 Müller, C. B. & Godfray, H. C. J. 1999 Indirect interactions in aphid–parasitoid communities. *Res. Popul. Ecol.* **41**, 93–106. (doi:10.1007/PL00011986)
 - 40 Blüthgen, N. 2010 Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. *Basic Appl. Ecol.* **11**, 185–195. (doi:10.1016/j.baec.2010.01.001)
 - 41 Neutel, A. M., Heesterbeek, J. A. P., Van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C., Berendse, F. & de Ruiter, P. C. 2007 Reconciling complexity with stability in naturally assembling food webs. *Nature* **449**, 599–602. (doi:10.1038/nature06154)
 - 42 Grace, J. B. 2006 *Structural equation modeling and natural systems*. Cambridge, UK: Cambridge University Press.
 - 43 R Development Core Team. 2008 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.r-project.org>.
 - 44 Dormann, C., Gruber, B. & Fründ, J. 2008 Introducing the bipartite package: analysing ecological networks. *R News* **8**, 8–11.
 - 45 Dormann, C., Fründ, J., Blüthgen, N. & Gruber, B. 2009 Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecol. J.* **2**, 7–24. (doi:10.2174/1874213000902010007)
 - 46 Fox, J. 2006 Structural equation modeling with the SEM package in R. *Struct. Equ. Modeling* **13**, 465–486. (doi:10.1207/s15328007sem1303_7)

- 47 Lawton, J. H. 1983 Plant architecture and the diversity of phytophagous insects. *Annu. Rev. Entomol.* **28**, 23–39. (doi:10.1146/annurev.en.28.010183.000323)
- 48 Murdoch, W. W., Evans, F. C. & Peterson, C. H. 1972 Diversity and pattern in plants and insects. *Ecology* **53**, 819–829. (doi:10.2307/1934297)
- 49 Stinson, C. S. A. & Brown, V. K. 1983 Seasonal changes in the architecture of natural plant communities and its relevance to insect herbivores. *Oecologia (Berlin)* **56**, 67–69. (doi:10.1007/BF00378218)
- 50 Tschardtke, T., Rand, T. A. & Bianchi, F. J. J. A. 2005 The landscape context of trophic interactions: insect spillover across the crop–non-crop interface. *Ann. Zool. Fenn.* **42**, 421–432.
- 51 Marino, P. C. & Landis, D. A. 1996 Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecol. Appl.* **6**, 276–284. (doi:10.2307/2269571)
- 52 Menalled, F. D., Marino, P. C., Gage, S. H. & Landis, D. A. 1999 Does agricultural landscape structure affect parasitism and parasitoid diversity? *Ecol. Appl.* **9**, 634–641. (doi:10.1890/1051-0761(1999)009[0634:DALSAP]2.0.CO;2)
- 53 Vollhardt, I. M. G., Tschardtke, T., Wäckers, F. L., Bianchi, F. J. J. A. & Thies, C. 2008 Diversity of cereal aphid parasitoids in simple and complex landscapes. *Agr. Ecosyst. Environ.* **126**, 289–292. (doi:10.1016/j.agee.2008.01.024)
- 54 Purtauf, T., Thies, C., Ekschmitt, K., Wolters, V. & Dauber, J. 2005 Scaling properties of multivariate landscape structure. *Ecol. Indic.* **5**, 295–304. (doi:10.1016/j.ecolind.2005.03.016)
- 55 Leather, S. R. 1993 Overwintering in six arable aphid pests: a review with particular relevance to pest management. *J. Appl. Entomol.* **116**, 217–233. (doi:10.1111/j.1439-0418.1993.tb01192.x)
- 56 Hawkins, B. A. 1992 Parasitoid–host food webs and donor control. *Oikos* **65**, 159–162. (doi:10.2307/3544898)
- 57 Scherber, C. *et al.* 2010 Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**, 553–556. (doi:10.1038/nature09492)
- 58 Hawkins, B. A. & Cornell, H. V. 1994 Maximum parasitism rates and successful biological control. *Science* **266**, 1886. (doi:10.1126/science.266.5192.1886)
- 59 Höller, C., Borgemeister, C., Haardt, H. & Powell, W. 1993 The relationship between primary parasitoids and hyperparasitoids of cereal aphids: an analysis of field data. *J. Anim. Ecol.* **62**, 12–21. (doi:10.2307/5478)
- 60 Höller, C., Christiansen-Weniger, P., Micha, S. G., Siri, N. & Borgemeister, C. 1991 Hyperparasitoid–aphid and hyperparasitoid–primary parasitoid relationships. *Redia* **74**, 153–161.
- 61 Leslie, T. W., Van Der Werf, W., Bianchi, F. J. J. A. & Honěk, A. 2009 Population dynamics of cereal aphids: influence of a shared predator and weather. *Agric. Forest Entomol.* **11**, 73–82. (doi:10.1111/j.1461-9563.2008.00405.x)