

# Effect of plant species loss on aphid–parasitoid communities

Jana S. Petermann<sup>1\*‡</sup>, Christine B. Müller<sup>1†</sup>, Alexandra Weigelt<sup>2§</sup>, Wolfgang W. Weisser<sup>2</sup> and Bernhard Schmid<sup>1</sup>

<sup>1</sup>Institute of Evolutionary Biology and Environmental Sciences, University of Zurich, Winterthurerstr. 190, 8057 Zurich, Switzerland; and <sup>2</sup>Institute of Ecology, University of Jena, Dornburger Str. 159, 07743 Jena, Germany

## Summary

1. The consequences of species loss on ecosystem functioning within a single trophic level have been extensively studied. However, the loss of basal species is likely to have profound impacts on the abundance, richness and ecosystem functioning of species at higher trophic levels.

2. Here, we used experimentally established plant communities with a species richness gradient to study the effects of plant species loss on a multi-trophic insect community in the field. We measured densities and species richness of aphids and parasitic wasps (primary, secondary and facultative tertiary parasitoids of aphids) that naturally colonized the grassland plots.

3. Furthermore, we calculated two ecosystem functions: aphid load (the number of aphid individuals per host plant biomass used as a proxy for herbivory) and parasitism rate. We used structural equation models to explore pathways of direct and indirect effects of plant species richness on higher trophic levels.

4. We found that the densities and richness of species at all trophic levels were influenced by changes in plant species richness. The effects were rarely direct, but instead mediated by the abundance and species richness of aphid host plants and subsequent trophic levels.

5. The herbivore and primary parasitoid levels were most directly affected by changes in plant species richness, with highest insect densities and species richness occurring at intermediate plant species richness. The densities and species richness of secondary parasitoids declined linearly with plant species richness owing to sparser resources, resulting in shorter food chains in communities with the highest plant species richness.

6. Aphid load was highest at intermediate plant species richness and negatively affected by both host plant biomass and host plant species richness. Parasitism rate was mostly affected indirectly via aphid density and overall only weakly negatively related to plant species richness.

7. Our results demonstrate that plant species richness can have strong cascading effects up to high trophic levels. However, their direction may differ at the lower and higher ends of the plant species richness spectrum, cautioning against simplifying consequences of plant species loss for specialist food webs that may become limited by sparse resources at high plant richness.

**Key-words:** biodiversity effects, bottom–up control, herbivores, multi-trophic interactions, species richness

\*Correspondence author. E-mail: petermann@zoology.ubc.ca

†Christine Müller died on 7 March 2008. She is sadly missed.

‡Present address: Department of Zoology, University of British Columbia, 2370-6270 University Blvd., Vancouver BC, Canada V6T 1Z4

§Present address: University of Leipzig, Institute of Biology I, Johannisalle 21-23, 04103 Leipzig, Germany

## Introduction

The consequences of the prevalent loss of species have been thoroughly studied over the past decade. The effect of terrestrial plant species loss on primary productivity has certainly received most attention, with studies largely in agreement that a decline in plant species negatively affects ecosystem

functioning at the plant level (reviewed, e.g. by Hooper *et al.* 2005; Balvanera *et al.* 2006). However, studies have rarely considered diversity loss in a multi-trophic context (Duffy *et al.* 2007; Thébault, Huber & Loreau 2007). For example, the loss of plant species is likely to have profound bottom-up effects via cascading secondary extinctions and subsequent loss of ecosystem function at higher trophic levels (Joshi *et al.* 2004; Kagata & Ohgushi 2006; Thébault & Loreau 2006; Thébault *et al.* 2007; Schmid *et al.* 2009).

In fact, a large number of hypotheses regarding multi-trophic consequences of plant diversity loss exist, but they are often contradictory and rarely reflected in empirical results even for herbivores, the first trophic level above plants. For example, the classical resource concentration hypothesis and the enemies' hypothesis (Root 1973) predict high specialist herbivore loads at low plant diversity owing to a concentration of resources and a low efficiency of generalist predators. However, some studies have found exactly the opposite: weaker herbivory at low plant diversity (Prieur-Richard *et al.* 2002; Scherber *et al.* 2006), lower herbivore loads with increased host plant abundance (i.e. a resource dilution effect; Koricheva *et al.* 2000; Otway, Hector & Lawton 2005) and increased predator efficiency at low plant diversity (Aquilino, Cardinale & Ives 2005).

The higher the trophic level, the more complex are the predictions for plant diversity effects that have been proposed, especially because effects are often not direct but mediated by other trophic levels (Abrams *et al.* 1996; Siemann *et al.* 1998; Tschardt & Hawkins 2002; Dyer & Letourneau 2003; Dyer & Stireman 2003; Balvanera *et al.* 2006; Schmid *et al.* 2009; Viketoft *et al.* 2009). For example, direct effects of plant diversity on higher trophic levels could include effects of plant architecture (Root 1973; Hochberg & Hawkins 1992; Brose 2003; Langellotto & Denno 2004; Vanbergen *et al.* 2007) or floral resources (e.g. Langellotto & Denno 2004; Araj *et al.* 2008). Indirect effects could be mediated by density, species richness or life-history traits (e.g. body size) of the species at lower trophic levels (Abrams *et al.* 1996; Knops *et al.* 1999; Bukovinszky *et al.* 2008).

Although plant species richness is often assumed to underlie food web change across habitats (e.g. Perner *et al.* 2003; Unsicker *et al.* 2006; Albrecht *et al.* 2007; Macfadyen *et al.* 2009) it is rarely explicitly manipulated. However, to disentangle effects of plant species loss and correlated factors on higher trophic levels, controlled experiments are necessary. Few such experiments have been conducted and the most rigorous ones have been lab experiments (e.g. Aquilino *et al.* 2005). Field experiments typically only consider one, rarely two, trophic levels above the primary producers (e.g. Siemann *et al.* 1998; Knops *et al.* 1999; Mulder *et al.* 1999; Koricheva *et al.* 2000; Symstad, Siemann & Haarstad 2000; Haddad *et al.* 2001, 2009; Prieur-Richard *et al.* 2002; Otway *et al.* 2005; Scherber *et al.* 2006) or focus on single or few plant species out of the entire community (e.g. Prieur-Richard *et al.* 2002). Furthermore, almost all field studies associate herbivores, predators, parasitoids and plant communities based on co-occurrences (e.g. Siemann *et al.* 1998; Knops

*et al.* 1999; Koricheva *et al.* 2000; Haddad *et al.* 2001, 2009), rarely quantifying actual interactions between trophic levels. To address these shortcomings, this study examined quantified aphid-parasitoid food webs comprising three to four trophic levels above plants in a grassland field experiment that directly manipulated plant species richness (i.e. a random-loss scenario; Schmid & Hector 2004).

Aphids are attacked by primary parasitoid wasps that lay a single egg into their host's body. The aphids continue to feed for a few days before dying and developing into hard-shelled 'mummies' in which the primary parasitoid larva eventually pupates. Two guilds of secondary parasitoid wasps attack primary parasitoids: hyperparasitoids lay their egg into the developing primary parasitoid larva inside the living aphid and delay their development until the primary parasitoid larva has killed the aphid host; they are koinobiont endoparasitoids. Mummy parasitoids, however, lay their egg onto the primary parasitoid larva inside the dead and mummified aphid; they are idiobiont ectoparasitoids (Godfray 1994). Because hyperparasitoid larvae have to deal with the primary parasitoid's immune system, they are usually more specialized than mummy parasitoids (Müller *et al.* 1999; Bukovinszky *et al.* 2008). Mummy parasitoid larvae can furthermore feed on primary parasitoid larvae and hyperparasitoid larvae (facultative tertiary parasitism, Müller *et al.* 1999). Thus, mummy parasitoids represent a trophic level slightly above hyperparasitoids, that is, in our case a facultative fifth level in the community. With aphids being sedentary herbivores and all parasitoids being solitary (i.e. a single parasitoid developing from a single host), links between food web members can be established and fully quantified.

Aphid-parasitoid food webs are frequently used as ecological model systems for this reason (Müller *et al.* 1999), but also because they are important in an agricultural context (e.g. Schmidt *et al.* 2003; Brewer & Elliott 2004). Herbivory by aphids constitutes a central ecosystem function within the aphid-parasitoid community, albeit an unpopular one with farmers. Aphids can reduce crop yield considerably and aphid load, that is, in our case the number of aphids per biomass of the host plant, is typically positively correlated with the magnitude of plant damage (e.g. Larsson 2005). We therefore measured aphid load and used it as a proxy for aphid herbivory. Parasitism of aphids by parasitic wasps is another ecosystem function of the aphid-parasitoid community, but one that is promoted by farmers as biocontrol against aphids. These two important ecosystem functions could be affected by changes in plant diversity, either directly or indirectly via the density or richness of the involved organisms.

Here we report results from 47 quantified aphid-parasitoid food webs associated with experimental plant communities of varying plant species richness and test the following hypotheses: (i) the loss of plant species affects densities and species richness of all trophic levels; (ii) the loss of plant species has strong direct effects on lower trophic levels with indirect effects cascading up the food web; (iii) ecosystem

functions at higher trophic levels, such as herbivory (herbivore load) and parasitism are affected by a loss of plant species.

## Materials and methods

### EXPERIMENTAL DESIGN

This study was conducted at the site of the Jena Experiment, a large grassland biodiversity–ecosystem functioning experiment in Jena, Germany (Roscher *et al.* 2004). This experiment was established in 2002 on a former agricultural field in the floodplain of the Saale River. The plant species pool of the experiment used for this study contained nine dominant species from semi-natural, species-rich, mesophilic grassland typical of the area (Roscher *et al.* 2004, 2005). The 3.5- × 3.5-m plots did not receive fertilizer but were mown twice a year in June and September, a typical management regime for these grasslands. Among the nine species were five grasses [*Alopecurus pratensis*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Phleum pratense*, *Poa trivialis*, all plant nomenclature follows Rothmaler (2002)], two forbs (*Anthriscus sylvestris*, *Geranium pratense*) and two legumes (*Trifolium pratense*, *Trifolium repens*). Species richness levels were 1, 2, 3, 4, 6 and 9 plant species. Spontaneously colonizing plant species were removed by weeding to maintain the original species compositions. The plots were arranged into four blocks located at increasing distance from the river and at a distance of about 50 m from each other, with each block containing an equal number of plots (Roscher *et al.* 2004, 2005). Paths between the plots were sown with plant species that were not part of the experimental pool (*Festuca arundinacea*, *Poa compressa*, *Agrostis gigantea* and *Festuca rubra* ssp. *commutata*) and were kept short by frequent mowing. Plots belonging to another experiment (Roscher *et al.* 2004) and natural grasslands surrounded our plots.

Aphids naturally colonized four of the nine plant species in the experiment (*A. elatius*, *P. pratense*, *A. sylvestris* and *T. pratense*); so, we randomly selected plots containing at least one of these plant species at an abundance of >5% (based on cover estimates in May 2006). This selection resulted in 47 plots: 7 monocultures, 19 two-species mixtures, 7 three-species mixtures, 7 four-species mixtures, 4 six-species mixtures and 3 nine-species mixtures (Table S1). Nine of the plots were located in Block 1, 14 in Block 2, nine in Block 3 and 15 in Block 4. The unbalanced structure of the design, especially with regard to the number of replicates at each species richness level, limits the potential for interpretation and we have to exercise caution in drawing our conclusions, in particular regarding the high richness levels (see Discussion).

### DATA COLLECTION

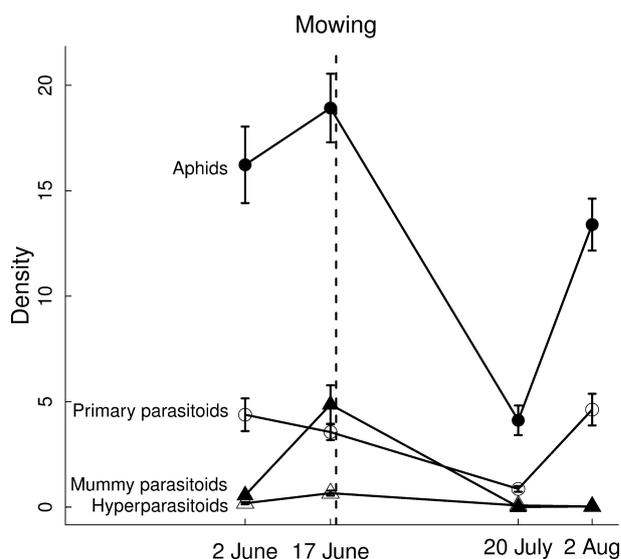
We counted naturally occurring aphids and collected parasitized aphids (mummies) four times from May (first appearance of aphids at the field site) to August 2006 (almost no aphids found after the fourth sampling period). Sampling was usually completed within 1 week and was carried out twice before the first mowing of the field site (around 2 June and 17 June) and twice between the first and the second mowing (20 July and 2 August). After the initial identification of all aphid species in the lab, aphids were identified *in situ* and counted on all plants along a transect of 3 × 0.2 m across the middle of the plot. Mummies were collected in the same transects at the same time and, additionally, in a larger area (usually 1.1 × 3.5 m) to be able to detect the entire parasitoid community of a plot. Mummies

were placed individually in gelatine capsules and kept in the lab until the emergence of the parasitoid. After 3 months at room temperature, non-emerged mummies were subjected to two cold (4 °C) periods of 1 month with a warm period of 1 month in-between to induce emergence. All emerged parasitoids were identified to the species level under a binocular microscope using specialist keys (e.g. Starý 1966, 1976; Fergusson 1980; Kavallieratos *et al.* 2005; Japoshvili & Abrantes 2006). Plant biomass was cut 3 cm above-ground in two randomly selected areas of 20 × 50 cm in the plots in May and August, just before mowing. The biomass was sorted to species level, dried to constant mass at 70 °C for 48 h and weighed (see also Roscher *et al.* 2005; Marquard *et al.*, in press).

### DATA ANALYSIS

Plant biomass, separated into the different host and non-host plant species, was summed over the whole season. Densities of aphids, primary parasitoids, hyperparasitoids and mummy parasitoids were used as sums over all sampling dates in the analyses but are shown separately for the sampling dates in Fig. 1. ‘Species richness’ is the total number of species in each group in the sampled area over all sampling dates. Although sampling was standardized by area, we additionally examined the effect of varying insect densities on insect species richness using individual-based rarefaction (Gotelli & Colwell 2001; Appendix S1).

Two ecosystem functions of aphid–parasitoid communities were considered in this study: aphid herbivory and parasitism. Because the effect of sucking insects on plants could not be measured directly, aphid load (the number of aphid individuals per host plant biomass) was used as a proxy for herbivory. Parasitism rate (the proportion of parasitized aphids) was calculated as the number of all parasitoids divided by the sum of the number of aphids and parasitoids. Secondary parasitoids were included in this rate because mummies from which secondary parasitoids emerged had originally been parasitized



**Fig. 1.** Mean insect density (individuals per square metre) ± SE for the four sampling periods in 2006 in all sampled plots. Aphids, filled circles (actual density scaled down by one order of magnitude); primary parasitoids, open circles; mummy parasitoids, filled triangles; hyperparasitoids, open triangles. The date of the mowing is indicated by a dashed line.

by primary parasitoids. Insect densities and richness were square-root-transformed whereas aphid load and parasitism rate were arc-sine-square-root-transformed prior to statistical analyses. Plot means of host plant biomass, insect densities and host plant and insect richness were analysed using multiple regression and analysis of variance, with the term 'block' fitted first in the model to account for spatial variation (ANOVA; for more details on statistical analyses in biodiversity experiments, see Schmid *et al.* 2002). The following model was used for all response variables: 'response variable'  $\sim$  'block' + 'plant species richness' + '(plant species richness)<sup>2</sup>'. Additional spatial variables (linear and squared *x*- and *y*-coordinates of the plots and their respective interactions) were fitted in initial models but their inclusion did not alter the results and they were omitted from final models.

Structural equation models (Hair *et al.* 1995) were used to separate direct and indirect effects of plant species richness on organisms and ecosystem functions at higher trophic levels. For these analyses, four *a priori* models based on our hypotheses, were constructed: first model for the effect of plant species richness on insect densities (Fig. S1), second for the effect of plant species richness on insect species richness (Fig. S1), third for the effect of plant species richness on aphid load (Fig. S2a) and a fourth model for the effect of plant species richness on parasitism rate (Fig. S2b). The first two models included all possible direct and indirect bottom-up paths to higher trophic levels. The only exception was the variable '(plant species richness)<sup>2</sup>', which we only expected (after the first analyses) to have an influence on aphids and primary parasitoids. Furthermore, we included covariances between mummy parasitoids and hyperparasitoids and between plant species richness and '(plant species richness)<sup>2</sup>'. The initial models for aphid load and parasitism rate were constructed according to results from the models for densities and species richness and *a priori* expectations. All initial models were based on correlation matrices and then simplified. Simplification and model selection followed standard procedures (Anderson & Gerbing 1988). Final models were evaluated by several goodness-of-fit statistics, such as the Tucker-Lewis Non-Normed Fit Index and the Comparative Fit Index (Hair *et al.* 1995). However, intermediate and final models were also assessed considering their biological coherence and meaningfulness. Because our sample size ( $n = 47$ ) is large for a multi-trophic study but small for using structural equation models (Kline 2005; Bentler 2006) our results cannot be interpreted as being confirmatory but rather have to be seen as being exploratory.

Several food web properties were calculated for the sampled communities (Bersier, Banasek-Richter & Cattin 2002). However, because all insect species proved to be highly host-specific at the field site during the study year, average link density was close to 1, connectance was highly negatively correlated with species richness and link diversity measures (e.g. the number, Shannon diversity and evenness of links) were identical to their species-based counterparts. Therefore, these metrics do not provide any additional information and are not presented.

Data were analysed with the free software R, version 2.7.2 (R Development Core Team, <http://www.r-project.org>), including the

SEM package version 0.9-12 for structural equation modelling (Fox 2006).

## Results

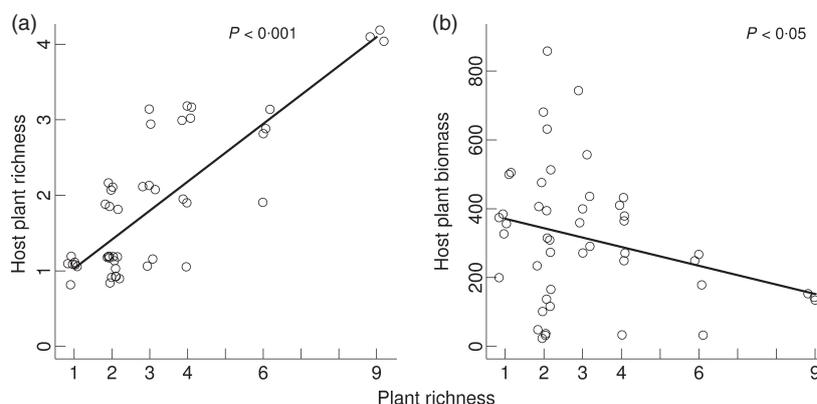
Aphids were parasitized by chalcidoid and ichneumonoid wasps, secondary parasitoids included cynipoid, chalcidoid and ceraphronoid wasps (complete species list in Table S2). In the study year, aphids appeared at the end of May after a cold spring (Fig. 1). Aphid densities peaked shortly before the first mowing in June and increased again after the plants had re-grown. The last aphids were observed on the plots shortly after the end of the fourth sampling period at the beginning of August. Primary parasitoid densities remained relatively constant throughout the year whereas secondary parasitoid densities showed a peak in June. Aphids and associated parasitoids were found on four host plant species in differing densities (Table 1), with highest aphid densities (individuals/square metre) on *P. pratense* and highest parasitoid densities on *A. sylvestris*. Only aphids on *P. pratense* were found throughout the season; all other aphids were restricted to one or two sampling dates. Almost all insect species in the aphid-parasitoid communities proved to be monophagous; very few species were oligophagous during our study. In total, 10 aphid species, 8 primary parasitoid species, 7 hyperparasitoid species and 7 mummy parasitoid species were found, with the highest aphid and parasitoid richness and the highest parasitism rate on *A. sylvestris*.

### OVERALL EFFECTS OF PLANT DIVERSITY

Host plant species richness (hereafter 'host plant richness') increased with increasing overall plant species richness (hereafter 'plant richness') as a feature of the experimental design. In contrast, total host plant biomass in the plots decreased linearly with increasing plant richness (Fig. 2 and Table 2). Aphid and primary parasitoid densities tended to show a unimodal relationship with plant richness, with maximum densities at intermediate plant richness levels (Fig. 3 and Table 2). Hyperparasitoid density was negatively affected by plant richness whereas mummy parasitoid density showed no relationship with plant richness. Aphid and primary parasitoid richness were again a unimodal function of plant richness; hyperparasitoid richness decreased linearly and mummy parasitoid richness did not change with changing plant richness. Although insect densities and species richness

**Table 1.** Mean densities  $\pm$  SE (individuals per square metre) of insects on the four host plants; sums over all sampling dates

Plant species	Aphids	Primary parasitoids	Hyperparasitoids	Mummy parasitoids
<i>Anthriscus sylvestris</i>	317 $\pm$ 77	14.6 $\pm$ 3.7	1.19 $\pm$ 0.46	11.56 $\pm$ 3.89
<i>Arrhenatherum elatius</i>	168 $\pm$ 49	8.3 $\pm$ 3.1	0.02 $\pm$ 0.02	0.02 $\pm$ 0.02
<i>Phleum pratense</i>	545 $\pm$ 132	4.9 $\pm$ 1.2	0.78 $\pm$ 0.48	0.06 $\pm$ 0.04
<i>Trifolium pratense</i>	109 $\pm$ 20	1.3 $\pm$ 0.5	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01



**Fig. 2.** (a) Host plant richness and (b) host plant biomass as a function of overall plant richness in the plots. For statistical analyses, see Table 2.

were correlated (see next and Fig. 7), insect richness was not solely a result of varying insect densities in the plots (Appendix S1, Fig. S3 and Table S3).

Ecosystem functioning in terms of aphid load and parasitism rate showed unimodal (aphid load) or weakly negative (parasitism rate) relationships with plant richness (Fig. 4). The effect of the presence of legumes in plant communities was tested as a separate contrast in initial analyses because this particular plant functional group has been shown to influence ecosystem functioning in terms of biomass production (e.g. Spehn *et al.* 2002) and life-history characteristics of aphids and parasitoids (Jana S. Petermann, unpublished data). However, legumes did not have important effects in any of these analyses, and thus the term was removed from the models.

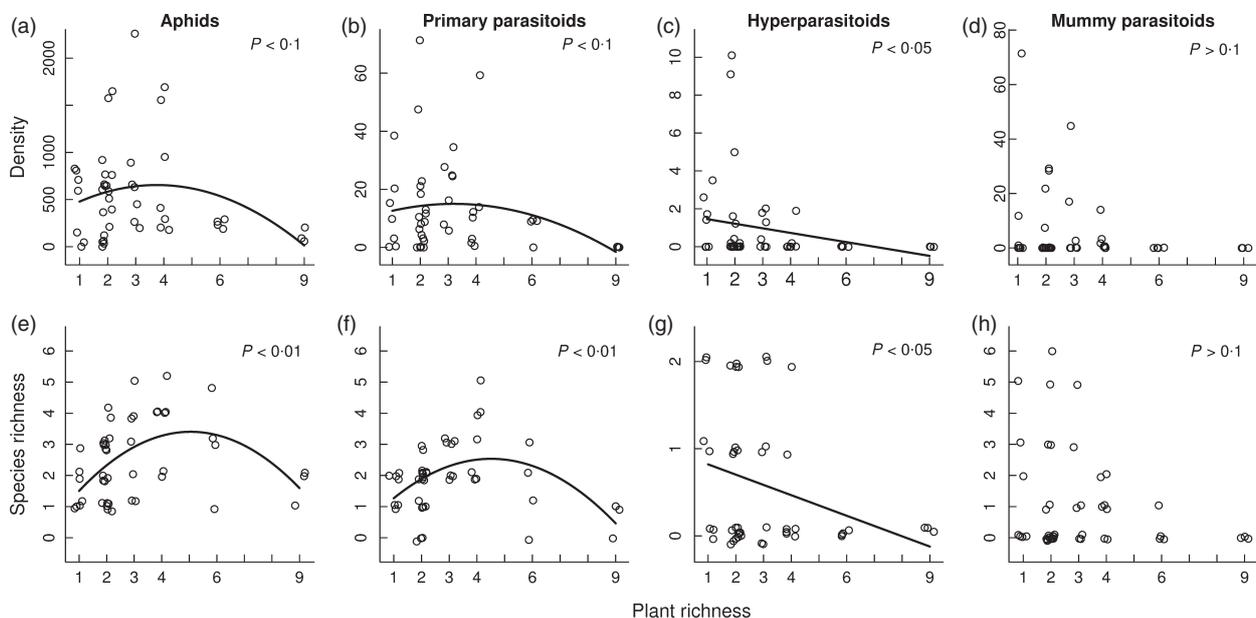
#### DIRECT AND INDIRECT EFFECTS OF PLANT DIVERSITY

Using structural equation modelling, we explored direct and indirect effects of plant richness on higher trophic levels. After sequential deletion of terms from the initial *a priori* models (Figs S1 and S2), we arrived at final models with minimal Bayesian information criteria scores and adequate fit (Hair *et al.* 1995). The most parsimonious model for the effects of plant richness on insect densities (Fig. 5a) indicated that all significant effects on higher trophic levels were indirect. Plant richness had an indirect positive effect on host plant biomass via increased host plant richness but a strong direct negative effect, resulting in the weak negative overall effect of plant richness on host plant biomass (Fig. 2b). Aphid density was positively influenced by primary

**Table 2.** Summary of regression models (with normal errors and identity link) testing the linear and quadratic effects of plant richness on the density and species richness of the organisms in the community and on ecosystem functions (aphid load and parasitism rate). The model formula was in all cases: 'response variable'  $\sim$  'block' + 'plant species richness' + '(plant species richness)<sup>2</sup>. Insect densities and richness were square-root-transformed whereas aphid load and parasitism rate were arcsine-square-root-transformed. Regression models on untransformed variables using other errors and link functions (Poisson models with log link for insect density and insect species richness and binomial models with logit link for aphid load and parasitism rate) produced similar results

Response	Res. d.f.	Plant richness			(Plant richness) <sup>2</sup>		
		%SS	<i>F</i>	<i>P</i>	%SS	<i>F</i>	<i>P</i>
<b>Density</b>							
Total host plant biomass	43	9.0	4.57	<b>0.038</b>	0.2	0.09	0.768
Aphids	43	3.4	1.66	0.204	6.9	3.37	<b>0.073</b>
Primary parasitoids	43	6.5	3.20	<b>0.081</b>	6.3	3.12	<b>0.084</b>
Hyperparasitoids	43	9.6	4.63	<b>0.037</b>	0.8	0.40	0.530
Mummy parasitoids	43	4.0	1.82	0.185	0.1	0.03	0.871
<b>Species richness</b>							
Host plants	43	67.2	96.57	<b>&lt; 0.001</b>	0.4	0.61	0.439
Aphids	43	1.6	0.90	0.348	19.5	10.97	<b>0.002</b>
Primary parasitoids	43	2.1	1.10	0.300	15.3	7.94	<b>0.007</b>
Hyperparasitoids	43	10.5	5.06	<b>0.030</b>	0.1	0.04	0.852
Mummy parasitoids	43	3.4	1.57	0.217	1.9	0.86	0.360
<b>Function</b>							
Aphid load	41	0.0	0.01	0.919	10.8	5.05	<b>0.030</b>
Parasitism rate	41	8.3	3.89	<b>0.055</b>	2.4	1.12	0.297

*P*-values  $< 0.1$  are given in bold. Res. d.f., residual degrees of freedom; %SS, per cent sum of squares explained.



**Fig. 3.** Density (individuals per square metre) and species richness of aphids, primary parasitoids and secondary parasitoids (hyperparasitoids and mummy parasitoids) as a function of plant richness in the plots. Note the different scale of axes for the different trophic levels. Fitted lines are drawn for relationships significant at  $P < 0.1$ . Untransformed data are shown but  $P$ -values refer to transformed data. For statistical analyses, see Table 2.

parasitoid density which in turn was positively influenced by densities of both groups of secondary parasitoids. There was no significant direct quadratic effect of plant richness.

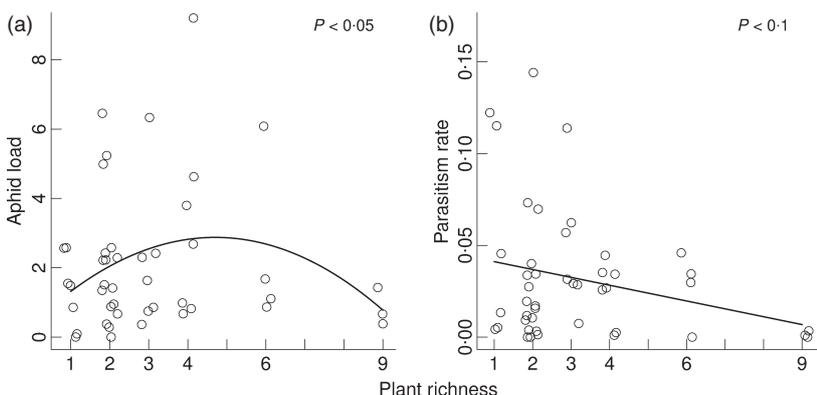
In contrast, insect species richness was not affected by changes in host plant biomass according to the final structural equation model (Fig. 5b). However, plant richness and host plant richness directly and indirectly influenced the richness of higher trophic levels. These effects were strongest at the herbivore level. Plant richness had a direct quadratic effect on aphid richness that resulted in the unimodal relationship (Fig. 3e). At the same time, host plant richness was found to have a strong positive linear effect on aphid richness. In general, species richness at trophic levels directly below the respective insect group showed strong positive influences, whereas direct effects from lower levels were either weakly positive or negative. The signs for direct and indirect effects were often opposing, leading to weak overall effects.

Aphid load was influenced by a number of variables in the structural equation model and showed a direct linear and

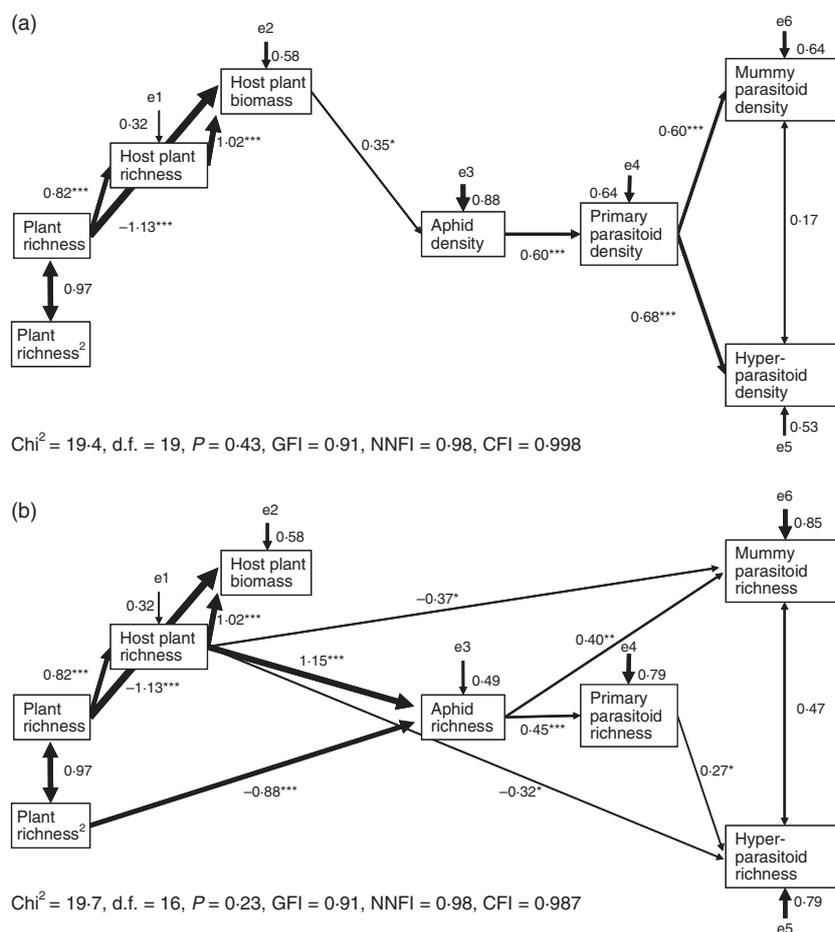
quadratic effect of plant richness, a negative effect of host plant richness and host plant biomass and a positive effect of aphid density (Fig. 6a). Aphid richness did not influence aphid load. Parasitism rate was expectedly strongly affected by primary parasitoid density and aphid density (Fig. 6b). However, there was an additional negative effect of host plant richness and a positive effect of primary parasitoid richness on parasitism rate. Plant richness appeared to have no direct effect on parasitism rate; instead indirect positive and negative effects nearly cancelled each other out, resulting in a weak negative overall effect of plant richness on parasitism rate (Fig. 4b).

#### CHANGES IN INSECT COMMUNITY STRUCTURE

Previously, we presented separate structural equation models for the effects of plant richness on insect densities and insect species richness. However, insect density and species richness were correlated at each trophic level (Fig. 7). The higher the



**Fig. 4.** (a) Aphid load (aphid individuals per host plant biomass) and (b) parasitism rate (proportion of parasitized aphids) as a function of plant richness in the plots. Untransformed data are shown but  $P$ -values refer to transformed data. For statistical analyses, see Table 2.



**Fig. 5.** Final, most parsimonious structural equation models for plant richness effects on: (a) insect density and (b) insect species richness. Insect density and species richness were square-root-transformed. Standardized path coefficients are given next to path arrows with significances depicted by \**P* < 0.05, \*\**P* < 0.01 and \*\*\**P* < 0.001. Unexplained variance is denoted by ‘e’ and double-headed arrows indicate covariance. All arrow widths are proportional to path coefficients. For initial *a priori* models, see Fig. S1. GFI, Goodness-of-Fit Index; NNFI, Tucker–Lewis Non-Normed Fit Index; CFI, Comparative Fit Index.

trophic level, the steeper the slope of the density–richness relationship on the log–log scale (aphids: slope = 0.12, *r* = 0.37, d.f. = 45, *t* = 2.71, *P* = 0.009; primary parasitoids: slope = 0.15, *r* = 0.56, d.f. = 40, *t* = 4.23, *P* < 0.001; hyperparasitoids: slope = 0.21, *r* = 0.73, d.f. = 16, *t* = 4.22, *P* < 0.001; mummy parasitoids: slope = 0.29, *r* = 0.89, d.f. = 17, *t* = 8.23, *P* < 0.001), that is, the stronger the decline in species richness with a similar decline in density.

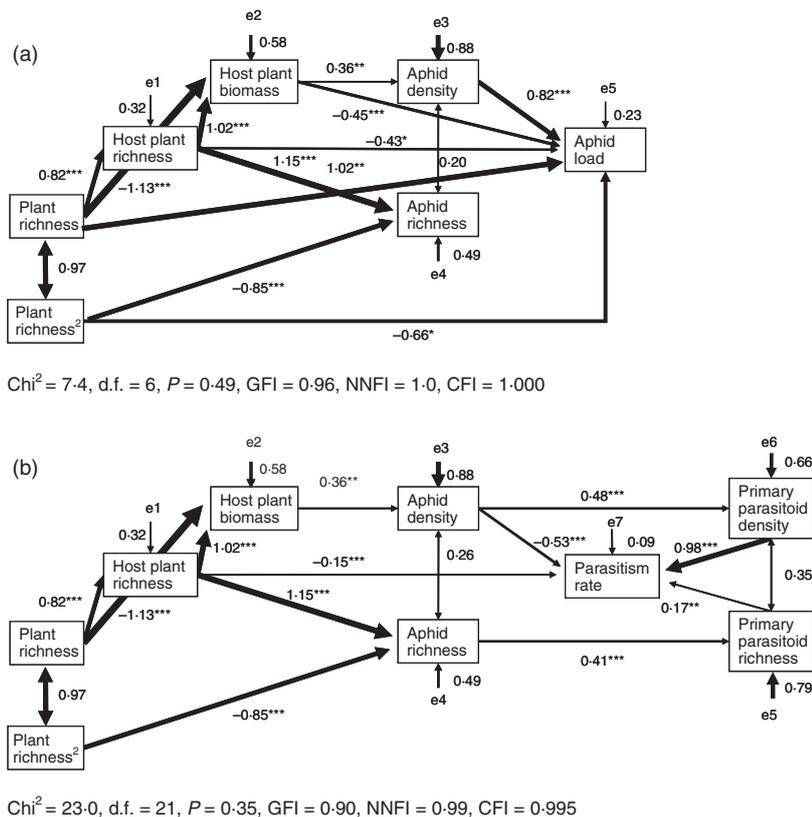
Insect densities at high trophic levels were generally low to start with and with increasing plant richness and associated decreases in host plant biomass, their densities declined (Fig. 3). The higher the trophic position, the lower the plant richness level at which this decline in density set in and the lower the plant richness level at which the insect species were absent from the community. The most dramatic insect community change could be seen in the six-species mixture where the facultative tertiary parasitoids (mummy parasitoids) did no longer occur, and then in the nine-species mixtures where the entire secondary parasitoid level was missing (Fig. 3g,h).

## Discussion

### APHID DENSITY AND SPECIES RICHNESS

Confirming our first hypothesis, plant richness in artificially established communities affected higher trophic levels of

plant–aphid–parasitoid food webs in the field. Furthermore, plant richness had more direct and stronger effects on lower levels of the food web, confirming our second hypothesis. Previous studies have found both positive and negative effects of plant richness on herbivore density, richness and herbivory (e.g. Siemann *et al.* 1998; Knops *et al.* 1999; Jactel & Brockerhoff 2007; Unsicker *et al.* 2008; Schmid *et al.* 2009). Nevertheless, most studies agree that specialist herbivores are predominantly controlled by the presence, density and richness of their host plants (Koricheva *et al.* 2000; Joshi *et al.* 2004; Otway *et al.* 2005; Jactel & Brockerhoff 2007). Indeed, we found that the density of aphids, a relatively specialized group of herbivores, was mainly driven by the biomass of their host plants. Overall, the opposing direct and indirect effects at the plant level were apparently responsible for the hump-backed relationships of aphid density and aphid richness with plant richness; that is, intermediate plant richness being most favourable for aphids. At the lower end of the plant richness gradient, aphids seemed to benefit from an increase in host plant richness. Towards the higher end, they were increasingly limited by low host plant biomass or potentially by the additional structure of non-host plants affecting the searching efficiency of winged aphid colonizers (e.g. Joshi *et al.* 2004). This conclusion is supported by the fact that aphids are generally inefficient at locating host plants (Dixon *et al.* 1987). However, we interpret the data



**Fig. 6.** Final, most parsimonious structural equation models for plant richness effects on: (a) aphid load (aphid individuals per host plant biomass) and (b) parasitism rate (proportion of parasitized aphids). Insect density and species richness are square-root-transformed whereas aphid load and parasitism rate are arcsine-square-root-transformed. Standardized path coefficients are given next to path arrows with significances depicted by \**P* < 0.05, \*\**P* < 0.01 and \*\*\**P* < 0.001. Unexplained variance is denoted by 'e' whereas double-headed arrows indicate covariance. All arrow widths are proportional to path coefficients. For initial *a priori* models, see Fig. S2. GFI, Goodness-of-Fit Index; NNFI, Tucker–Lewis Non-Normed Fit Index; CFI, Comparative Fit Index.

with caution because we sampled few species-rich plant communities and therefore, our data set is unbalanced with respect to the plant richness gradient.

Although this study focussed on bottom–up effects of plant richness on higher trophic levels, herbivores are not only controlled by their food plants but also by their predators and parasitoids (Hairston, Smith & Slobodkin 1960; Lawton & McNeill 1979). To assess the strength of these top–down effects and interactions between bottom–up and top–down forces, experiments that simultaneously manipulate species richness at lower and higher trophic levels are necessary. So far, such experiments have been scarce (but see Aquilino *et al.* 2005) and they are especially challenging to be performed in a field setting.

#### PARASITOID DENSITY AND SPECIES RICHNESS

We found that all higher trophic levels were influenced by changes in plant richness in our study, but rarely in a direct way. Densities of primary and secondary parasitoids seemed to be strongly dependent on the densities of their food sources. Likewise, primary and secondary parasitoid richness were driven by the species richness of their prey. Hence, their relationship with plant richness largely followed the relationship of aphid density and richness with plant richness. Richness-mediated indirect effects were typically stronger than density-mediated indirect effects, which is in accordance with the findings of previous studies (Siemann *et al.* 1998; Knops *et al.* 1999).

Plant richness had a negative overall effect on the highest trophic levels in our food webs, which was partly obscured by the indirect interactions. Although density and richness within a trophic level were correlated for all trophic levels, the higher the trophic level, the stronger the decline in species richness with a similar decline in density (steeper slopes of the density–richness correlations for primary and secondary parasitoids). Parasitoid densities in our plots were generally low: with a plot size of about 12 m<sup>2</sup>, the resulting parasitoid populations in each plot were usually supported by less than 100 newly emerging primary parasitoid individuals and even less secondary parasitoids over all sampling dates. When plant richness increased beyond a certain threshold, parasitoid densities dropped to very low levels and parasitoid species richness declined rapidly. The highest trophic level (secondary parasitoids) was even entirely absent from the communities with the highest plant richness, denoting a reduction of total food chain length as a result of low population sizes at top trophic levels.

While bearing the low sample size for communities with a high plant richness in mind, it still seems reasonable to believe that aphid population sizes in the 3.5- × 3.5-m patches of plant communities with a high species richness in our experiment were too low to sustain stable populations of specialist parasitoids (Kruess & Tschamtkke 1994). In a parallel study, we found that parasitoid emergence success and proportions of females decreased with increasing plant richness (Jana S. Petermann, unpublished data). This could have contributed to the observed decline in parasitoid abundance. However,

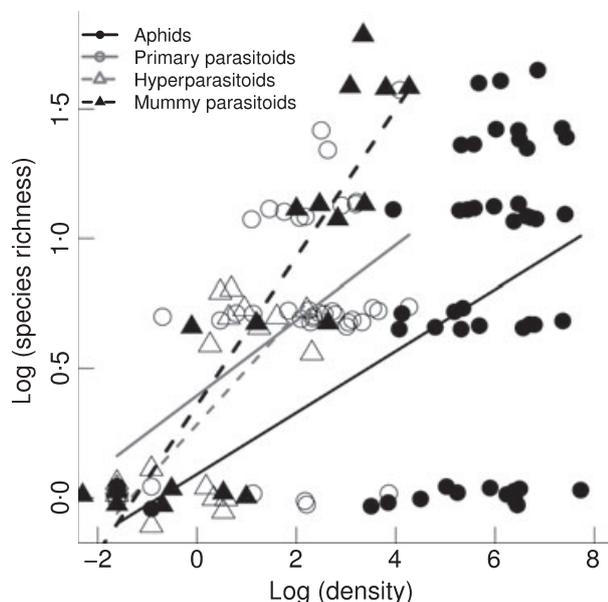


Fig. 7. Density–species richness relationships for the four insect groups on a log–log scale. Aphids, filled circles and black line; primary parasitoids, open circles and grey line; hyperparasitoids, open triangles and dashed grey line; mummy parasitoids, filled triangles and dashed black line. Fitted lines are drawn over the observed ranges of density. For statistical analyses, see text.

because parasitoids are usually more mobile than aphids, their abundance in the plots does not necessarily reflect demographic effects of habitat quality but may be rather a result of foraging behaviour. In this context, high surrounding plant richness could have led to a low detectability of small host populations, essentially creating refuges for aphids (Hochberg & Hawkins 1992).

All insect species in our aphid–parasitoid communities behaved as specialists. Aphids are a relatively specialized group of herbivores in general, and parasitoids typically show narrower host ranges than predators (Memmott, Martinez & Cohen 2000). However, the species we found may prove to be more generalized in the study area if communities are followed over several years (Petanidou *et al.* 2008). The results we obtained, especially the strong dependency of food webs on specific aphid host plants and the associated absence of certain species at higher trophic levels at high plant richness, obviously, only apply to the specialized aphid–parasitoid subcommunity within the total arthropod community.

A general caveat of our study that is shared with most published food web studies is its relatively short duration. However, by repeatedly sampling whole food webs in replicated plant communities across a diversity gradient we focused on covering as much within-season and between-community variability as possible. Several multi-season food web studies (usually two seasons) have found that although insect incidences and densities may vary, the species richness and food web properties generally remained stable across years (Müller *et al.* 1999; van Veen *et al.* 2002; Albrecht *et al.* 2007; Petanidou *et al.* 2008). Irregular aphid and parasitoid surveys at the field site in the following year support these findings

(Jana S. Petermann, personal observation). Nevertheless, studies sampling quantified aphid–parasitoid food webs at different plant richness levels repeatedly across several years would be greatly desirable.

#### ECOSYSTEM FUNCTIONING

In addition to the effects of plant richness on insect density and richness we measured the effects of plant richness on two ecosystem functions of the aphid–parasitoid system: aphid load and parasitism rate. Confirming our third hypothesis, these functions were influenced by plant richness. Similar to density and species richness of aphids, aphid load showed a unimodal relationship with plant richness. Furthermore, aphid load was negatively affected by host plant biomass and host plant richness but positively by plant richness, at least at lower plant richness levels. Previous studies have suggested that herbivore load or herbivory increase with host plant abundance as a result of the improved detectability of abundant hosts (the resource concentration hypothesis; Root 1973) and consequently decrease with plant richness (Knops *et al.* 1999). This hypothesis was sometimes used to explain devastating insect infestations in agricultural monocultures (reviewed by Andow 1991). However, the opposite, a decrease in herbivore loads with increasing host plant abundance, has recently been found in a biodiversity experiment (a resource dilution effect; Otway *et al.* 2005). In our study, aphid densities were positively influenced by host plant biomass but densities did not increase proportionally with host plant biomass; thus, aphid load declined with increasing host plant biomass, consistent with a resource dilution effect (Joshi *et al.* 2004; Otway *et al.* 2005). Population growth effects could be responsible for this result (Otway *et al.* 2005). Species-specific searching efficiency and arrival events could also explain the decreased herbivore load but these effects would have been masked in our community-level study.

Parasitism rate tended to decline with increasing plant richness and was negatively affected by host plant richness in our study, potentially as a result of decreased parasitoid searching efficiency or aphid quality (Jana S. Petermann, unpublished data). Furthermore, parasitism rate was negatively influenced by the density of hosts, indicative of a resource dilution effect at a higher trophic level. Aphid species richness did not have a clear effect on parasitism rates, even though resource diversity could be expected to influence ecosystem functioning at the next trophic level. However, this influence could either be positive owing to an increased resource partitioning potential (Tylianakis *et al.* 2008) or negative because of a stronger resistance or decreased parasitoid efficiency (Vos *et al.* 2001; Montoya, Rodriguez & Hawkins 2003; Schmid *et al.* 2009). Possibly, opposing mechanisms were operating simultaneously in our study. Indeed, primary parasitoids appeared to exhibit niche complementarity or facilitation because increasing primary parasitoid species richness increased parasitism rates (Cardinale *et al.* 2003; Aquilino *et al.* 2005).

In summary, we have shown that plant richness can influence all trophic levels of an aphid–parasitoid community. Whereas effects of plant richness on herbivore density and richness were direct and easily detectable, effects at higher trophic levels were generally mediated by lower trophic levels and obscured by positive and negative interactions between the respective organisms. Interestingly, food chains were shorter in communities of high plant richness, possibly because of the resource limitation and subsequently low population sizes of species at high trophic levels. As a result of changes in aphid and parasitoid density and richness, ecosystem functions performed by these insects were affected by plant species loss.

The results we obtained from experimental grasslands could be applied to agricultural settings, where, for example, promoting the species richness of the parasitoid community could provide benefits in terms of aphid biocontrol. One of our main findings is that bottom–up effects of plant species loss may cascade up to at least the fourth trophic level of the community. Thus, the assessment of effects of species loss on ecosystems should take multi-trophic interactions into account. In conclusion, very low plant richness is not only detrimental to ecosystem functioning at the plant level (Hooper *et al.* 2005) but also involves smaller and poorer aphid–parasitoid food webs. However, in patchy grassland communities of high plant richness, specialist insect populations experience a higher risk of extinction owing to low host abundance. Increasing habitat area and avoiding fragmentation is therefore essential for maintaining stable insect populations and species-rich aphid–parasitoid communities.

## Acknowledgements

The authors thank Frank van Veen for help with parasitoid identification, Anne Hausteiner for field work assistance and numerous gardeners and helpers for the maintenance of the field site. Ernst-Detlef Schulze provided scientific input at the start of the Jena Experiment and comments by Pascal Niklaus and two anonymous reviewers greatly improved the manuscript. The Jena Experiment is funded by the German Research Foundation (FOR 456) and supported by the Friedrich-Schiller-University of Jena and the Max-Planck-Institute for Biogeochemistry, Jena. Additional support was provided by the Swiss National Science Foundation (grant no. 31-65224-01 to B.S.).

## References

- Abrams, P., Menge, B.A., Mittelbach, G.G., Spiller, D. & Yodanis, C.L. (1996) The role of indirect effects in food webs. *Food Webs: Integration of Patterns and Dynamics* (eds G.A. Polis & K.O. Winemiller), pp. 371–395. Chapman & Hall, New York.
- Albrecht, M., Duelli, P., Schmid, B. & Müller, C.B. (2007) Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *Journal of Animal Ecology*, **76**, 1015–1025.
- Anderson, J.C. & Gerbing, D.W. (1988) Structural equation modeling in practice: a review and recommended two-step approach. *Psychological Bulletin*, **103**, 411–423.
- Andow, D.A. (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology*, **36**, 561–586.
- Aquilino, K.M., Cardinale, B.J. & Ives, A.R. (2005) Reciprocal effects of host plant and natural enemy diversity on herbivore suppression: an empirical study of a model tritrophic system. *Oikos*, **108**, 275–282.
- Araj, S.E., Wratten, S., Lister, A. & Buckley, H. (2008) Floral diversity, parasitoids and hyperparasitoids – a laboratory approach. *Basic and Applied Ecology*, **9**, 588–597.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.
- Bentler, P.M. (2006) *EQS 6: Structural Equations Program Manual*. Multivariate Software Inc, Encino, CA.
- Bersier, L.F., Banasek-Richter, C. & Cattin, M.F. (2002) Quantitative descriptors of food-web matrices. *Ecology*, **83**, 2394–2407.
- Brewer, M.J. & Elliott, N.C. (2004) Biological control of cereal aphids in North America and mediating effects of host plant and habitat manipulations. *Annual Review of Entomology*, **49**, 219–242.
- Brose, U. (2003) Bottom–up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, **135**, 407–413.
- 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.
- 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. *Ecology Letters*, **6**, 857–865.
- Dixon, A.F.G., Kindmann, P., Leps, J. & Holman, J. (1987) Why there are so few species of aphids, especially in the tropics. *The American Naturalist*, **129**, 580–592.
- Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thebault, E. & Loreau, M. (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, **10**, 522–538.
- Dyer, L.A. & Letourneau, D. (2003) Top–down and bottom–up diversity cascades in detrital vs. living food webs. *Ecology Letters*, **6**, 60–68.
- Dyer, L.A. & Stireman, J.O. (2003) Community-wide trophic cascades and other indirect interactions in an agricultural community. *Basic and Applied Ecology*, **4**, 423–432.
- Fergusson, N.D.M. (1980) A revision of the British species of *Dendrocerus* Ratzeburg (Hymenoptera: Ceraphronoidea) with a review of their biology as aphid hyperparasites. *Bulletin of the British Museum of Natural History (Entomology)*, **41**, 255–314.
- Fox, J.W. (2006) Structural equation modeling with the SEM package in R. *Structural Equation Modelling*, **13**, 465–486.
- Godfray, H.C.J. (1994) *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, NJ.
- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M. & Knops, J.M.H. (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist*, **158**, 17–35.
- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H. & Tilman, D. (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, **12**, 1029–1039.
- Hair, J.F., Anderson, R.E., Tatham, R.L. & Black, W.C. (1995) *Multivariate Data Analysis with Readings*. Prentice Hall, Englewood Cliffs, NJ.
- Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control and competition. *The American Naturalist*, **94**, 421–425.
- Hochberg, M.E. & Hawkins, B.A. (1992) Refuges as a predictor of parasitoid diversity. *Science*, **255**, 973–976.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeyem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Jactel, H. & Brockerhoff, E.G. (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters*, **10**, 835–848.
- Japoshvili, G. & Abrantes, I. (2006) *Aphelinus* species (Hymenoptera: Aphelinidae) from the Iberian Peninsula, with the description of one new species from Portugal. *Journal of Natural History*, **40**, 855–862.
- Joshi, J., Otway, S.J., Koricheva, J., Pfisterer, A.B., Alpehi, J., Roy, B.A., Scherer-Lorenzen, M., Schmid, B., Spehn, E.M. & Hector, A. (2004) Bottom–up effects and feedbacks in simple and diverse experimental grassland communities. *Insects and Ecosystem Function* (eds W.W. Weisser & E. Siemann), pp. 116–134. Springer, Berlin.
- Kagata, H. & Ohgushi, T. (2006) Bottom–up trophic cascades and material transfer in terrestrial food webs. *Ecological Research*, **21**, 26–34.
- Kavallieratos, N.G., Tomanovic, Z., Stary, P., Athanassiou, C.G., Fasseas, C., Petrovic, O., Stanisavljevic, L.Z. & Veroniki, M.A. (2005) *Praon* Haliday (Hymenoptera: Braconidae: Aphidiinae) of southeastern Europe: key, host range and phylogenetic relationships. *Zoologischer Anzeiger – A Journal of Comparative Zoology*, **243**, 181–209.

- Kline, R.B. (2005) *Principles and Practice of Structural Equation Modeling*. The Guilford Press, New York.
- Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarsstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E. & Groth, J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 286–293.
- Koricheva, J., Mulder, C.P.H., Schmid, B., Joshi, J. & Huss-Danell, K. (2000) Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia*, **125**, 271–282.
- Kruess, A. & Tscharntke, T. (1994) Habitat fragmentation, species loss, and biological control. *Science*, **264**, 1581–1584.
- Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.
- Larsson, H. (2005) A crop loss model and economic thresholds for the grain aphid, *Sitobion avenae* (F.), in winter wheat in southern Sweden. *Crop Protection*, **24**, 397–405.
- Lawton, J.H. & McNeill, S. (1979) Between the devil and the deep blue sea: on the problems of being an herbivore. *Population Dynamics* (eds R.M. Anderson, B.D. Turner & L.R. Taylor), pp. 223–244. Blackwell Scientific, Oxford.
- Macfadyen, S., Gibson, R., Polaszek, A., Morris, R.J., Craze, P.G., Planqué, R., Symondson, W.O.C. & Memmott, J. (2009) Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecology Letters*, **12**, 229–238.
- Marquard, E., Weigelt, A., Temperton, V.M., Roscher, C., Schumacher, J., Buchmann, N., Fischer, M., Weisser, W. & Schmid, B. (in press) Plant species richness and functional composition drive overyielding in a 6-year grassland experiment. *Ecology*, **90**, 3290–3302.
- Memmott, N.D., Martinez, N.D. & Cohen, J.E. (2000) Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology*, **69**, 1–15.
- Montoya, J.M., Rodriguez, M.A. & Hawkins, B.A. (2003) Food web complexity and higher-level ecosystem services. *Ecology Letters*, **6**, 587–593.
- Mulder, C.P.H., Koricheva, J., Huss-Danell, K., Högberg, P. & Joshi, J. (1999) Insects affect relationships between plant species richness and ecosystem processes. *Ecology Letters*, **2**, 237–246.
- Müller, C.B., Adriaanse, I.C.T., Belshaw, R. & Godfray, H.C.J. (1999) The structure of an aphid–parasitoid community. *Journal of Animal Ecology*, **68**, 346–370.
- Otway, S.J., Hector, A. & Lawton, J.H. (2005) Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *Journal of Animal Ecology*, **74**, 234–240.
- Perner, J., Voigt, W., Bahrmann, R., Heinrich, W., Marsteller, R., Fabian, B., Gregor, K., Lichter, D., Sander, F.W. & Jones, T.H. (2003) Responses of arthropods to plant diversity: changes after pollution cessation. *Ecography*, **26**, 788–800.
- Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P. & Pantis, J.D. (2008) Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters*, **11**, 564–575.
- Prieur-Richard, A.-H., Lavelle, S., Linhart, Y. & Dos Santos, A. (2002) Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. *Oecologia*, **130**, 96–104.
- Root, R.B. (1973) Organization of a plant–arthropod association in simple and diverse habitats: the fauna of Collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95–124.
- Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W.W., Schmid, B. & Schulze, E.-D. (2004) The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, **5**, 107–121.
- Roscher, C., Temperton, V.M., Scherer-Lorenzen, M., Schmitz, M., Schumacher, J., Schmid, B., Buchmann, N., Weisser, W.W. & Schulze, E.-D. (2005) Overyielding in experimental grassland communities – irrespective of species pool or spatial scale. *Ecology Letters*, **8**, 419–429.
- Rothmaler, R. (2002) *Exkursionsflora von Deutschland*. Spektrum, Heidelberg-Berlin.
- Scherber, C., Mwangi, P.N., Temperton, V.M., Roscher, C., Schumacher, J., Schmid, B. & Weisser, W.W. (2006) Effects of plant diversity on invertebrate herbivory in experimental grassland. *Oecologia*, **147**, 489–500.
- Schmid, B. & Hector, A. (2004) The value of biodiversity experiments. *Basic and Applied Ecology*, **5**, 535–542.
- Schmid, B., Hector, A., Huston, M.A., Inchausti, P., Nijs, I., Leadley, P.W. & Tilman, D. (2002) The design and analysis of biodiversity experiments. *Biodiversity and Ecosystem Functioning* (eds M. Loreau, S. Naeem & P. Inchausti), pp. 61–75. Oxford University Press, Oxford.
- Schmid, B., Balvanera, P., Cardinale, B.J., Godbold, J., Pfisterer, A.B., Raffaelli, D., Solan, M. & Srivastava, D.S. (2009) Consequences of species loss for ecosystem functioning: a meta-analysis of data from biodiversity experiments. *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective* (eds S. Naeem, D.E. Bunker, A. Hector, M. Loreau & C. Perrings), pp. 14–29. Oxford University Press, Oxford.
- Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. & Tscharntke, T. (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 1905–1909.
- Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist*, **152**, 738–750.
- Spohn, E.M., Scherer-Lorenzen, M., Schmid, B., Hector, A., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Jumpponen, A., O'Donovan, G., Pereira, J.S., Schulze, E.-D., Troumbis, A.Y. & Körner, C. (2002) The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos*, **98**, 205–218.
- Starý, P. (1966) *Aphid Parasites of Czechoslovakia. A Review of the Czechoslovak Aphidiidae (Hymenoptera)*. W. Junk, The Hague.
- Starý, P. (1976) *Aphid Parasites (Hymenoptera: Aphidiidae) of the Mediterranean Area*. W. Junk, The Hague.
- Symstad, A.J., Siemann, E. & Haarstad, J. (2000) An experimental test of the effect of plant functional group diversity on arthropod diversity. *Oikos*, **89**, 243–253.
- Thébault, E. & Loreau, M. (2006) The relationship between biodiversity and ecosystem functioning in food webs. *Ecological Research*, **21**, 17–25.
- Thébault, E., Huber, V. & Loreau, M. (2007) Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos*, **116**, 163–173.
- Tscharntke, T. & Hawkins, B.A. (2002) *Multitrophic Level Interactions*. Cambridge University Press, Cambridge.
- Tylianakis, J.M., Rand, T.A., Kahmen, A., Klein, A.-M., Buchmann, N., Perner, J. & Tscharntke, T. (2008) Resource heterogeneity moderates the biodiversity–function relationship in real world ecosystems. *PLoS Biology*, **6**, 947–956.
- Unsicker, S.B., Baer, N., Kahmen, A., Wagner, M., Buchmann, N. & Weisser, W.W. (2006) Invertebrate herbivory along a gradient of plant species diversity in extensively managed grasslands. *Oecologia*, **150**, 233–246.
- Unsicker, S., Oswald, A., Köhler, G. & Weisser, W. (2008) Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia*, **156**, 313–324.
- Vanbergen, A.J., Jones, T.H., Hails, R.S., Watt, A.D. & Elston, D.A. (2007) Consequences for a host–parasitoid interaction of host–plant aggregation, isolation, and phenology. *Ecological Entomology*, **32**, 419–427.
- van Veen, F.J.F., Müller, C.B., Adriaanse, I.C.T. & Godfray, H.C.J. (2002) Spatial heterogeneity in risk of secondary parasitism in a natural population of an aphid parasitoid. *Journal of Animal Ecology*, **71**, 463–469.
- Viketoft, M., Bengtsson, J., Söhlenius, B., Berg, M.P., Petchey, O., Palmborg, C. & Huss-Danell, K. (2009) Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. *Ecology*, **90**, 90–99.
- Vos, M., Berrocal, S.M., Karamaouna, F., Hemerik, L. & Vet, L.E.M. (2001) Plant-mediated indirect effects and the persistence of parasitoid–herbivore communities. *Ecology Letters*, **4**, 38–45.

Received 16 July 2009; accepted 27 January 2010  
Handling Editor: Frank van Veen

## Supporting Information

Additional Supporting Information may be found in the online version of this article.

### Appendix S1. Rarefaction.

**Fig. S1.** Initial *a priori* model for effects of plant richness on insect densities or insect species richness.

**Fig. S2.** Initial *a priori* model for effects of plant richness on: (a) aphid load (aphid individuals per host plant biomass); (b) parasitism rate (proportion of parasitized aphids).

**Fig. S3.** Rarefied species richness of: (a) aphids, (b) primary parasitoids, (c) hyperparasitoids and (d) mummy parasitoids as a function of plant richness in the plots.

**Table S1.** List of all 47 sampled plots with their block number, plot number, composition code, plant species richness, the presence of legumes, the presence of the nine plant species in the plant assemblage and the total host plant biomass (sum across all host plant species and both harvests in 2006)

**Table S2.** List of all species in observed plant–aphid–parasitoid communities, sorted by trophic level, with average densities across all

plots (biomass in gram per square metre for plants, individuals per square metre for aphids and parasitoids, sums over all sampling dates)

**Table S3.** Summary of regression models (with normal errors and identity link) testing the linear and quadratic effects of plant richness on the rarefied species richness (square-root-transformed) of the insects in the community

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.