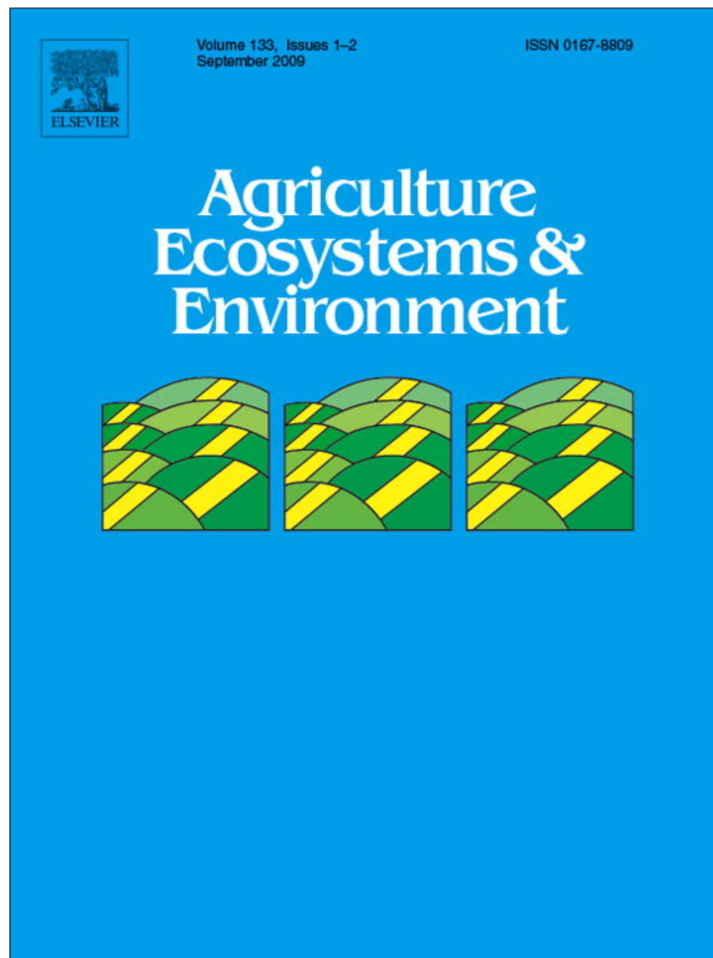
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Agriculture, Ecosystems and Environment 133 (2009) 14–18

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Parasitoid control of aphids in organic and conventional farming systems

Sarina Macfadyen [a,b,*], Rachel Gibson [b], Lorna Raso [c], Daniela Sint [c], Michael Traugott [c], Jane Memmott [b]

[a] CSIRO Entomology, Black Mountain, GPO Box 1700, Canberra, ACT 2601, Australia
[b] School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS6 7EU, UK
[c] Mountain Agriculture Research Unit, Institute of Ecology, University of Innsbruck, Technikerstrasse 25, A-6020 Innsbruck, Austria

ARTICLE INFO

Article history:
Received 31 December 2008
Received in revised form 3 April 2009
Accepted 19 April 2009
Available online 23 May 2009

Keywords:
Biological control
Natural enemies
Parasitoids
Sitobion avenae
Molecular parasitoid detection

ABSTRACT

Organic farmers cannot use most commonly available synthetic insecticides to control crop pests and reduce economic losses due to pest outbreaks. Instead, they rely heavily on the activities of naturally occurring predators and parasitoids, particularly in broad-acre crops such as cereals. It is still unclear whether organic farms which typically support greater levels of biodiversity also experience greater levels of pest control services. We assess whether organic farming systems were better able to control cereal aphids due to a greater diversity and activity of naturally occurring parasitoid species. We anticipated greater parasitism rate of aphids in organic arable fields due to closer proximity to plants that provide resources for adult parasitoids and places that are suitable for overwintering, and the presence of alternate aphid hosts when cereals are absent. Aphids were collected from organic and conventional cereal crops, and screened for parasitoid DNA using diagnostic polymerase chain reaction (PCR). Aphid abundance was low across the season, however organic cereal fields had significantly greater aphid abundance. From the 1446 aphids screened we detected 12 parasitoid taxa. There was no difference in parasitism rate between the farming systems (org. mean mortality 20.9 ± 3.3% s.e., con. 29.8 ± 4.9%). Furthermore, there was no difference between farming systems in hyperparasitoid attack and multi-parasitism rates, parasitoid richness and parasitoid community diversity. The most abundant species recorded on organic and conventional farms was the generalist aphid primary parasitoid *Ephedrus plagiator*. It appears that the extra plant diversity and greater area of semi-natural habitats on organic farms offer no advantage for increasing cereal aphid parasitoid diversity, at least at the aphid abundances encountered during the sampling period.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

When pests such as aphids attack annual crops their populations are most often controlled by the use of synthetic insecticides. Alternative techniques such as the use of resistant crop varieties, barriers, and introduced biological control agents (e.g. lacewing larvae) can be very effective for aphid control in greenhouse crops (Zehnder et al., 2007). However for broad-acre crops such as cereals, a greater emphasis on naturally occurring predators and parasitoids is necessary to reduce reliance on synthetic insecticides. There are few successful examples of the control of aphids in annual crops, and this may be due to the fact that specialist parasitoid populations must invade from some other habitat in each growing season (Murdoch et al., 2006). This process can take time and allow aphid populations to build up undisturbed. This has led some to conclude that generalist natural enemies that utilize a range of prey and so can exist year-round may be more important for aphid control particularly early in the season (Symondson et al., 2002; Murdoch et al., 2006). However, Schmidt et al. (2003) found that parasitoids were more important than generalist predators for the control of aphids in wheat fields in Germany. Furthermore, Langer et al. (1997) showed that parasitoids that are active early in the year are important to avoid high aphid densities.

A gradual loss in biodiversity from intensive agricultural landscapes has been shown to be associated with the loss of some important ecosystem services (Biesmeijer et al., 2006; Costanza et al., 2007). Naturally occurring pest control is one example of a free ecosystem service that is a result of the interactions between species within a complex community of prey and natural enemies. Organic farming practices, characterized by high proportions of semi-natural habitat on farms (Langer, 2001), greater plant diversity (Gibson et al., 2007) within arable fields and reduced pesticide usage (Lampkin, 1999), are thought to lead to increased diversity of up to 30% for some taxa (Bengtsson et al., 2005; Hole et al., 2005). Pest control by naturally occurring predators and parasitoids occurs on both organic and conventionally managed farms; however, organic farmers rely more heavily

* Corresponding author at: CSIRO Entomology, Black Mountain, GPO Box 1700, Canberra, ACT 2601, Australia.
E-mail address: sarina.macfadyen@csiro.au (S. Macfadyen).

0167-8809/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.agee.2009.04.012

Author's personal copy

on this service as they cannot use synthetic insecticides to control insect pest outbreaks (Lampkin, 1999). We would expect parasitism rate of aphids in organic arable fields to be greater due to the closer proximity of alternative plants that provide resources for adult parasitoids, the presence of alternate aphid hosts on these different plant species when cereals are absent, and closer proximity to places that are suitable for overwintering (Langer, 2001).

The better characterization of the complex relationships between aphid hosts, their parasitoid community, and the provision of ecosystem service of pest control is essential for understanding their efficacy in different farming systems. This approach could provide the data needed to more fully exploit the potential pest control advantages of parasitoids in both conventionally and organically managed systems alike. We collected aphids from cereal crops on replicate organic and conventional managed farms and used a novel DNA-based technique to identify endoparasitoids. Traditional rearing techniques require little specialist equipment, but maintaining individuals in the laboratory, and subsequent taxonomic identification can be very time consuming. Moreover, parasitism rates established by rearing can be biased by the host and parasitoid mortality encountered when maintaining individuals in the laboratory (Gariepy et al., 2008). In contrast DNA-based techniques require specialist equipment, and can be costly to set-up, however once developed they offer an efficient and reliable technique for screening large numbers of hosts to determine parasitism rate and parasitoid species diversity (Greenstone, 2006; Traugott et al., 2008). Molecular approaches also allow detection of the species involved in multiparasitism and hyperparasitism, though it remains unclear which species would eventually emerge from the host. Here we screen cereal aphids from organic and conventional fields for parasitoid DNA to determine if farming system has an impact on aphid parasitism rates and parasitoid community assemblage.

2. Materials and methods

Twenty farms (10 organic and 10 conventional) located around the city of Bristol in southwest England were selected for the study (Gibson et al., 2007; Macfadyen et al., 2009). Organic farms had been certified as organic for an average of 7.3 years at the start of the study. Cereal crops (mostly winter wheat, and to a lesser extent spring barley) were sampled in summer 2007 from the time of ear emergence until too ripe to support aphid feeding (beginning of June to end of July). Only 7% of the transects in which aphids were present were in barley fields (the other 93% were in wheat) and there was no difference in sowing time (spring versus winter) between the farming systems. Gibson et al. (2007) showed that overall the organic farms in this study contained less total area of arable fields than conventional farms however the diversity of crop types was not different. Insecticide use on the conventional farms was sporadic in the years preceding the aphid sampling (one farm sprayed in 2006 to control midge, and two farms sprayed in 2004/2005 to control aphids). Each farm was sampled three times throughout the growing season, and a pair of farms was sampled in a day, with the treatment sequence alternating (organic in morning then conventional in afternoon, next visit conventional in morning then organic in afternoon, etc.). Up to three cereal fields per farm (some farms only contained one or two cereal fields) were sampled, and within each field, a transect (30 m × 1 m) was laid out starting at least 10 m in from the field edge. Within each transect two ears per m^2 were systematically checked for the presence of aphids. If colonized ears were found they were collected in individual polythene bags, and chilled for transportation back to the laboratory. The transect and surrounding crop were then searched for a further 30 min, or until 20 ears with aphids were collected. After being transported back to the laboratory, the aphids were transferred into individual 1.5 mL centrifuge tubes and frozen at −40 °C.

2.1. Rearing parasitoids from field-collected aphids

Parasitoids were reared from field-collected aphids to evaluate and extend a previously developed molecular detection system for aphid parasitoids (Traugott et al., 2008). Up to 10 ears with aphids per field were collected and transported back to the laboratory. Each ear was placed in an individual 50 mL plastic vial, and sealed with fine horticultural fleece. A moist paper towel was laid across the tops of the vials to increase the moisture levels inside the vials. The vials were maintained until adult parasitoids emerged or all aphids died. Aphid mummies collected from the field were placed in clear capsule containers with the minimal amount of plant material and stored until an adult parasitoid emerged. The parasitoid rearing yielded 51 individuals which were identified by Dr. Ines Vollhardt (University of Göttingen, Germany).

2.2. DNA extraction from field-collected aphids

Aphid samples were stored before DNA extraction below −27 °C. DNA of field-collected aphids was extracted by adding 47 μL phosphate buffered saline (PBS, Sigma), 3 μL Proteinase K (20 mg/mL, Sigma) and glass balls (5–6 balls Φ 1 mm, 1 ball Φ 3 mm) to a 1.5 mL Eppendorf tube. Samples were milled using a ball mill (MM301, Retsch, Germany) for 2 min at 30 Hz. After a 1 min spin at 13,000 rpm, 200 μL of a 10% Chelex (BioRad) solution was added and samples incubated overnight at 56 °C. Thereafter samples were heated to 94 °C for 15 min and then stored at −28 °C. Within each batch of 48 samples one extraction negative control was included. Controls were tested with aphid- and *Aphidius*-specific primer pairs (see below) to test for potential carry-over of DNA between samples. All extractions and pre-PCR work were done in a pre-PCR laboratory.

2.3. Screening aphids for parasitoid DNA

New primer pairs were designed from mitochondrial cytochrome oxidase subunit I (COI) gene sequences following the procedure described in Traugott et al. (2008). No primers were developed for the hyperparasitoids *Phaenoglyphis* sp. and *Asaphes vulgaris*. In the former species this was due to the fact that only one individual was reared from the aphids collected at the different farms, indicating its minor importance. In *A. vulgaris* high intraspecific variability in the mtCOI gene prohibited the design of species-specific primers (see Traugott et al., 2008). The primers used for *Praon gallicum* (S123/A127) and *Praon volucre* (S117/A119) as well as the primer pair targeting the hyperparasitoid *Dendrocerus carpenteri* (S120/A122) (for details see Traugott et al. (2008)) were substituted in the present study's multiplex PCR by group-specific primer pairs S126/A130 and S148/A144 targeting two *Praon* species (*P. gallicum* and *P. volucre*) and two *Dendrocerus* species (*D. carpenteri* and *D. aphidium*), respectively (Table 1, Fig. 1). Moreover, a species-specific primer pair for *D. aphidium* (S130/A131, see below) was developed.

A multiplex PCR system was developed to simultaneously detect DNA from several parasitoid taxa within one reaction. Each 10 μL multiplex PCR reaction mix contained 1.5 μL of extracted DNA, 1× multiplex PCR master mix (Qiagen), 2 μL of PCR-water (Qiagen), 0.5 μL bovine serum albumin (BSA, 10 mg/mL, Sigma) and the primers at their respective concentration (Table 1). The cycling conditions were 15 min at 95 °C, 35 cycles of 30 s at 94 °C, 1.5 min at 62.5 °C, 1.5 min at 72 °C and final elongation for 10 min at 72 °C. Within all PCRs 1:6 diluted DNA of the target species was

Author's personal copy

Table 1
Primer pairs designed from mtDNA COI sequences of primary and secondary aphid parasitoid species as well as a primer pair targeting the grain aphid *Sitobion avenae*. Columns show the primer targets, primer names (S and A denotes forward and reverse primers, respectively), sequences, the expected product size, and the concentration (con.) of the primers used within the multiplex PCR. The primer pair for *Aphidius*-group targets five *Aphidius* species (*A. ervi*, *A. picipes*, *A. rhopalosiphi*, *A. uzbekistanicus*, *Aphidius* sp.), the *Praon*-group pair targets *P. gallicum* and *P. volucre*, and the *Dendrocerus*-group pair targets *D. carpenteri* and *D. aphidium*.

Target	Primer names & sequences (5′–3′)	Size (bp)	Con. (μM)
Aphidius-group	S108: TRACWYTAGGDCATAGAGGTGTAG A107: GCTCCTGCTAAAACAGGTAAT	215	0.2
Ephedrus plagiator	S115: GGATCAGATATAGCTTTCCCA A115: CATCCAGTTCCAACACCAT	114	0.2
Praon-group	S126: GKATACCTGGWAGATTAATTGGAAG A130: CTAAATCTACAGAAATTCCYCTATGTCTA	313	0.2
Alloxysta victrix	S119: GATATAGCTTTCCCTCGTCTT A121: CCGGCCAATACAGGTAAT	342	0.2
Dendrocerus-group	S148: CCTTAACKTCTAAYYTAAGMCACGC A144: ATGGTTTTATTATCARTARAGTTGAYAA	130	0.6
Sitobion avenae	S101: ATTAGATTTTGAYTACTACCACCA A103: TCTCCTCCTCCTGCTGGA	383	0.4

included as a positive control as well as a minimum of six negative controls (PCR-H_2O substituting DNA). Note that the multiplex PCR included a *Sitobion avenae*-specific primer pair to test for false-negative PCR results (see Traugott et al., 2008). To account for other cereal aphid species, all samples which failed to produce an amplicon with the *S. avenae*-specific primer or the parasitoid primers were tested with general metazoan primers as described in Traugott et al. (2008) and those samples which did not amplify were excluded from the analysis.

Samples testing positive with a group-specific primer were assayed with species-specific primers in singleplex PCR to identify the parasitoid species present in the aphid sample. In addition to the species-specific parasitoid primers given in Traugott et al. (2008), primer pair S130/A131 (S130: 5′-GACTCTTACCCCCTTCTT-TATTAC-3′; A131: 5′-TAAAAATTGATCAACAAAATAATGAG-3′) amplifying a 261 bp DNA fragment was used to identify *D. aphidium*. Singleplex PCRs were carried out in 10 μL reaction volumes containing 1.5 μL of DNA, 0.2 mM dNTPs (Invitrogen), 1 μM of each primer, 1 μL 10× buffer (Invitrogen), 3 mM $MgCl_2$ and 0.75 U Taq DNA polymerase (Invitrogen). Initial denaturation was done at 94 °C for 2 min, followed by 35 cycles at 94 °C for 20 s, 62.5 °C for 30 s, 72 °C for 1 min and final elongation at 72 °C for 3 min.

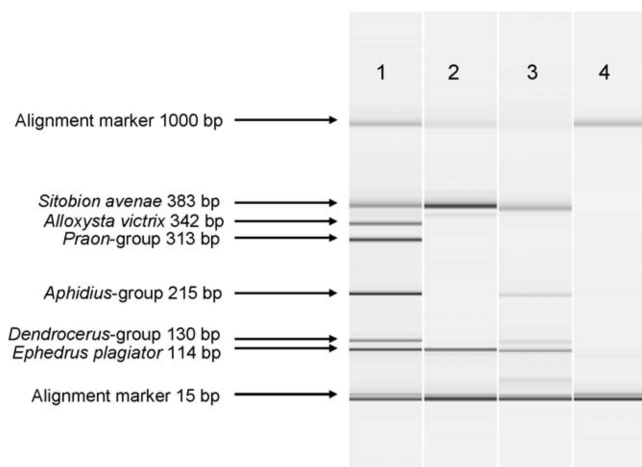


Fig. 1. Multiplex PCR products separated and visualized by QIAxcel. Lane 1 shows a DNA mixture of the six target species used as PCR template, lanes 2 and 3 show PCR-products from field-collected aphids, lane 4 shows negative control (DNA substituted by ddH_2O).

All PCRs were carried out in Eppendorf Mastercyclers. Multiplex PCR products were separated and detected using the QIAxcel System (Qiagen). Electropherograms were analyzed and scored using BioCalculator Fast Analysis Software version 3.0 (Qiagen). Singleplex PCR products were separated on ethidium bromide-stained agarose gels and visualized using a UV light-transiluminator. Besides the cross-reactivity tests described in Traugott et al. (2008) all primers used in this study were tested for their specificity against DNA from *Phaenoglyphis* sp. and *D. aphidium*. All primers proved to be specific for their respective target species/group of species.

2.4. Data analysis

As multiple fields were sampled within one farm (so each field was not independent) aphid abundance and parasitism rate were compared on a per farm basis. Aphid abundance was calculated per metre for each cereal field sampled then averaged across all fields per farm. Aphid abundance from organic and conventional fields was compared using nonparametric Mann–Whitney *U*-test. Parasitism rate was calculated per farm. The number of aphids that scored positive for one or more parasitoid genera was divided by the total number of aphids screened per farm. A binomial generalized linear model (GLM) in GenStat (logit link function) was used to compare the total number of aphids collected per farm to the numbers of parasitized aphids. This approach allowed us to account for variation in host abundance when calculating parasitism rate.

A MANOVA was used to test if there was an effect of farming system on the numbers of aphids which contained primary parasitoids (only 1 parasitoid species per aphid, after excluding aphids with hyperparasitoids), multiple parasitoid species (>1 parasitoid species per aphid, after excluding aphids with hyperparasitoid species), and hyperparasitoids (aphids parasitized by *Alloxysta victrix*, *D. carpenteri* or *Dendrocerus* sp.). The influence of farming system on parasitoid assemblage was tested by MANOVA using the species level identifications (12 taxa) and then by lumping to the genera level (5 taxa). The analysis used the total number of times each species or genus was detected per farm. For both MANOVA's the data was $\log_{10}(x+1)$ transformed prior to analysis and a single conventional farm was removed because of low numbers. The number of parasitoid taxa per farm, and the number of times each taxa produced a positive result in the PCR assay (a surrogate for abundance) were used to calculate the Shannon diversity index for each farm. A nonparametric

Author's personal copy

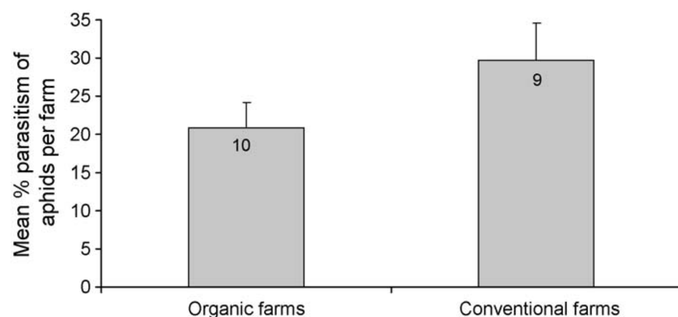


Fig. 2. Mean parasitism rates of aphid hosts in organic and conventional cereal fields. Organic and conventional farms in the southwest of England were sampled for aphids during the summer cropping season. 10 organic farms and 10 conventional farms were sampled. Data from one conventional farm was removed due to low aphid numbers. Diagnostic PCR was then used to detect parasitoid DNA within each individual host. Lines above the bars represent standard error and the number within the bars shows the number of farms sampled.

Mann–Whitney *U*-test was used to compare the diversity indices between the farming systems. Aphids from which DNA did not amplify were removed from the dataset. Samples that scored positive using genera-specific primers but failed to work with the species-specific primers were included in the parasitism rate calculations and grouped into genera.

3. Results

Aphid abundance was low in both farming systems never reaching one aphid per metre in cereal fields (mostly winter wheat and spring barley). Organic cereal fields had significantly greater aphid abundance per metre (org. mean 0.29 ± 0.055 s.e., con. 0.13 ± 0.017, $Z = -2.798$, $P < 0.01$). Amplifiable DNA could be extracted from a total of 1446 aphids (identified as *S. avenae*) and these were screened using diagnostic PCR (mean org. 98.6 per farm $\pm$ 18.8 s.e., con. 50.4 ± 7.2). The percentage of parasitized aphids ranged between 1.2% and 43.6% per farm (mean parasitism rates shown in Fig. 2), but the binomial GLM showed no difference in parasitism rate (predicted mean proportions org. = 0.232, s.e. = 0.035, con. = 0.264, s.e. = 0.054, analysis of deviance assuming binomial errors $P = 0.623$) between the farming systems. There was no significant influence of the farming system on primary parasitism (org. 14.7%, con. 21.2%), multiparasitism (org. 2.1%, con. 3.9%), and hyperparasitism (org. 4.1%, con. 4.7%) (Wilk's Lambda = 0.881, $P = 0.555$).

The molecular approach allowed us to detect 12 taxa of aphid parasitoids (Table 2). The most abundant species recorded on organic and conventional farms was the generalist aphid primary parasitoid *Ephedrus plagiator*. There was no significant difference in the parasitoid assemblage on organic versus conventional farms at the species level (Wilk's Lambda = 0.188, $P = 0.177$) and at the genera level (Wilk's Lambda = 0.749, $P = 0.526$). There was no difference between organic and conventional farms in the number of parasitoid taxa per farm (org. mean 5.90 ± 0.87 s.e., con. mean 5.70 ± 0.75, $P = 0.821$), and Shannon diversity index per farm (org. mean = 1.35 ± 0.16 s.e., con. mean = 1.43 ± 0.19, $P = 0.818$).

4. Discussion

We found no difference between organic and conventional fields in the level of cereal aphid mortality due to parasitoids, the levels of primary parasitism, hyperparasitism and multiparasitism, or parasitoid diversity. There were significantly more aphids in organic cereal fields, however overall aphid populations were low on all farms during the study. Previous studies have shown that arthropod abundance and diversity generally increases in organically managed fields, however there is large variation in response across taxa (Hole et al., 2005). A meta-analysis by Bengtsson et al. (2005) suggested that natural enemies are negatively affected by conventional management to a larger extent than other insects. However, we did not see an increase in cereal aphid parasitoid diversity in organic fields in our study. A whole-farm level analysis of these farms suggest that overall parasitoid diversity (across a range of groups) is greater on organic farms, however this does not necessarily translate into the greater provision of ecosystem services such as pest control on organic farms (Macfadyen et al., 2009). Parasitism rate across a range of herbivore hosts (Lepidoptera and Diptera) also showed no difference with respect to farming system (Macfadyen et al., 2009).

The landscape context in which the study was based may have had an influence on the results obtained. The region is relatively heterogeneous and clear differences between diversity on organic and conventional farms may be more obvious in more homogeneous landscapes (Roschewitz et al., 2005a; Rundlof et al., 2008). However, Roschewitz et al. (2005b) found that organic farming was related to a lower abundance of cereal aphids, but not higher parasitism. Furthermore, Vollhardt et al. (2008) found that arable fields in high intensity agricultural landscapes, with little non-crop area, supported a similar diversity of cereal aphid parasitoids (collected via sweep netting) as those in structurally complex landscapes. The authors attributed this result to the fact that in intensive cereal production landscapes these parasitoids do not require alternative aphid hosts, on other plant species, and so are capable of finding all necessary resources even in simple

Table 2
Parasitoid taxa found parasitizing cereal aphids on organic and conventional farms. The final two columns show the proportion (as a percentage) each species represents of the total number of parasitoids returning a positive in the PCR assay. Data from all 10 organic farms and 10 conventional farms were combined. The genus only identifications indicate parasitoids that were amplified using the group-specific primers but not with species-specific primers.

Parasitoid species	Family	Organic	Conventional
Alloxysta victrix^{H}	Alloxystidae	1.46	0.65
Aphidius ervi	Braconidae	7.30	20.00
Aphidius picipes	Braconidae	2.19	7.10
Aphidius rhopalosiphi	Braconidae	4.74	9.03
Aphidius sp.	Braconidae	12.41	14.19
Aphidius uzbekistanicus	Braconidae	0.73	0.65
Ephedrus plagiator	Braconidae	39.78	30.32
Praon gallicum	Braconidae	0.36	0.65
Praon sp.	Braconidae	11.31	1.29
Praon volucre	Braconidae	5.84	3.87
Dendrocerus carpenteri^{H}	Megaspilidae	10.22	10.32
Dendrocerus sp.^{H}	Megaspilidae	3.65	1.94

H: Hyperparasitoid species.

Author's personal copy

landscapes. If this is the case then the greater plant diversity seen in organic cereal fields (Gibson et al., 2007) and the greater area of semi-natural habitats on these organic farms (average 13.6 ± 1.4% of total farm area for organic farms and 7.8 ± 1.3% for conventional farms, Gibson et al., 2007) would have little impact on parasitoid diversity. The relatively high levels of aphid mortality (up to 44% parasitism per farm), suggests that all farms, regardless of farming system, had adequate levels of parasitoid activity at least at the aphid abundances encountered while sampling. This is further supported by the fact that aphid populations in both farming systems were below the threshold of 1–7 aphids/tiller suggested as the point at which economic losses occur (Larsson, 2005). Bianchi and Van Der Werf (2003) found that landscapes with 9–16% non-crop habitat provided enough resources for local populations of ladybeetles to control aphid outbreaks. If aphid parasitoids require a similar area of non-crop resources the majority of farms used in this study would meet this minimum threshold.

By detecting parasitoids using specific primers, species not targeted by these molecular markers will have been missed. However, the current assay allowed screening for 12 parasitoid species, which correlates well with the results of Vollhardt et al. (2008) who collected ~14 parasitoid species in wheat fields via sweep netting. Furthermore, as indicated by samples which tested positive with the group-specific markers but failed to amplify using species-specific markers, additional species within the genera *Aphidius*, *Dendrocerus* and *Praon* will have been targeted. A comparative study of conventional and molecular methods for the evaluation of host–parasitoid associations by Gariepy et al. (2008) found that parasitism levels estimated by all methods were similar but molecular analysis detected parasitoids earlier than dissection and rearing. Furthermore, data loss as a result of host and parasitoid mortality during the rearing process does not occur when using molecular methods. Our study further demonstrates the utility of using molecular methods to investigate host–parasitoid associations, particularly in cases where the host is difficult to rear. Using molecular techniques similar to those used here Traugott et al. (2008) found only 1.6% of wheat aphids to be multiparasitized, suggesting that aphid primary parasitoids effectively avoid multiple parasitism. The present findings indicate that this seems to hold true for both conventional and organic farming systems. Overall, it appears that there is little difference between the two farming systems in levels of aphid mortality from naturally occurring parasitoid species, however other important predator and parasitoid groups may respond differently.

Acknowledgements

This study was funded by the Biotechnology and Bio-Resources Research Council UK, and the Lady Emily Smyth Agricultural Research Station (Bristol University). Dr. Ines Vollhardt (University of Göttingen) was involved in the taxonomic identification of parasitoid adults. Thank you to the landholders involved in the project who allowed us access to their farms. Two anonymous reviewers, Tek Tay and W.O.C. Symondson offered many helpful comments on drafts of the manuscript.

References

Bengtsson, J., Ahnstrom, J., Weibull, A.C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. Journal of Applied Ecology 42, 261–269.

Bianchi, F., Van Der Werf, W., 2003. The effect of the area and configuration of hibernation sites on the control of aphids by *Coccinella septempunctata* (Coleoptera: Coccinellidae) in agricultural landscapes: a simulation study. Environmental Entomology 32, 1290–1304.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313, 351–354.

Costanza, R., Fisher, B., Mulder, K., Liu, S., Christopher, T., 2007. Biodiversity and ecosystem services: a multi-scale empirical study of the relationship between species richness and net primary production. Ecological Economics 61, 478–491.

Gariepy, T., Kuhlmann, U., Gillott, C., Erlandson, M., 2008. A large-scale comparison of conventional and molecular methods for the evaluation of host-parasitoid associations in non-target risk-assessment studies. Journal of Applied Ecology 45, 708–715.

Gibson, R.H., Pearce, S., Morris, R.J., Symondson, W.O.C., Memmott, J., 2007. Plant diversity and land use under organic and conventional agriculture: a whole-farm approach. Journal of Applied Ecology 44, 792–803.

Greenstone, M.H., 2006. Molecular methods for assessing insect parasitism. Bulletin of Entomological Research 96, 1–13.

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, F., Evans, A.D., 2005. Does organic farming benefit biodiversity? Biological Conservation 122, 113–130.

Lampkin, N., 1999. Organic Farming. Farming Press, Tonbridge.

Langer, A., Stilmant, D., Verbois, D., Hance, T., 1997. Seasonal activity and distribution of cereal aphid parasitoids in Belgium. Entomophaga 42, 185–191.

Langer, V., 2001. The potential of leys and short rotation coppice hedges as reservoirs for parasitoids of cereal aphids in organic agriculture. Agriculture Ecosystems & Environment 87, 81–92.

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.

Macfadyen, S., Gibson, R., Plaszek, A., Morris, R., Craze, P., Planque, 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.

Murdoch, W.W., Swarbrick, S.L., Briggs, C.J., 2006. Biological control: lessons from a study of California red scale. Population Ecology 48, 297–305.

Roschewitz, I., Gabriel, D., Tscharntke, T., Thies, C., 2005a. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. Journal of Applied Ecology 42, 873–882.

Roschewitz, I., Hucker, M., Tscharntke, T., Thies, C., 2005b. The influence of landscape context and farming practices on parasitism of cereal aphids. Agriculture Ecosystems & Environment 108, 218–227.

Rundlof, M., Nilsson, H., Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumble bees. Biological Conservation 141, 417–426.

Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M., Tscharntke, T., 2003. Relative importance of predators and parasitoids for cereal aphid control. In: Proceedings of the Royal Society of London Series B: Biological Sciences, 270. pp. 1905–1909.

Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47, 561–594.

Traugott, M., Bell, J.R., Broad, G.R., Powell, W., van Veen, F.J.F., Vollhart, I.M.G., Symondson, W.O.C., 2008. Endoparasitism in cereal aphids: molecular analysis of a whole parasitoid community. Molecular Ecology 17, 3928–3938.

Vollhardt, I.M.G., Tscharntke, T., Wäckers, F.L., Bianchi, F.J.J.A., Thies, C., 2008. Diversity of cereal aphid parasitoids in simple and complex landscapes. Agriculture, Ecosystems & Environment 126, 289–292.

Zehnder, G., Gurr, G.M., Kuhne, S., Wade, M.R., Wratten, S.D., Wyss, E., 2007. Arthropod pest management in organic crops. Annual Review of Entomology 52, 57–80.