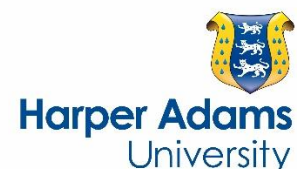


Do natural enemies really make a difference? Field scale impacts of parasitoid wasps and hoverfly larvae on cereal aphid populations.

by Ramsden, M., Menendez Martinez, M.R., Leather, S.R. and Leopold, F.L.

Copyright, Publisher and Additional Information: This is the author accepted manuscript. The final published version (version of record) is available online via Wiley Online Please refer to any applicable terms of use of the publisher.

DOI: 10.1111/afe.12191



Ramsden, M., Menendez Martinez, M.R., Leather, S.R. and Leopold, F.L. 2016. Do natural enemies really make a difference? Field scale impacts of parasitoid wasps and hoverfly larvae on cereal aphid populations. *Agricultural and Forest Entomology*.

27 September 2016

1 Full Title: Do natural enemies really make a difference? Field scale impacts of
2 parasitoid wasps and hoverfly larvae on cereal aphid populations.

3 Running title: Do natural enemies really make a difference

4 Correspondence author: Mark Ramsden

5 Address: ADAS UK Ltd, Pendeford House, Pendeford Business Park,
6 Wolverhampton, UK

7 Contact number: 01902 271290

8 Contact email: Mark.Ramsden@adas.co.uk

9

10 Additional authors:

11 Rosa Menendez;

12 Lancaster Environment Centre, Lancaster University, Lancaster, UK

13 Simon Leather;

14 Crop and environmental Sciences, Harper Adams University, Shropshire, UK

15 Felix Wäckers;

16 Lancaster Environment Centre, Lancaster University, Lancaster, UK

17

18 **Key words:** Cereal aphids, conservation biological control, pest management, natural enemies

19

20

21

22

23

24

25

26

1 **Abstract**

- 2 1. Naturally occurring predators and parasitoids are known to reduce the abundance of pest
3 invertebrates in arable crops, yet current treatment thresholds do not account for this
4 contribution to pest management.
- 5 2. Here, we provide evidence for the presence of natural enemies correlating with a
6 subsequent reduction in pest population growth.
- 7 3. The abundance of cereal aphid pests and two key aphidophagous natural enemies,
8 parasitoid wasps (Aphidiinae) and hoverfly larvae (Syrphinae) were assessed at field
9 boundaries and interiors in southeast England.
- 10 4. The highest rate of aphid population growth was associated with locations where no natural
11 enemies were found. The presence of either Aphidiinae wasps or predatory Syrphinae larvae
12 was associated with a reduction in the rate of aphid population growth irrespective of
13 location within the field, and overall aphid population growth was negatively correlated with
14 increasing natural enemy abundance.
- 15 5. This work indicates that natural enemies contribute significantly to pest control, and
16 provides further evidence in support of using management strategies to promote their
17 occurrence in agro-ecosystems.
- 18 6. Aphid predators and parasitoids make an important contribution to aphid pest control
19 within cereal fields, and thresholds for insecticide application should account for this to
20 avoid unnecessary treatments.

21
22
23
24
25
26

1 **Introduction**

2 The potential cost of pest insect outbreaks are highly unpredictable and can lead to reductions in
3 yield far in excess of the cost of insecticide application (Larsson, 2005; Oerke, 2006; Jacquemin *et al.*,
4 2014). Pest thresholds provide farmers with a basis for deciding when to apply treatments.
5 However, the low direct cost of insecticide applications and high risks associated with failure to
6 prevent pest outbreaks mean that calendar sprays have become common practice. The difficulty in
7 accurately predicting insect populations in large crop areas and in managing fields accordingly has
8 further encouraged calendar sprays with little, if any, pest assessment (Bailey *et al.*, 2009; Reisig *et*
9 *al.*, 2012). The resulting gratuitous use of pesticides has reduced the biological control potential of
10 natural enemies of crop pests and selected for insecticide resistance in pests (Geiger *et al.*, 2010;
11 Foster *et al.*, 2014), increasing the risk of long term crop losses (Bass *et al.*, 2014). Insecticides are
12 not the only tool for controlling invertebrate pests, and European legislation (Sustainable Use
13 Directive 2009/128/EC) requires professional users of pesticides to follow the general principles of
14 Integrated Pest Management (IPM), in which chemical control is used as a last resort as part of a
15 management plan (Bruce, 2010; Sabatier *et al.*, 2013). The majority of farmers employ cultural
16 control, such as crop rotation and soil cultivations, to help reduce pests, but enhancement of natural
17 enemies is rarely practiced (Bommarco *et al.*, 2013; Ramsden *et al.*, 2014). This may be due to a
18 combination of factors, including a lack of awareness of the contribution natural enemies can have
19 in arable pest control, and a lack of knowledge about how to promote natural enemies in
20 agricultural landscapes. Previous work investigating epigeal predators in cereal fields has shown that
21 their impact on pest control declines with distance to the crop edge (Griffiths *et al.* 2008). Relatively
22 little information is available on whether or not this occurs for flight capable natural enemies.

23 We used cereal aphids and two key natural enemy groups in winter wheat as a model to
24 study crop/pest/natural enemy interactions. The grain aphid, *Sitobion avenae* (Fabricius)
25 (Hemiptera: Aphididae), is the most important aphid pest of wheat during the spring and early
26 summer, causing losses in yield and grain quality through direct feeding (Larsson, 2005). The Bird

1 cherry-oat aphid, *Rhopalosiphum padi* (Linnaeus) (Hemiptera: Aphididae) can also cause damage by
2 direct feeding during spring (Leather *et al.*, 1989), but is more important as a vector of barley yellow
3 dwarf virus (BYDV) in autumn (Riedell *et al.*, 2007). A third aphid, the rose grain aphid,
4 *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae), is rarely an economic pest (Howard and
5 Dixon, 1995). Summer populations in UK wheat crops are normally dominated by *S. avenae*, which is
6 found on the underside of upper leaves, on the stem, and on the ears. Current guidelines
7 recommend treatment of aphid infestation in spring/summer when half the tillers are infested prior
8 to growth stage (GS) 61, when two-thirds are infested between stem extension to flag-leaf
9 emergence, or when more than two thirds of tillers are infested and numbers are increasing
10 between flowering and watery ripe (George and Gair, 1979; AHDB, 2014). Available thresholds are
11 only based on pest levels and do not consider natural enemy population levels (Zhang and Swinton,
12 2009).

13 Syrphinae larvae (Diptera: Syrphidae) are naturally occurring predators which consume large
14 numbers of aphids until they pupate (Chambers and Adams, 1986), whilst adult Aphidiinae
15 (Hymenoptera: Braconidae) lay their eggs inside aphids (Shaw and Huddleston, 1991). Once
16 hatched, the wasp larvae consume their host from within and transform the aphid's body into a
17 cocoon, or 'mummy', from which the adult wasp subsequently emerges (Shaw and Huddleston,
18 1991). Most aphid parasitoids found in cereal fields are polyphagous, capable of parasitising all three
19 key species, though host preference is partially conditioned by prior host selection (Powell and Zhi-
20 Li, 1983, Pungertl, 1986; Höller, 1991). Some Syrphinae species may show preference for different
21 aphid prey, but there is no evidence for any selection between the three cereal aphids in wheat
22 (Chambers and Adams, 1986; Sadeghi *et al.* 2000). Therefore both Syrphinae and Aphidiinae are
23 capable of reducing aphid populations, and are frequently used on protected crops to control aphid
24 pests (Hågvar and Hofsvang, 1991; Pineda and Marcos-Garcia, 2008). Cereal aphids and their natural
25 enemies can be collected using water traps, and catch rates are representative of abundance on the

1 crop; however there is little published data available on the interactions between aphid
2 populations and their natural enemies (Vorley and Wratten, 1987; Ramsden *et al.*, 2014).

3 The aim of this study was to investigate the relationship between the abundance of natural
4 enemies and subsequent changes in the abundance of cereal aphid abundance during summer
5 infestations, and whether this relationship differed with respect to location within-field. This was
6 done by adapting the model used in Chaplin-Kremer *et al.* (2013) to correlate the number of natural
7 enemies caught per unit area with a subsequent change in pest numbers caught. We then discuss
8 the results of our study in relation to current thresholds for applying insecticide treatments for
9 summer aphid infestations.

10

11 **Materials and methods**

12 *Study site and experimental design*

13 Cereal aphids and their natural enemies were collected using water traps in winter wheat fields on
14 three arable farms in the UK. Two of the farms were in Berkshire: Stern Farm (Latitude: 51° 12' 45"
15 N, Longitude: 0° 56' 14" W) and Manor Farm (Latitude: 51° 12' 29" N, Longitude 1° 3' 15" W), and a
16 third was in Essex: Fingrith Hall Farm (Latitude: 51° 42' 28" N, Longitude 0° 19' 39" E). At each farm
17 three winter wheat fields of 200 metres width or greater were selected at random giving nine fields
18 in total. In each field, all field edges bordering a second cereal crop were identified, from which one
19 edge of 200 metres was selected at random. All field margins were dominated by grass species,
20 alongside hawthorn-dominated hedgerows. There were few floral herbs at any of the sites. No
21 insecticides were applied to any of the fields throughout the experiment.

22 Two transects were installed parallel to the selected edge in each field; one was 10 metres
23 from the field margin (boundary), and the other was 100 metres into the crop from the field margin
24 (Interior). In both transects five brown water traps were placed 20 metres apart and fixed below
25 crop height at 30 centimetres above the ground. In this way the traps collect arthropods that got
26 swept off the plants, as well as flying individuals. Each water trap was 20 centimetres in diameter

1 and three centimetres deep, made using a plastic plant pot saucer fixed to a 40cm wooden stake
2 driven 10cm into the ground. A second saucer was placed into the first, and filled with 1 litre of 10%
3 ethylene glycol solution to preserve samples and 1 mL of detergent to break surface tension and
4 ensure any trapped insects sunk and drowned. We chose brown water traps as a way to passively
5 collect invertebrates, as yellow or white traps can disproportionately attract individuals searching for
6 floral resources (Bowie, 1999; Laubertie *et al.*, 2006). Other sampling methods, such as sweep
7 netting and vacuum sampling, were not used as they can cause damage to plants, affecting their
8 physical condition and releasing volatiles which can influence visitation of pests and natural enemies
9 to the area over repeat visits (Paré and Tumlinson, 1999).

10 The traps were set on 28th June, and reset each week until 19th July 2010, after which the
11 aphid population underwent the mid-season crash (Karley *et al.*, 2004). Samples were preserved in
12 industrial methylated spirits and were later identified following keys in Powell (1982), Shaw and
13 Huddleston (1991), Goulet and Huber (1993), Blackman and Eastop (2000), and Stubbs and Falk
14 (2002). All aphids, including the common agricultural pests, *M. dirhodum*, *R. padi* and *S. avenae*,
15 were grouped together as “cereal aphids”, though samples were dominated by *S. avenae*. In this
16 study we focussed on parasitic wasps (Aphidiinae spp.), and hoverfly larvae (Syrphinae spp.), both of
17 which were collected using the water traps. Syrphidae larvae were identified to functional group
18 (aphidophagous Syrphinae), and all Syrphinae adults were identified to species to determine the
19 common species. A random selection of 315 adult Aphidiinae were identified to species where
20 possible to determine the most common species.

21

22 *Statistical analyses*

23 To assess the impact of natural enemies on cereal aphids, changes in aphid density were
24 related to the abundance of the natural enemies (adapted from Chaplin-Kramer *et al.* 2013). The
25 change in aphid density (population growth) was defined as:

26

1 $\Delta A =$ aphids per trap in week (t)/mean weekly number of aphids trapped per trap in previous two
2 weeks

3

4 Generalized Linear Mixed Model (GLMMs) via *lme4* and *languageR* packages in R version

5 2.14.1 (R Development Core Team, 2005; Bates and Maechler, 2009; Baayen, 2012) were used to

6 assess the relationship between aphid population growth and the abundance of Aphidiinae and

7 Syrphinae during the previous two weeks (Chaplin-Kramer *et al.*, 2013). As these models produced

8 estimated F statistics, degrees of freedom are not reported. The response of aphids (ΔA) to natural

9 enemy abundance was also investigated with respect to the distance from the field margin

10 (Boundary versus Interior). Models included farm, the field within farm, and the distance along each

11 transect within field as nested random effects and the week in which aphid trapping took place as a

12 random effect. The abundance of aphids and their natural enemies were count data, so a Poisson

13 error structure and a log link function with the Laplace approximation were used for the analyses.

14 The data were explored following the protocol in Zuur *et al.* (2010) and model assumptions were

15 checked using the R package *LMERConvenienceFunctions* (Tremblay, 2012). Where relevant,

16 stepwise deletion from the maximal model was carried out to determine the minimal adequate

17 model, including the interaction between the abundance of both groups of natural enemies

18 (Crawley, 2007). The significance of each factor and their interactions were identified using z-values,

19 and subsequent changes in deviance between models with and without individual terms were tested

20 using chi-squared (χ^2) tests (Zuur *et al.*, 2010). The χ^2 values and p-values from the relevant model

21 comparisons are provided in the results. Estimates calculated by the minimal adequate model for

22 mean and standard errors were back transformed for graphical representation.

23

24 **Results**

1 A total of 9,664 cereal aphids were collected between 28th June and 19th July. Variation in aphid
2 abundance among sampling locations was very high, and there was no significant difference
3 between the boundary and interior transects ($\chi^2 = 3.4107$, $p = 0.066$, Figure 1).

4 ##Figure 1##

5 During the sampling period 1,113 Aphidiinae were collected. The most common species identified in
6 the randomly select 315 sampled were *Aphidius ervi* (Haliday), *A. rhopalosiphi* (De Stefani-Perez),
7 *Praon volucre* (Haliday), and *P. gallicum* (Stary), which together represented 54% identified to
8 species level. *Aphidius picipes* (Nees), *A. uzbekistanicus* (Luzhetzhi) and *Ephedrus plagiator* (Nees)
9 made up a further 7% (Supplementary Table 1). During the sampling period 741 Syrphinae larvae
10 were collected. Adult Syrphinae were collected to determine the species present but were not
11 included in the analysis. Four species were identified: *Platycheirus manicatus* (Meigen), *P. clypeatus*
12 (Meigen), *Syrphini ribesii* (Linnaeus) and *Episyrphus balteatus* (de Geer), of which *E. balteatus* was
13 the most abundant.

14 The change in number of cereal aphids caught over time was not affected by distance into
15 the crop, but was significantly affected by the abundance of natural enemies in the previous two
16 weeks (Table 1). As the abundance of Aphidiinae or Syrphinae larvae increased, the aphid
17 population growth slowed (Figure 2 ab).

18 ##Figure 2 ab ##

19 There was no significant interaction between the two natural enemy groups. From the model it is
20 possible to estimate the average number of natural enemies collected in previous weeks that
21 correlates with no change in the number of aphids collected, i.e. no increase in aphid population.
22 The collected number of Aphidiinae associated with no change in aphid catch was 2.86 ± 0.09 per
23 trap, while the number of Syrphinae larvae was 3.33 ± 0.11 per trap.

24 ##Table 1##

25

26 **Discussion:**

1 Our results show that the number of natural enemies trapped correlated with the subsequent
2 change in cereal aphid abundance. We found that in this respect, increase abundance of natural
3 enemies recorded led to a reduction in the rate of change of aphids caught. The relationship
4 between natural enemies and subsequent abundance of aphids caught in cereal fields was
5 unaffected by location, either at 10 metres or 100 metres from the field boundary.

6 On average, where no Syrphinae larvae or Aphidiinae were trapped the subsequent number
7 of aphids collected increased. The presence of either natural enemies reduced the rate of increase.
8 The importance of natural enemies in preventing invertebrate pest outbreaks is well recognised
9 (Chambers and Adams, 1986). Despite this, their population levels are not considered in current pest
10 threshold models and limited targeted actions are taken to promote them in arable crops (Kean *et*
11 *al.*, 2003, Ramsden *et al.*, 2014). Our results also indicate that increasing numbers of natural
12 enemies can have an increasing impact on the reducing aphid abundance. This further supports the
13 provision of additional resources in agro-ecosystems through conservation biological control (Olson
14 and Wäckers, 2006).

15 Syrphinae larvae and Aphidiinae were found to impact aphid numbers in both the boundary
16 and interior of the crop. In previous field experiments, epigeal natural enemy populations were
17 shown to have limited dispersal from alternative habitats at the field boundary, and this is
18 considered to limit their reliability as part of a pest management programme (Griffiths *et al.* 2008).
19 Our results show that flight capable natural enemies are not restricted in this way in winter wheat,
20 also observed in other crops (Gillespie *et al.*, 2011). This is important, because if the impact of
21 natural enemies is to be increased using field margins, these should ideally have an impact at a
22 landscape scale rather than only providing benefits to the crop immediately adjacent. These non-
23 crop landscape elements are necessary as Syrphinae and Aphidiinae have a wider resource
24 requirement than those normally found within cereal crops. Like their aphid prey, both these
25 natural enemies overwinter outside cropped areas, and follow their prey into the crops in spring
26 (Landis *et al.*, 2000; Vialatte *et al.*, 2007; Ramsden *et al.*, 2014). Moreover, adult Syrphinae

1 commute between the crop and non-crop vegetation to feed on pollen - a vital source of proteins for
2 egg maturation, and nectar for sustenance (Hogervorst *et al.*, 2007; Choate and Lundgren, 2013; Van
3 Rijn *et al.*, 2013; van Rijn and Wäckers, 2016). Aphidiinae do not exploit adult protein sources, but do
4 require carbohydrates for survival. While honeydew from their aphid hosts is widely utilised by these
5 parasitoids, floral nectar found outside the crop can be superior to honeydew for sustaining adults
6 and will be of particular relevance under conditions of low host availability (Wäckers, 2000; Lee *et*
7 *al.*, 2004; Wäckers *et al.*, 2008). Individual parasitoids are unlikely to commute in and out of the
8 crop, and it is more likely that in this study the aphid populations were sufficient to support the
9 Aphidiinae population up to 100 m from the crop margin. Both Syrphinae and Aphidiinae
10 populations would benefit from additional resource provision during periods of the year when cereal
11 aphid populations are not widely available (Karley *et al.*, 2004; Roitberg and Gillespie, 2014;
12 Ramsden *et al.*, 2014).

13 Cereal aphids overwinter outside the crop in habitats such as grass margins, which can
14 provide a significant source of infestation in adjacent crops, leading to initially higher pest levels
15 close to field boundaries (Lewis, 1969; Vialatte *et al.*, 2007). The original source of infestation has
16 little effect on subsequent within-field aphid distribution and abundance (Winder *et al.*, 1999;
17 Vialatte *et al.*, 2005; Al Hassan *et al.*, 2013), and the continuous re-infestation of the crop by alate
18 aphids throughout the season contributes to high variation within fields and over time, as we
19 observed in this study (Cocu *et al.*, 2005; Vialatte *et al.*, 2005; Klueken *et al.*, 2009). This variation
20 makes it difficult to assert whether or not infestations will lead to a reduction in yield and limits the
21 reliability of current thresholds. Furthermore, current UK treatment threshold do not account for the
22 impact of environmental conditions, such as plant health or the presence of natural enemies
23 (George and Gair, 1979). A more recent threshold was defined by Larsson (2005) as 1 aphid/tiller at
24 GS59, 4 at GS69 and 7 at GS75. This threshold was determined using data in Sweden and has not
25 been checked for UK conditions. It also does not account for additional factors that may affect the
26 crops ability to tolerate damage or which may reduce aphid population growth. While simple

1 thresholds are essential in making them implementable, confidence in over-simplistic thresholds is
2 limited. The absence of natural enemy contribution from these thresholds also undermines efforts
3 to promote IPM strategies, and encouraging risk-averse application of insecticides.

4 Our study indicates that increasing abundance of natural enemies has a significant impact on
5 reducing subsequent aphid population growth rates, suggesting that the abundance of natural
6 enemies in the crop should be considered as an important factor in the decision to apply
7 insecticides. More research is needed to make thresholds for treatment accurate and
8 implementable, and the incorporation of natural enemies into agronomic decision making could help
9 reduce the reliance on insecticides at a time when restrictions on chemical applications is increasing
10 (Griffiths *et al.*, 2008; Caballero-López *et al.*, 2012; Hillocks, 2012; Holland *et al.*, 2012; Popp *et al.*,
11 2013). A key challenge remains the convenience and low purchase cost of insecticide applications
12 and the fact that environmental and long term costs of pesticide use are not incorporated in the
13 price of insecticides.

14 In our study we did not relate aphid catch rates to numbers of aphids on the crop, or assess
15 impact on yield. To establish crop protection programmes that account for biological control further
16 work is needed to investigate the implications of tri-trophic interactions on yield loss. The water
17 traps used are likely to have underestimated the abundance of Syrphinae larvae (Bowie *et al.* 2001),
18 however, as we were not comparing abundance across different habitats the relative catch rate
19 remains a valid method for monitoring these predators. We only assessed the impact of two natural
20 enemies in this work, as other important predators (e.g. *Chrysoperla carnea* (Stephens) (Neuroptera:
21 Chrysopidae)) were not collected in sufficient abundance on which to carry out analysis. As the
22 relative importance of different natural enemy species change with agricultural landscapes over
23 time, multi-year experiments would be useful in exploring the impact of other beneficial species
24 (Tscharntke *et al.* 2007).

25

26 **Conclusion**

1 Our aim was to provide evidence for the role of natural enemies in reducing aphid pest abundance in
2 cereal crops, and investigate whether this was limited at the field scale by distance from the field
3 margin. We found that as the number of natural enemies caught increased, the subsequent growth
4 rate of cereal aphid population caught was reduced. The relationship between natural enemy
5 abundance and subsequent aphid abundance was unaffected by distance into a field from the
6 boundary. Long-term studies need to relate the contribution of biological control to reducing yield
7 losses, however, the results of this study provide further evidence that natural enemy abundance
8 should be a factor in decisions to apply insecticide treatments to pest infestations. They also suggest
9 that targeted resource provision for natural enemies has the potential for improving biological
10 control of cereal aphid, though impacts must always be considered in the context of the landscape
11 matrix in which they are placed.

12

13 **Acknowledgments:**

14 This project was funded by Biotechnology and Biological Sciences Research Council. We are grateful
15 for the time and effort that Chris Bucknell, Paul Sigley and Steve Berry put into providing assistance
16 with the management of the land used in the study, and to Jeffery Pullinger for his assistance in the
17 field. We thank Steve Ellis and Rosie Burdon for their comments on the work, and are grateful for
18 the constructive comments of three anonymous reviewers.

19

20 **References**

21 AHDB (2014) Encyclopaedia of pests and natural enemies in field crops. AHDB 2014, 200pp
22 Almohamad, R., Verheggen, F.J., Francis, F. and Haubruge, E. (2007) Predatory hoverflies select their
23 oviposition site according to aphid host plant and aphid species. *Entomologia Experimentalis et*
24 *Applicata*, 125, 13–21.
25 Baayen, R.H. (2012) Data sets and functions with analyzing linguistic data: a practical introduction to
26 statistics. CRAN.

1 Bailey, A.S., Bertaglia, M., Fraser, I.M., Sharma, A. and Douarin, E. (2009) Integrated pest
2 management portfolios in UK arable farming: results of a farmer survey. *Pest management science*,
3 65, 1030–9.

4 Bass, C., Puinean, A.M., Zimmer, C.T., Denholm, I., Field, L.M., Foster, S.P., *et al.* (2014) The evolution
5 of insecticide resistance in the peach potato aphid, *Myzus persicae*. *Insect Biochemistry and*
6 *Molecular Biology*, 51, 41–51.

7 Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. and Tscharntke, T. (2012) Responses of plant, insect
8 and spider biodiversity to local and landscape scale management intensity in cereal crops and
9 grasslands. *Agriculture, Ecosystems and Environment*, 146, 130–136.

10 Bates, D. and Maechler M. (2012) Linear mixed-effects models using S4 classes. CRAN.
11 system processes and services via functional traits. *Biodiversity and Conservation*, 19, 2873–2893.

12 Blackman R.L. and Eastop V.F. (2000) Aphids on the world's crops: An identification and information
13 guide, 2nd edition. John Wiley & Sons, Chichester, 414 pp., 59 figs, 51 plates

14 Bommarco, R., Kleijn, D., and Potts, S.G. (2013) Ecological intensification: harnessing ecosystem
15 services for food security. *Trends in Ecology and Evolution*, 28, 230–238.

16 Bowie, M.H. (1999) Effects of distance from field edge on aphidophagous insects in a wheat crop and
17 observations on trap design and placement. *International Journal of Pest Management*, 45, 69–73.

18 Bowie M.H., Gurr M., and Framptthreshold
19 parasitoid fauna in wheat in New South Wales, Australia. *New Zealand Entomologist*, 24, 3-6

20 Bruce, T.J.A. (2010) Tackling the threat to food security caused by crop pests in the new millennium.
21 *Food Security*, 2, 133–141.

22 Caballero-López, B., Bommarco, R., Blanco-Moreno, J.M., Sans, F.X., Pujade-Villar, J., and Rundlöf, M.
23 (2012) Aphids and their natural enemies are differently affected by habitat features at local and
24 landscape scales. *Biological Control*, 63, 222–229.

1 Chambers, R.J. and Adams, T.H.L. (1986) Quantification of the impact of hoverflies (Diptera,
2 Syrphidae) on cereal aphids in winter wheat: an analysis of field populations. *The Journal of Applied*
3 *Ecology*, 23, 895–904.

4 Chaplin-Kramer, R., Valpine, P. de, Mills, N.J. and Kremen, C. (2013) Detecting pest control services
5 across spatial and temporal scales. *Agriculture, Ecosystems and Environment*, 181, 206–212.

6 Choate, B.A. and Lundgren, J.G. (2013) Why eat extrafloral nectar? Understanding food selection by
7 *Coleomegilla maculata* (Coleoptera: Coccinellidae). *BioControl*, 58, 359–367.

8 Cocu, N., Harrington, R., Hulle, M. and Rounsevell, M.D.A. (2005) Spatial autocorrelation as a tool for
9 identifying the geographical patterns of aphid annual abundance. *Agricultural and Forest*
10 *Entomology*, 7, 31–43.

11 Crawley, M. J. (2007) Data Input, in *The R Book*, John Wiley & Sons, Ltd, Chichester, UK.

12 Foster, S.P., Paul, V.L., Slater, R., Warren, A., Denholm, I., Field, L.M. and Williamson, M.S. (2014) A
13 mutation (L1014F) in the voltage-gated sodium channel of the grain aphid, *Sitobion avenae*, is
14 associated with resistance to pyrethroid insecticides. *Pest Management Science*, 70, 1249-1253

15 George, K.S. and Gair, R. (1979) Crop loss assessment on winter wheat attacked by the grain aphid,
16 *Sitobion avenae*, (F.), 1974-77. *Plant Pathology*, 28, 143-149.

17 Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P.,
18 Liira, J., Tschantke, T., Winqvist, C., Eggers, S., Bommarco, R., Part, T., Bretagnolle, V., Plantegenest,
19 M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C.,
20 Flohre, A., Hanke, S., Fischer, C., Goedhart, P.W., and Inchausti, P. (2010) Persistent negative effects
21 of pesticides on biodiversity and biological control potential on European farmland. *Basic and*
22 *Applied Ecology*, 11, 97-105.

23 Gillespie, M., Wratten, S., Sedcole, R. and Colfer, R. (2011) Manipulating floral resources dispersion
24 for hoverflies (Diptera: Syrphidae) in a California lettuce agro-ecosystem. *Biological Control*, 59, 215–
25 220.

1 Goulet, H. and Hubert, J. F. (1993) Hymenoptera of the world. An identification guide to families. —
2 Research Branch, Agricultural Canada Publication. Canada Communication Group-Publishing,
3 Ottawa. 668 Seiten. Griffiths, G.J.K., Holland, J.M., Bailey, A. and Thomas, M.B. (2008) Efficacy and
4 economics of shelter habitats for conservation biological control. *Biological Control*, 45, 200–209.
5 Hågvar, E.B. and Hofsvang, T. (1991) Aphid parasitoids (Hymenoptera, Aphidiidae): biology, host
6 selection and use in biological control. *Biocontrol News and Information*, 12, 13–41.
7 Hassan, D. Al, Georgelin, E., Delattre, T., Burel, F., Plantegenest, M. and Kindlmann, P. (2013) Does
8 the presence of grassy strips and landscape grain affect the spatial distribution of aphids and their
9 carabid predators? *Agricultural and Forest Entomology*, 15, 24–33.
10 Hillocks, R.J. (2012) Farming with fewer pesticides: EU pesticide review and resulting challenges for
11 UK agriculture. *Crop Protection*, 31, 85–93.
12 Hogervorst, P.A.M., Wäckers, F.L. and Romeis, J. (2007) Detecting nutritional state and food source
13 use in field-collected insects that synthesize honeydew oligosaccharides. *Functional Ecology*, 21,
14 936–946.
15 Holland, J.M., Oaten, H., Moreby, S., Birkett, T., Simper, J. and Southway, S. (2012) Agri-environment
16 scheme enhancing ecosystem services: A demonstration of improved biological control in cereal
17 crops. *Agriculture, Ecosystems and Environment*, 155, 147–152.
18 Höller, C.A. (1991) Evidence for the existence of a species closely related to the cereal aphid
19 parasitoid *Aphidius rhopalosiphi* De Stefani-Perez based on host ranges, morphological characters,
20 isoelectric focusing banding patterns, cross-breeding experiments and sex pheromone specificities
21 (Hymenoptera, Braconidae, Aphidiinae). *Systematic Entomology*, 16, 15-28
22 Howard, M. T. and Dixon, A. F. G. (1995) Factors determining the pest status of the rose-grain aphid,
23 *Metopolophium dirhodum* (Walker), on winter barley in the United Kingdom. *Annals of Applied*
24 *Biology*, 127: 1–10.

1 Jacquemin, G., Chavalle, S. and Proft, M. De. (2014) Forecasting the emergence of the adult orange
2 wheat blossom midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae) in Belgium. *Crop*
3 *Protection*, 58, 6–13.

4 Karley, A. J., Parker, W.E., Pitchford, J.W. and Douglas, A. E. (2004) The mid-season crash in aphid
5 populations: Why and how does it occur? *Ecological Entomology*, 29, 383–388.

6 Kean, J., Wratten, S., Tylianakis, J. and Barlow, N. (2003) The population consequences of natural
7 enemy enhancement, and implications for conservation biological control. *Ecology Letters*, 6(7),
8 pp.604-612.

9 Klueken, A.M., Hau, B., Ulber, B. and Poehling, H.M. (2009) Forecasting migration of cereal aphids
10 (Hemiptera: Aphididae) in autumn and spring. *Journal of Applied Entomology*, 133, 328–344.

11 Landis, D.A., Wratten, S.D., and Gurr, G.M. (2000) Habitat management to conserve natural enemies
12 of arthropod pests and in agriculture. *Annu. Rev. Entomol.* 45, 175–201. Larsson, H. (2005) A crop
13 loss model and economic thresholds for the grain aphid, *Sitobion avenae* (F.), in winter wheat in
14 southern Sweden. *Crop Protection*, 24, 397–405.

15 Laubertie, E. A., Wratten, S.D. and Sedcole, J.R. (2006) The role of odour and visual cues in the pan-
16 trap catching of hoverflies (Diptera: Syrphidae). *Annals of Applied Biology*, 148, 173–178.

17 Leather, S.R., Walters, K.F.A., and Dixon, A.F.G. (1989) Factors determining the pest status of the bird
18 cherry-oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), in Europe: a study and review.
19 *Bulletin of Entomological Research*, 79, 345-360.

20 Lee, J.C., Heimpel, G.E. and Leibee, G.L. (2004) Comparing floral nectar and aphid honeydew diets on
21 the longevity and nutrient levels of a parasitoid wasp. *Entomologia Experimentalis et Applicata*, 111,
22 189–199.

23 Lewis, T. (1969) The diversity of the insect fauna in a hedgerow and neighbouring fields. *Journal of*
24 *Applied Ecology*, 6, 453-458.

25 Oerke, E.-C. (2006) Crop losses to pests. *The Journal of Agricultural Science*, 144, 31.

1 Olson, D.M. and Wäckers, F.L. (2006) Management of field margins to maximize multiple ecological
2 services. *Journal of Applied Ecology*, 44, 13–31.

3 Paré P.W. and Tumlinson J.H. (1999) Plant Volatiles as a Defense against Insect Herbivores. *Plant*
4 *Physiology*, 121, 325-332

5 Pineda, A. and Marcos-Garcia, M., A. (2008) Use of selected flowering plants in greenhouses to
6 enhance aphidophagous hoverfly populations (Diptera: Syrphidae). *Annales De La Societe*
7 *Entomologique De France*, 44, 487–492.

8 Popp, J., Peto, K. and Nagy, J. (2013) Pesticide productivity and food security. A review. *Agronomy*
9 *for Sustainable Development*, 33, 243–255.

10 Powell, W. (1982) The identification of hymenopterous parasitoids attacking cereal aphids in Britain.
11 *Systematic Entomology*, 7, 465-473

12 Powell W., and Zhi-Li Z. (1983) The reactions of two cereal aphid parasitoids, *Aphidius uzbekistanicus*
13 and *A. ervi*, to host aphids and their food-plants. *Physiological Entomology*, 8, 439-443

14 Pungertl N.B. (1986) Morphometric and electrophoretic study of *Aphidius* species (Hymenoptera:
15 Aphidiidae) reared from a variety of aphid hosts. *Systematic Entomology*, 11, 327-354

16 R Development Core Team (2005) R: A Language and Environment. R Foundation for Statistical
17 Computing, Vienna, Austria ISBN 3-900051-07-0.

18 Ramsden, M.W., Menéndez, R., Leather, S.R. and Wäckers, F. (2014) Optimizing field margins for
19 biocontrol services: The relative role of aphid abundance, annual floral resources, and overwinter
20 habitat in enhancing aphid natural enemies. *Agriculture, Ecosystems and Environment*, 199, 94–104.

21 Reisig, D.D., Bacheler, J.S., Herbert, D.A., Kuhar, T., Malone, S., and Philips, C. (2012) Efficacy and
22 value of prophylactic vs. integrated pest management approaches for management of cereal leaf
23 beetle (Coleoptera: Chrysomelidae) in wheat and ramifications for adoption by growers. *Journal of*
24 *Economic Entomology*, 105, 1612–1619.

25 Riedell, W.E., Osborne, S.L. and Jaradat, A. a. (2007) Crop mineral nutrient and yield responses to
26 aphids or barley yellow dwarf virus in spring wheat and oat. *Crop Science*, 47, 1553–1560.

1 Rijn, P.C.J. Van, Kooijman, J. and Wäckers, F.L. (2013) The contribution of floral resources and
2 honeydew to the performance of predatory hoverflies (Diptera: Syrphidae). *Biological Control*, 67,
3 32–38.

4 Rijn P.C.J. Van, and Wäckers, F.L. (2016) Nectar accessibility limits fitness, flower choice and
5 abundance of zoophagous hoverflies. *Journal of Applied Ecology*, 53, 925-933

6 Roitberg, B.D. and Gillespie, D.R. (2014) Natural enemies on the landscape - Integrating life-history
7 theory and landscapes. *Biological Control*, 75, 39–47.

8 Sabatier, R., Meyer, K., Wiegand, K. and Clough, Y. (2013) Non-linear effects of pesticide application
9 on biodiversity-driven ecosystem services and disservices in a cacao agroecosystem: A modeling
10 study. *Basic and Applied Ecology*, 14, 115–125.

11 Sadeghi, H. and Gilbert, F. (2000) Aphid suitability and its relationship to oviposition preference in
12 predatory hoverflies. *Journal of Animal Ecology*, 69, 771–784.

13 Shaw, M.R. and Huddleston, T. (1991) Classification and Biology of Braconid Wasps. *Handbooks for*
14 *the identification of British Insects*, 7. Royal Entomological Society of London, London.

15 Stubbs, A.E. and Falk, S. (2002) *British hoverflies, an illustrated identification guide*. Second
16 edition. British Entomological and Natural History Society, Reading.

17 Sutherland, J.P., Sullivan, M.S. and Poppy, G.M. (2001) Distribution and abundance of
18 aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats.
19 *Agricultural and Forest Entomology*, 3, 57–64.

20 Tremblay, A. (2012) A suite of functions of back-fit effects and forward-fit random effects, as well as
21 other miscellaneous functions. CRAN.

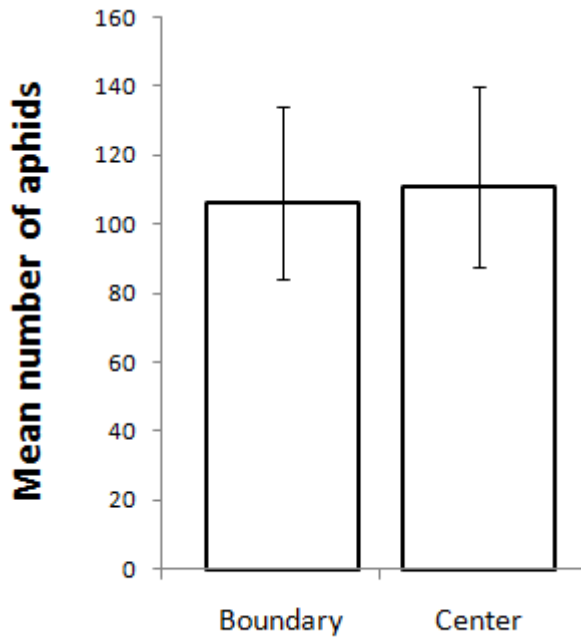
22 Tschardtke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J. M., van
23 Nouhuys, S., and Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape
24 scale. *Biological Control*. 43, 294–309.

- 1 Vialatte, A., Dedryver, C.-A., Simon, J.-C., Galman, M. and Plantegenest, M. (2005) Limited genetic
2 exchanges between populations of an insect pest living on uncultivated and related cultivated host
3 plants. *Proceedings of the Royal Society B: Biological Sciences*, 272, 1075–1082.
- 4 Vialatte, A., Plantegenest, M., Simon, J.C. and Dedryver, C.A. (2007) Farm-scale assessment of
5 movement patterns and colonization dynamics of the grain aphid in arable crops and hedgerows.
6 *Agricultural and Forest Entomology*, 9, 337–346.
- 7 Vorley, V.T., and Wratten, S.D. (1987) Migration of parasitoids (Hymenoptera: Braconidae) of cereal
8 aphids (Homoptera: Aphididae) between grassland, early-sown cereals and late-sown cereals in
9 southern England. *Bulletin of Entomological Research*, 77, 555-568
- 10 Wäckers, F.L. (2000) Do oligosaccharides reduce the suitability of honeydew for predators and
11 parasitoids ? A further facet to the function of insect-synthesized honeydew sugars. *Oikos*, 90, 197–
12 201.
- 13 Wäckers, F.L., Rijn, P.C.J. van and Heimpel, G.E. (2008) Honeydew as a food source for natural
14 enemies: Making the best of a bad meal? *Biological Control*, 45, 176–184.
- 15 Winder, L., Perry, J.N. and Holland, J.M. (1999) The spatial and temporal distribution of the grain
16 aphid *Sitobion avenae* in winter wheat. *Entomologia Experimentalis Et Applicata*, 93, 277–290.
- 17 Zhang W., and Swinton S. (2009) Incorporating natural enemies in an economic threshold for
18 dynamically optimal pest management. *Ecological Modelling*, 220, 1315-1324
- 19 Zuur, A.F., Ieno, E.N. and Elphick, C.S. (2010) A protocol for data exploration to avoid common
20 statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

21

22

1

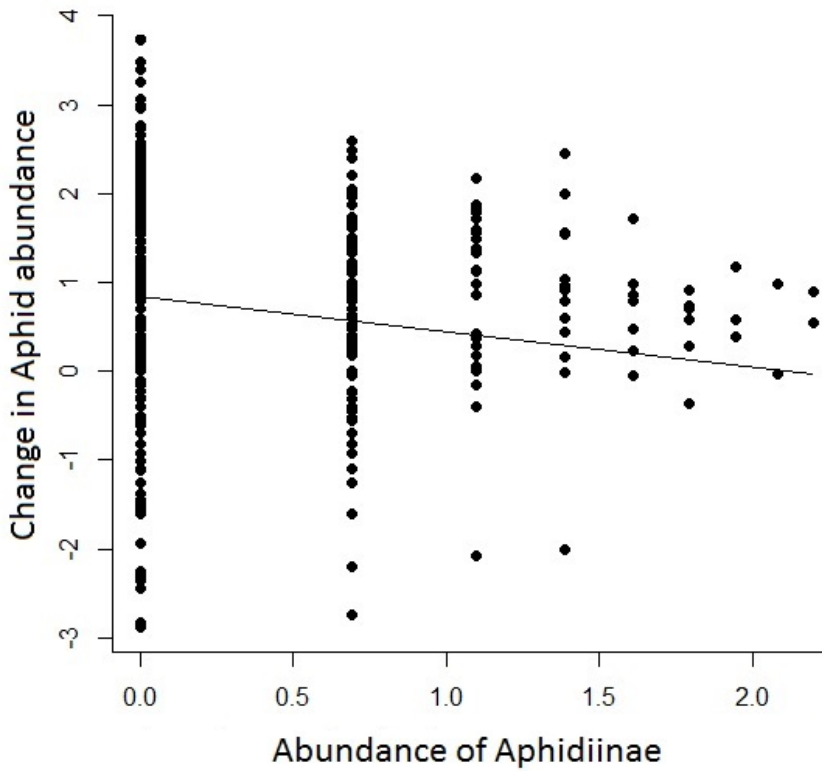


2

3 Figure 1: The overall mean number of cereal aphids per trap \pm SE. ($\chi^2 = 3.4107$, $p = 0.066$).

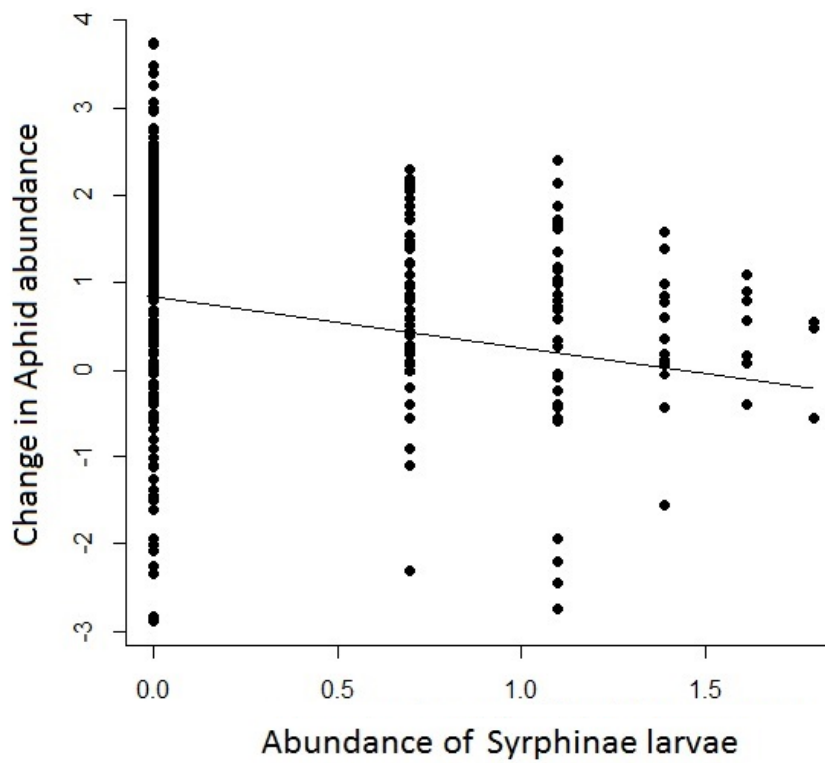
4

5 a)



6

7 b)



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Figure 2. The change in aphid abundance (log transformed) against the abundance (log transformed) of (a) Aphidiinae, and (b) Syrphinae larvae, in the previous two weeks. The line indicates the overall linear relationship estimated by the models; $\chi^2 = 21.10$, $P < 0.001$, and $\chi^2 = 48.99$, $P < 0.001$, respectively.

1 Table 1. Results of Generalised linear mixed models (χ^2 provided, see methods) for the effect of
 2 position within the crop (boundary v centre) and abundance of three natural enemies in the
 3 previous two weeks, on the change in aphid abundance in cereal fields, and the effect of the
 4 interactions between these factors. For all groups, sample size = 90 traps (nested in 9 fields and 3
 5 farms).

Effects	χ^2	P
Transect (T)	1.19	0.275
Aphidiinae adults (A)	21.10	<0.001
Syrphinae larvae (S)	48.99	<0.001
T x A	2.99	0.084
T x S	1.00	0.317
A x S	1.54	0.214
T x A x S	2.29	0.130

6

7

1 Supplementary Tables:

2

3 Supplementary Table 1: The species of Syrphinae and Aphidiinae adults identified in during the

4 study.

5

Natural enemies identified	Number identified
----------------------------	-------------------

Syrphinae (adults) Diptera: Syrphidae: Syrphinae (1)

<i>Platycheirus manicatus</i>	4
<i>Platycheirus ckyoeatus</i>	6
<i>Syrphini ribesii</i>	11
<i>Episyrphus balteatus</i>	17

Aphid parasitoids (adults) Hymenoptera: Braconidae: Aphidiinae (2)

<i>Aphidius ervi</i>	57
<i>Aphidius rhopalosiphi</i>	49
<i>Praon volucre</i>	41
<i>Praon gallicum</i>	23
<i>Aphidius pocopes</i>	9
<i>Aphidius uzbekistanicus</i>	6
<i>Ephedrus plagiator</i>	7
<i>Other Aphidius spp.</i>	32
<i>Other Praon spp.</i>	17
<i>Other Aphidiinae spp.</i>	38
<i>Indeterminate</i>	36

(1) Total number identified during sampling period.

(2) Number identified in randomly selected sample of 315 Aphidiinae wasps.

6

7