Revegetation by design, Queensland: natural resource management and IPM

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FINAL REPORT

Revegetation by design, Queensland: Natural resource management and IPM

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HAL Project VG07040

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This is the final report for VG07040 titled ‘Revegetation by Design, Queensland: Natural Resource Management and IPM’ which summarised the key findings and outlines plans for future research and industry adoption of better capture of the ecosystem service of pest control through the provision of non-crop perennial habitat, such as native vegetation, and on-farm refuges.

This project was funded for three years, conducted and completed in collaboration with key CSIRO staff including: Alejandro Costamagna, James Hereward, Felix Bianchi, Anna Marcora, Lynita Howie, and Andy Hulthen, and CSIRO French student intern Barthelemy, and DEEDI staff member Dave Carey. This project has been funded by HAL using the vegetable industry levy and matched funds from the Australian Government.

30 March 2012

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MEDIA SUMMARY

Invertebrate pests continue to cause substantial crop losses, while the standard methods of controlling them are often unsustainable. Capturing the services of natural pest control is one way to mitigate these losses. Such services are estimated to be worth ~$400 billion annually worldwide. Perennial habitat is increasingly recognized for the important role of providing habitat for beneficial insects and making them available to move into crops. This research focused on better capture of pest control services by investigating: the impact of early arrival and predation on pest populations in the Lockyer Valley, how pest suppression was affected by crop and non-crop habitat in the surrounding farm and landscape, the contribution of beneficial insects from on-farm refuges, and the voracity of two common predators on aphid pests.

Conducting extensive field experiments on growers' properties throughout the Lockyer Valley, and in the laboratory, we show that:

- The landscape surrounding fields and farms can greatly influence the abundance and movement of beneficials into crops.
- Landscapes with > 10% Lucerne provided more predators into the crop early, keeping pest populations lower for longer.
- Pest populations exploded in the absence of beneficials.
- Native vegetation is a source of beneficials, and may be important as a refuge when few crops are growing.
- Growers can enhance beneficial populations by providing on-farm refuge.
- An on-farm refuge for beneficial insects results in more beneficials accumulating in the crop. This effect is more pronounced when the landscape contribution of beneficial insects is low.
- Two common predators of crop pests consume 39 and 60 aphids per day, respectively, and the more aphids available the more they eat.

These findings show that early arrival of predators into crops keeps pest populations lower for longer. However, landscapes vary in the abundance of beneficial insects available to colonize. As part of an IPM program, growers can enhance pest suppression by managing an on-farm refuge. Future R&D should focus on trialling best-bet on-farm refuge options for vegetable production systems, and the development of accompanying decision-support tools to assist growers with plant selection, implementation and management.

TECHNICAL SUMMARY

The Problem At least two different mechanisms can explain higher levels of pest suppression in certain landscapes than in others. First, landscapes that are structurally complex may simply harbor more beneficials (eg. predators and parasitoids) than simple landscapes. A second mechanism may relate to the timing of predator arrival to the crop field, i.e. field crops located in landscapes with a higher proportion of natural enemy habitats are more likely to have one of those sources nearby, allowing quick response of beneficials to any pest colonising those crops. Each of these depends on their dispersal ability, which may be facilitated through the provision of 'on-farm' refuges such as unsprayed sections of crop, perennial Lucerne, or strips of planted native vegetation. However, in order to keep pest populations lower for longer, disadvantage the pests, and get more beneficials into the crop sooner, the key mechanisms must be understood, and linked with management options.

The Project Science The findings of HAL projects VG05014, and VG06024, show that beneficial predators and parasitoids were found on many species of native vegetation, with several beneficials spending time in the edge habitat between native remnant vegetation and crops, and moving into the crop at different times throughout the year. Building on these findings, we conducted experiments throughout the Lockyer Valley, QLD. We investigated: 1) the impact of early predation on pest populations and how pest suppression was affected by land use (e.g. crops, grassland, bushland) and the sources of natural enemies at multiple spatial scales, e.g. farm, neighbouring farms, and landscape; 2) the contribution of an on-farm refuge for beneficial insects in landscapes with few and many beneficial insect sources, and 3) the potential of two commonly observed predators to eat pests.

The Key Research Findings

• Farm Field Trials - Early predation and the role of the surrounding landscape:

- Early arrival of predators is crucial to achieve maximum pest suppression. Delay in predator arrival results in rapid aphid pest population growth.
- Landscapes vary in their 'pest suppressive' potential. Landscapes with > 10% Lucerne at a scale up to 1.5km from the focal fields were the most pest suppressive. More grassland resulted in the opposite.
- Non-crop habitat such as native remnant vegetation is a source of beneficials, but is not a driver for early predator colonisation. This habitat may be more important as a refuge when few crops are in the ground or when Lucerne is cut.

•Spatially-explicit modelling combined with an on-farm trial - Refuges near crops and the role of the surrounding landscape:

- Modelling results show that in landscapes devoid of predator source populations, mobile predators benefit from a refuge in the general area, whereas poor dispersing predators benefit from an on-farm refuge near the crop. In landscapes rich with predator sources, regardless of predator mobility, contribution of an on-farm refuge has negligible effect on accumulation of predators in the crop.
- Results of the field study that tested model predictions show an on-farm refuge for beneficial insects near the crop results in more beneficials (parasitic wasps) accumulating in the crop. This effect is more pronounced when the landscape contribution of beneficial insects is low.

• Student run laboratory experiment - How many pests do predators eat?:

- Two common predators of vegetable pests consume 39 and 60 aphids per day, respectively, and the more aphids available the more they eat.

Extension Highlights

- Results were communicated at four grower workshop, one national conference, two international conferences (funded invitation), one University lecture, three grower magazine articles, and two published manuscripts.

Recommendations Future R&D should focus on: 1) trialling best-bet on-farm refuge options for vegetable production systems in the different regions, 2) developing decision-support tools to assist growers with plant selection (both native and agronomic), sourcing seed and tube stock, and implementation, and 3) investigating how the condition of native remnant vegetation affects the pest load and habitat for beneficial insects. Some remnants contained mostly native plants, while others are overgrazed, contain broad-leaf weeds known to harbour pests and disease of vegetable crops.

INTRODUCTION

With increasing costs of inputs, pest damage, planned changes to land management legislation around water courses and continued pressure from urban encroachment, an integrated approach to vegetable pest management and land management is required. Further, trend forecasting is showing that consumers are becoming more conscious of environmental sustainability of production. These trends combined with our previous work (HAL projects VG05014, VG06024), results from this study, and studies from around the globe are highlighting the benefits of managing agricultural landscapes to capture ecosystem services of pest control. As we previously demonstrated in HAL projects VG05014 and VG06024:

1) most species of pests and natural enemies are multi-habitat users, and there appears to be species-specific preference for different habitats, 2) several pests of vegetable crops prefer weeds, e.g. jassids on exotic grasses and thrips on broad-leaf weeds, 3) the majority of native plants do not harbour pests of vegetable crops, and there are many no-low risk options for revegetation, 4) edge habitat between native remnant vegetation and crops support many species of beneficials and sometimes pests (e.g. Jassids on grasses) and there is a net immigration from remnant vegetation to crops at different times of the year. These findings tell us that pest control strategies need to be considered at the scale of the field, the farm and the surrounding landscape.

This project, HAL VG07040, was developed to integrate pest control at the different scales to disadvantage pests, and better capture natural pest control services. Beneficial insects provide important ecosystem services, controlling insect pests that result in savings of billions of dollars per year. For example, the annual ecosystem service of pest control is estimated to amount to US$ 4.49 billion in the USA alone (Losey and Vaughan 2006) and $400B/annually worldwide (Costanza *et al.* 2007). However, the mechanisms behind pest control by natural enemies have not been elucidated, and pest populations frequently reach outbreak levels. Pest populations are regulated by factors operating at multiple spatial scales. At the scale of a landscape, natural habitats and crops act as sources of beneficial insects that attack the pest in the field of interest, with increasing recognition that beneficial insects are affected at wider spatial scales, as they usually develop populations in multiple habitats (Polis *et al.* 1997; Landis *et al.* 2000; Tscharntke and Brandl 2004; Landis *et al.* 2005; Schellhorn *et al.* 2008). The abundance and richness of insect predators are affected by landscape structure (Thies *et al.* 2003), which in turn can result in higher predation on pests (Kruess and Tscharntke 1994; Gardiner *et al.* 2009; Chaplin-Kramer *et al.* 2011; Gagic *et al.* 2011). However, each of these mechanisms depends on the dispersal ability of the pests and their natural enemies.

Given that growers do not have control of land beyond their own property, the only active management option is on-farm refuge to capture, host and facilitate the movement of beneficial insects into crops. This may be achieved through the provision of “on-farm” refuges such as wildflower strips that provide resources for the predatory and parasitoid species sought for pest control, unsprayed sections of crop, perennial forages or strips of planted native vegetation, thereby conserving beneficials during spraying. To optimally design and place these refuges requires that we first understand the contribution that these on-farm or established habitats in relation to other sources of beneficial insects (namely environmental or landscape sources). If there is a large “landscape source” of beneficial insects nearby is there any value in maintaining an on-farm refuge? What is the cost of not maintaining an on-farm refuge when the landscape contribution is small? How does this change for beneficial insects with different dispersal capacities?

One of the key recommendations from past projects, HAL VG06024, was to determine the response time of beneficial insects to pests in cropping systems near remnant vegetation and the scale of changes in vegetation management to delay pest colonization. The aims of this project (HAL VG07040) were to investigate: 1) the impact of early predation on pest populations and how pest suppression was affected by land-use and the sources of natural enemies at multiple spatial scales, e.g. farm, neighbouring farms, and landscape; 2) the contribution of an on-farm refuge for beneficial insects in landscapes with few versus many sources of beneficial insects, and 3) the potential of two commonly observed predators to eat pests.

We answered these questions by: 1) conducting extensive landscape scale experiments on 28 fields on farms across the Lockyer Valley, 2) sampling for beneficial insects in 460 habitats throughout the valley, 3) developing a spatially explicit landscape model to determine: a) how the presence of natural enemy source habitat at the landscape scale influence the benefit of established on-farm predator refuges near crop fields, b) how the dispersal capacity of predators influences this process? 4) experimentally testing in the field the predictions of the spatially-explicit landscape model for refuge potential, and 5) conducting a student lead laboratory experiment testing the voracity of two common predators of a pest of vegetable crops.

In the research reports that follow the information generated from extensive landscape scale experiments and habitat sampling is found in Research Report I - *‘Is there a benefit from predators arriving early to the crop? What’s the role of the farm and the surrounding landscape?’* The information generated from developing spatially explicit landscape models and field testing of model predictions on the benefit of on-farm refuges is found in Research Report II - ‘*Early and fast crop colonization: the role of on-farm refuges in high beneficial landscapes versus low beneficial landscapes?*’ The information generated from laboratory studies evaluating the voracity of predators of a vegetable pest is found in Research Report III – *‘How many aphids can the striped ladybird beetle and the red and blue beetle eat?’*

I.

Early arrival of predators to crops: Is there a benefit and what's the role of the surrounding landscape?

Alejandro C. Costamagna, Nancy A. Schellhorn
CSIRO Ecosystem Sciences

Introduction

Beneficial insects provide important ecosystem services controlling insect herbivores (pests) that result in savings of billions of dollars per year. For example, the annual ecosystem service of pest control is estimated to amount US$ 4.49 billion in the USA alone (Losey and Vaughan 2006). However, the mechanisms behind pest control by natural enemies have not been elucidated, and pest populations frequently reach outbreak levels. Pest populations are regulated by factors operating at multiple spatial scales. At the scale of a landscape, natural habitats and crops act as sources of beneficial insects that attack the pest in the field of interest, with increasing recognition that natural enemies are affected at wider spatial scales, as they usually develop populations in multiple habitats (Polis *et al.* 1997; Landis *et al.* 2000; Tscharntke and Brandl 2004; Landis *et al.* 2005; Schellhorn, *et al.* 2008). The abundance and richness of insect predators are affected by landscape structure (Thies, *et al.* 2003), which in turn can result in higher predation on herbivores (Kruess and Tscharntke 1994; Gardiner *et al.* 2009; Chaplin-Kramer *et al.* 2011; Gagic *et al.* 2011).

At least two different mechanisms can explain higher levels of pest suppression in certain landscapes than in others. First, landscapes that are structurally complex may simply harbor more natural enemies than simple landscapes, a scenario corroborated in previous empirical studies (Kruess and Tscharntke 1994; Thies and Tscharntke 1999; Gardiner *et al.* 2009; Gardiner *et al.* 2009). A second mechanism may relate with the timing of predator arrival to the crop field, i.e. field crops located in landscapes with higher proportion of natural enemy habitats are more likely to have one of those sources nearby, allowing quick access of natural enemies to any pest colonizing those crops. It is important to assess the importance of this mechanism, as it has a practical application: if growers identify sources of natural enemies in the landscape, they can modify to certain extent the distribution of their crops in the farms in order to maximize pest suppression. Theoretical models suggest that to achieve pest suppression it is critical that predators attack pests as early as possible, when populations are still low (Chang and Kareiva 1999; Gardiner *et al.* 2009). Although there are empirical studies that support this theoretical prediction, those studies were not designed to separate the effect of early impact from the effect of longer impact of predators on pests (i.e. predators arriving early exert predation for a longer period of time than those arriving late) (Landis and Van der Werf 1997; Fox *et al.* 2004; Fox *et al.* 2005; Costamagna and Landis 2006).

We conducted a large scale field study to assess the effect of early predation on pest populations in the Lockyer Valley and how this control was affected by the sources of natural enemies at the landscape. Our hypothesis is that landscapes with more abundant and closer sources of beneficial insects will have better pest control by natural enemies. Thus, understanding what are the sources of beneficial insects and at what distance they need to be located to provide effective pest control, will allow developing habitat management plans for horticultural farms.

Materials & Methods

We used the melon aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) as a model insect pest. Melon aphids are polyphagous with a world-wide distribution and a reported host range of more than 700 plant species (Hollingsworth *et al.* 1994; Wool and Hales 1997; Capinera 2001). In Australia, *A. gossypii* has been collected from more than 200 different hosts, and is a major pest of horticultural crops and cotton (Swaine *et al.* 1991; Fitt 1994; Wool and Hales 1997; Herron *et al.* 2001). Insecticide applications are widely used to control *A. gossypii*, despite the potential for the development of insecticide resistance and the environmental costs of pesticides (Hollingsworth *et al.* 1994; Wilson *et al.* 1999; Herron *et al.* 2001).

We conducted our experiments on bare fields on grower properties that amongst several crops were also growing melon and pumpkin. This allowed us to standardize the treatment and capture the effects of the local versus landscape context on the predators of melon aphid attacking cucurbit plants. The field experiments were conducted in November 2009 (early season test) and March 2010 (late season test). We expected to have higher natural enemy populations and therefore higher aphid suppression at the late season test. We are aware that melon is not part of the vegetable industry levy, but it allows for a nice experimental system were we can produce seedlings, and pests, thereby establishing treatments in the field.

We selected 28 horticultural landscapes representing a gradient of natural vegetation areas and crop diversity in the Lockyer Valley (**Fig. 1**). In four cases it was possible to repeat the test in the same fields during both tests, but in most cases entirely new fields were used. We chose this approach because it allows for a broader representation of farms and greater complex of pests and natural enemies.

We also used melon plants infested with silverleaf whitefly nymph, but this part of the experiment was unsuccessful.

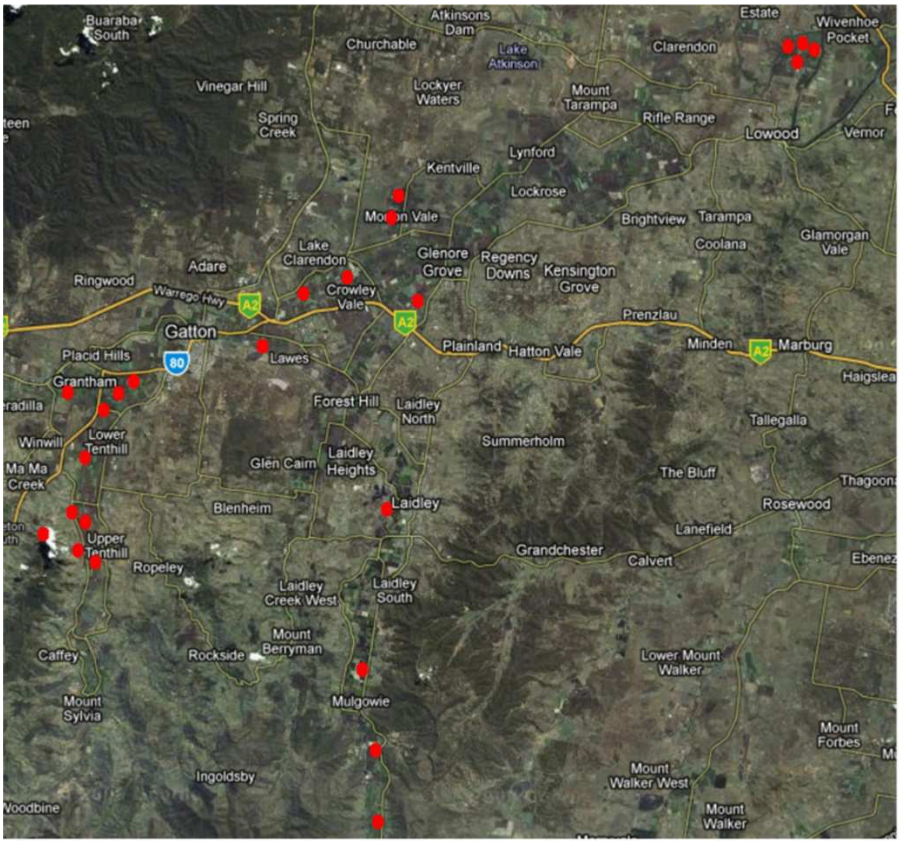


Fig. 1. Location of the 28 experimental field on farms in the Lockyer Valley (4 fields were used during both seasons and therefore the overlapping points do not show in the figure).

Early versus late predation effects

In each field we tested the effects of early versus late field colonization by natural enemies from habitats outside the field on melon aphid suppression. To rule out any potential local effect of the focal fields, we followed three strategies. First, the experiment was conducted on fallow fields (but always within pumpkin growing farms), to avoid confounding effects of different crop types and plant phenologies, and to minimize the number of predators present in the field before our manipulations. Second, we used sentinel potted plants, to rule out soil differences. And finally, all treatments were enclosed in cages (see below) that minimize the impact of resident predators (i.e. ants and ground predators), which are less affected by the landscape context, and therefore not expected to show significant responses to the presence of sources of beneficial insects outside the fields studied.

During the early season trial, in each bare-soil field selected for the study, eight locations within the field were used, locating four of them close (5 m), and four of them far (20 m) from the field border. Locations were separated between each other by 15 m. We did not observe differences between close and far from field border during the early season trial, and therefore for the late season trial we set five locations per field at an intermediate distance from the border (10 m). In each of the eight locations, four manipulations were conducted in a factorial design to separate the effect of early (first week of the experiment) versus late predation (second week), using natural enemy exclusion cages. Therefore, the four treatments conducted were: 1) continuous predation (cages open to predators), 2) early predation (cages open to predators for 1st week, then closed), 3) late predation (cages closed to predation during 1st week, then open for the 2nd week), and 4) continuous natural enemy exclusion **(Fig. 2)**. Early (2) and late (3) predation treatments were achieved by swapping the cage covers after the first week of manipulation. This design allow us to separate the intrinsic effects of predators suppressing aphids early in the pest colonization process (measured by the early predation treatment), from the effects of predation of predators arriving also in the first week but sustaining aphid suppression during the two weeks (measured by the continuous predation treatment), i.e. this last treatment combines both early predation with two weeks of predation.

All treatments were enclosed by two white rectangular plastic containers that contained a potted plant of pumpkin maintained in place by four empty pots (**Fig. 2**). The external plastic container was secured to the ground by a metal tent stake put through a hole in the bottom, therefore an inner container, without any bottom holes was included to prevent ants and other ground predators to enter the cages. The external container was coated in the outside with a strip (5 cm wide) of Fluon to create a slippery barrier that prevents ground predators to climb into the containers. The pumpkin plants within the predator exclusion cage were completely covered by a fabric of spun bonded polypropylene that allows natural sunlight to reach the plants but prevents insect movement (Greenharvest.com.au), supported by a plastic mesh (**Fig. 2**). The treatments exposed to predation were covered by a “sham cage” that consisted in the same plastic mesh as in the exclusion cage but covered only in the upper part by the polypropylene fabric, allowing predator access to the plants on all sides of the cage. This polypropylene “roof” served both as a control for microclimate conditions between treatments and as a protection from mortality cause by intense rainfall. Therefore, the “sham cages” used in the early (during first week), late (during second week) and continuous (during both weeks) predation treatments are designed to measure in a conservative manner the impact of predation as the only mortality factor acting upon the aphid populations. However, although in other systems sham cages have been used effectively to test for the impact of predation on aphids (Costamagna and Landis 2006; Costamagna *et al.* 2007; Costamagna *et al.* 2008), we cannot completely rule out any interference between the presence of the roof and the impact of predators, and therefore we added a fifth treatment of continuous predation without cover in seven of the fields in the late season trial. Comparison of this completely open with sham cages would measure interference of the sham cage with predation in the absence of significant rainfall events.

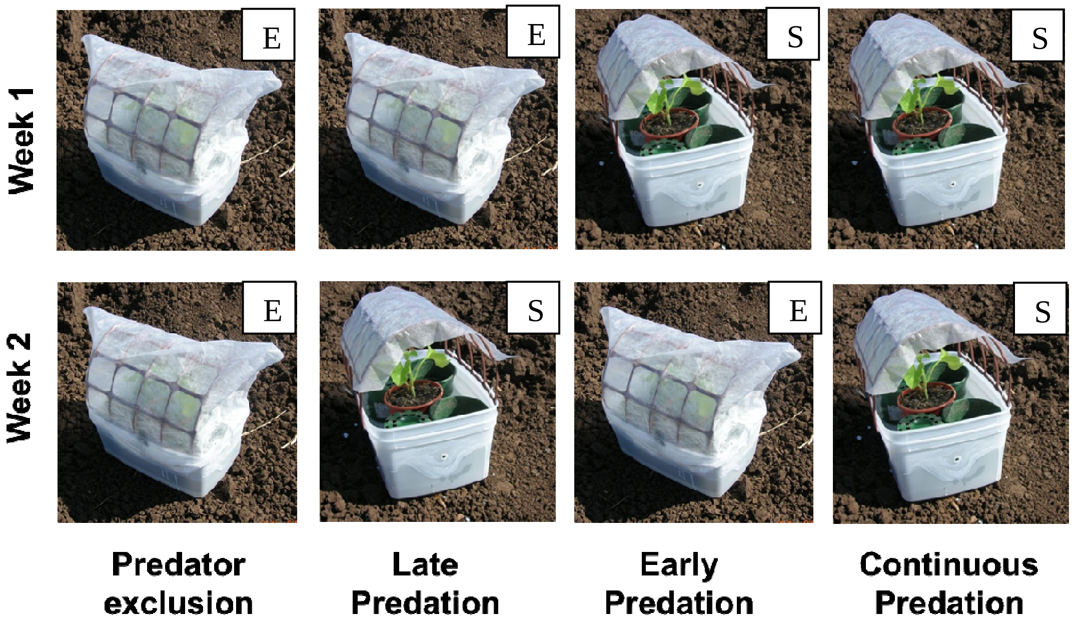


Fig. 2. Experimental design used to test the relative effects of early versus late predation on aphid pests: **E** = predator exclusion cages, **S** = sham cages (open to predation). During the second week of the experiment, E and S cages were swapped between late and early predation, to limit predation to only one week in both treatments.

In each pumpkin plant we placed 10 (early season trial) or 12 (late season trial) apterous (wingless) female melon aphids that were reproductive or nearly reproductive, following the methods described in Costamagna *et al.* (2006). After the first week of the experiment, we counted aphid populations in all plants and swapped cage covers between the early and late predation treatment, to generate the four final treatment combinations. A final count of aphids was performed after the second week of manipulation. A total of 763 aphid populations (eg. 7600+ aphids) in caged plants were manipulated and quantified for this experiment.

The plants used in these trials were initially grown under greenhouse conditions, and shortly before the field trials they were exposed to outside conditions to increase their hardiness. Pots were maintained in trays covered by double non-woven, spun-bound polypropylene cloth to maintain plants free of insects. Despite the efforts to increase their hardiness, plants response to field conditions varied in each landscape, resulting in some fields in which our potted plants performed poorly. This was more noticeable during the second trial, when record-high rainfalls during February 2010 delayed our field experiment for two weeks, and the plants had to be maintained under covered conditions to protect them from hail and strong rainfall. To account for this, we only included in the analysis of the results those fields in which the conditions were adequate for aphid population growth. We quantified the suitability for aphid growth by testing whether it was significant population growth (i.e. final number of aphids / initial number of aphids > 1) in the predator exclusion treatment, using one-sample t-tests. As a result of that condition, 19 fields (12 in 2009, 7 in 2010) were included in the final analysis.

Data analysis: aphid population growth was analysed using a generalized linear model with a negative binomial distribution and a log-link function (glm.nb function, Venables and Ripley 2002; R Development Core Team 2011). Using the log-link allow us to model aphid growth as exponential population growth, which has been demonstrated accurate for aphid populations during the time frames used in our experiment (Costamagna *et al.* 2007). Specifically, we fitted models that include initial number of aphids, treatment in week 1 x time, treatment in week 2 x time, field, year, and their interactions as fixed factors. Since most fields are not repeated across the two years of the experiment, fields and years were used in separate models. We present and analysis of deviance for all the significant competing models using Akaike's Information Criteria adjusted for sample size (AICc, lowest indicate best support by data) and Akaike's weights (*Wi*, highest indicate best support by data) to select the best models (Burnham and Anderson 2002). We used Log-likelihood ratio tests to evaluate the contribution of each additional variable to explain the data (Venables and Ripley 2002). Since we found a significant field x predator manipulation interaction, we further analyse the effects of predator manipulation using pre-planned contrasts among them within each field. One sample t-tests were performed using R (R Development Core Team 2011).

Landscape composition effects on pest suppression

Landscape composition around each field studied was quantified to a radius of 2 km, following the methods described in Thies *et al.* (2003) and Gardiner *et al.* (2009). We used aerial images from Google Earth as our basic template to digitalize the maps of each landscape using ARC GIS 9.1 (ESRI 2005). During the two field trials, we conducted intensive ground verification to obtain detail information of all the crops and vegetation covers present during the periods under study, and used that information to correct and update the original digital maps. Areas where access was not granted were given a value of zero and therefore excluded from analysis; these areas averaged only 2.4 ± 2.3% of the landscape (mean ± SD; range = 0 – 8.9%). We identify 30 different land cover types and used them to estimate habitat diversity, using Simpson's Diversity Index (Gardiner *et al.* 2009): $D = 1/\Sigma (p_i)^2$, where *pi* is the proportion of habitat in the *i*th land-cover category, with *D* increasing with habitat diversity. We estimated habitat diversity and % area occupied by major land cover categories at five spatial scales: 0.25, 0.5, 1.0, 1.5, and 2.0 km from the field center (**Fig. 3**). Crops that occupied less than 3% of the landscape were combined together in a category called "other crops", with the exception of Cucurbits, that were maintained separate for analysis, as they were the model system of our study.

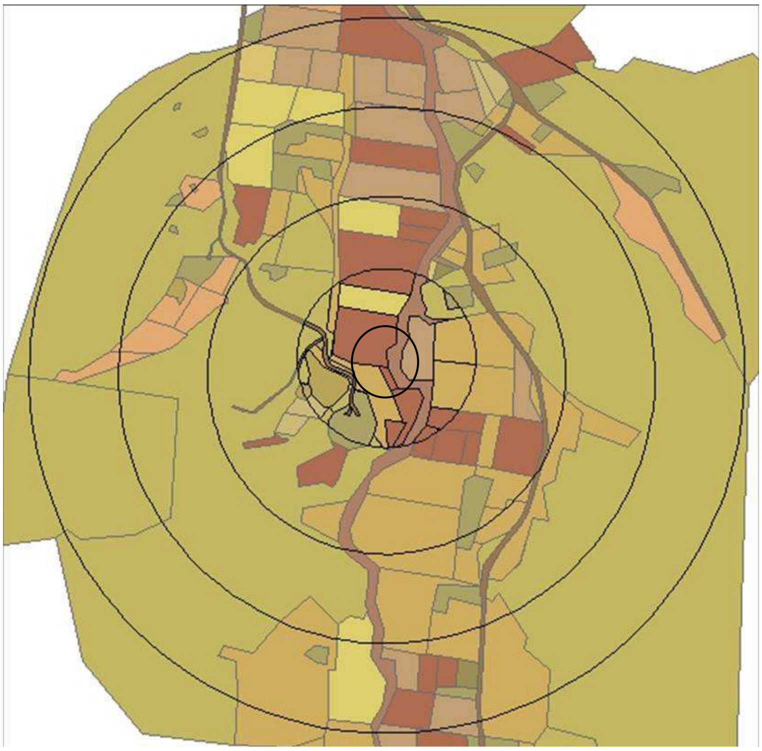


Fig. 3. Example of a digitalization of a landscape at the Lockyer Valley, Queensland, Australia. Different colours indicate different land cover categories. The five concentric circles represent radius of 0.25, 0.5, 1, 1.5 and 2 km from the field use for the experimental manipulations of predation. We calculated the area of each land cover within each circle and then estimated the percentage area cover by each of them at the five spatial scales

Data analysis: We investigated the relationship between aphid suppression and the composition of the horticultural landscapes using multiple linear regression analysis (MLR). We constructed separate MLR models for each predator manipulation treatment at each spatial scale. We used the number of aphids surviving in the predator exclusion treatment as a control for any environmental effects of each landscape on aphid growth, and therefore we introduce this as the first predictor in all models. We started with full models, including all the landscape predictors and using the *step* option in the *lm* package of R to perform stepwise backward selection of predictors, minimizing the AIC (R Development Core Team 2011). The resulting models were further investigated by removing correlated predictors, to minimize multi-collinearity (Neter *et al.* 1996). In addition, we fitted models for all other predictors that were individually correlated with the final number of aphids observed in each treatment (tested using Pearson coefficient to correlation) but were not included in the final model produced by stepwise regression. For each predation treatment and spatial scale studies we present all the models with substantial support by the data, following the rule of Burnham & Anderson (2002), i.e. models with $\Delta i < 2$. The model with the lowest AICc for each predator treatment indicates the landscape predictors with the most explanatory power and the scale at which they affect predation. Finally, we present partial correlation coefficients to indicate the strength and direction of the relationship between each predictor and aphid survivorship in the experimental manipulations.

Landscape functional effects on pest suppression

We classified each of the habitats within a scale of 1 km radius from the experimental fields as sources of natural enemies (i.e. natural enemies present) or matrix (i.e. areas that does not contribute to natural enemy populations in the landscape). We assessed the presence of natural enemies using sticky traps. Each sticky trap (ST) consisted of a transparent polypropylene cup (250 ml) coated with Tangletrap and held by bulldog clips to a bamboo stick just above the canopy level of the ground vegetation, or to a maximum height of approximately 50 cm above ground. In habitat with trees (i.e. Riparian non-crop, bush-land) we included a second ST attached to a tree at a height of 1.5 – 2 m from the ground.

We deployed one ST within 20 m from the corner of any accessible field or habitat with vegetation cover (i.e. crop, weed, or non-crop habitat (a mix of native vegetation and exotic weeds) within 1 km radius from our focal field in each landscape under study (17.9 ± 4.4 samples / landscape, mean ± SD). ST were deployed within the three initial days of the first week of experiment and recover in similar period of time during the second week of experiment, for mean collection times of 6.9 ± 0.9 days (2009, range 5 – 8 days), and 9.2 ± 0.4 days (2010, range 8 – 10 days). We sampled all major land cover types present in the landscapes, at a rate of (ST / land cover): Cucurbits = 72, Grassland = 44, Lucerne = 68, non-crop bush land (eg. mix of native vegetation and exotic weeds) = 25, Other Crops = 157 and Riparian non-crop vegetation (eg. mix of native vegetation specific to water courses and exotic weeds) = 94. We also deployed one ST at a central location within our caged manipulations, and those ST were replaced by new ones when cages were swapped during the first week of the experiment, obtaining a separate measure of natural enemy abundance for each week of the experiment (n = 262). All ST samples were expressed as number of insects / 7 days, to allow comparison among different collection times. Natural enemies in high versus low ST did not differ, and therefore those were combined, using their mean for statistical analysis.

Data analysis: we performed MLR models as described in the previous section to relate aphid suppression with predictors that classify the habitats according to their function, rather than their vegetation cover. We therefore constructed new predictors of aphid suppression, based on the areas that acted as sources of natural enemies. We considered that an area was a source if it contained at least one natural enemy in our sampling.

Landscape predictors were classified broadly as combining all land covers together or calculating specific values for the major land cover types (**Table 1**). For the first group we constructed eight predictors to test for: 1) natural enemy effects *per se* (i.e. without using information of the area of the land cover where they were collected), 2) the area with natural enemies in the landscape *per se* (i.e. classifying areas as with or without natural enemies), 3) natural enemy load effects (i.e. the number of natural enemies present multiplied by the area of that habitat), and 4) distance from source effects (i.e. how far natural enemies need to travel to reach the experimental field). These eight basic predictors were calculated for each of the three scales contained within the 1 km radius sampled with ST (i.e. 0.25, 0.5 and 1.0 km radius), resulting in a total of 24 predictors.

Table 1. Predictors of landscape effects on aphid suppression incorporating information about the natural enemies present on them.

Predictor	**Calculation**
Combining all Land Covers	
Natural Enemy (NE) effects	
Mean NE	Mean all ST in each landscape
Area effects	
Mean area with NE	$area_{(NE)}$ / # areas sampled with ST
Proportion area with NE	$area_{(NE)}$ / total area sampled with ST
Proportion number of areas with NE	# $ST_{(NE)}$ / total # ST
NE load effects	
Mean load NE	[Σ($area_{(NE)}$ x NE)] /# areas sampled ST
Adjusted load NE	Mean load NE / area sampled with ST
Distance from source effects	
Distance to nearest source	Distance to closest $area_{(NE)}$
Mean distance to source	Σ (distances to $area_{(NE)}$) / # $areas_{(NE)}$
Effects per Land Cover	
Area effects	
Mean $area_{(LC)}$ with NE	$area_{(LC)\ (NE)}$ / # $areas_{(LC)}$ sampled with ST
Proportion $area_{(LC)}$ with NE	$area_{(LC)\ (NE)}$ / total $area_{(LC)}$ sampled with ST
Proportion number of $areas_{(LC)}$ with NE	# $ST_{(LC)\ (NE)}$ / total # $ST_{(LC)}$
NE load effects	
Mean load $NE_{(LC)}$	[Σ ($area_{(LC)(NE)}$ x NE)] /# $areas_{(LC)}$ sampled with ST
Adjusted load $NE_{(LC)}$	Mean load $NE_{(LC)}$ / $area_{(LC)}$ sampled with ST

Notes: $area_{(NE)}$ = areas with at least one natural enemy; $area_{(LC)}$ = areas of an specific land cover; ST = sticky trap.

We also calculated in a similar way predictors for area and natural enemy load effects separately for each land cover, which resulted in 40 additional predictors. For this second approach, we extrapolated the number of natural enemies found in the fields sampled to all fields with that land cover present in the landscape. Therefore, this approach to develop landscape predictors constitutes a hybrid between using pure landscape metrics without information on natural enemies (the previous section and the most widely method used) and using only information about natural enemy abundance, disregarding the vegetation cover of the habitat sampled. We estimated the land cover predictors only at the 1 km radius scale, as there were not enough samples for all of them in each landscape at each of the two smaller spatial scales. Finally, we construct predictors separately for three different predator groupings: 1) mobile predators (insect with flying instars captured by ST), 2) spiders (capture by ST by ballooning, by proximity with crops canopy, or by climbing), and 3) all predators combined.

Due to the higher number of potential predictors than the actual number of landscapes, to avoid over-fitting effects we did not fit all the potential MLR models to the data. Instead, we explore separately the relation between each predictor and aphid suppression using Pearson correlations. We only incorporated into MLR models predictors that have significant correlation with aphid suppression (estimated conservatively at $P < 0.10$, in order to avoid overlooking important variables). Predictors were tested against predation in the continuous predation treatment only, as natural enemy sampling with ST at the landscape scale overlapped both the first and second week of the experiment, therefore preventing to estimate predator numbers separately for early and late predation. As with the MLR models use in the previous section, the number of aphids surviving in the predator exclusion treatment was used as the first predictor in the model to control for any potential landscape specific environmental effects on aphid population growth. Model selection statistics were estimated by the same methods described in the previous section. Comparisons of predator abundance among major land cover types were performed using Analysis of Variance, and treatments were compared using t-tests adjusted by the Bonferroni method for multiple comparisons (R Development Core Team 2011).

Results

Early versus late predation effects

Predation by flying natural enemies caused high mortality on melon aphid populations, with a 60% reduction observed when predators had continuous access to the aphids from the initial week of the experiment in comparison with the predator exclusion treatment (**Fig. 4**). When predation was restricted to just one week, we observed a small trend of higher aphid suppression if predators had access during the first week (early predation, 39% aphid reduction) than if predators arrive in the second week (late predation, 34% aphid reduction, **Fig. 4**). These results show that it is crucial that predators arrive to the field shortly after the pests to achieve maximum suppression. Statistical analysis of the data showed no difference between early and late season trials (season and its interaction term effects, **Table 2**).

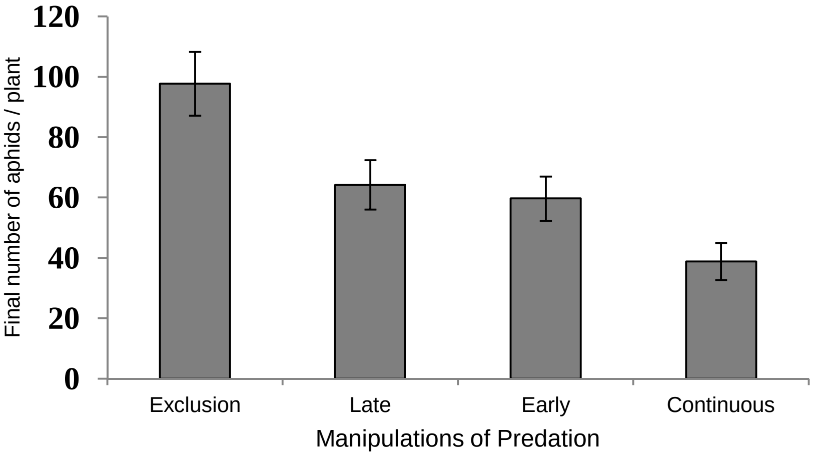


Fig. 4. Melon aphid populations after four predator manipulations during the two weeks of the experiment, combining all fields used in the study (mean ± SEM, n = 19 fields).

By contrast, predation and landscape have significant impacts in aphid population growth (**Table 1**). However, the model with the most support by the data was the model that included an interaction between predation and landscape (lowest AICc and Log-likelihood, highest *Wi*, **Table 2**), indicating that continuous, early, and late predation impacts varied across the landscapes studied.

Out of the 19 landscape tested, we observed significant aphid suppression in 14 landscapes when predators have continuous access to aphids, in 9 when they arrive early but only for one week, and in 6 when they arrive late (**Table 3**). Continuous predation resulted in higher suppression than either early or late predation (restricted to only one week) in 10 landscapes, and in 5 of those it was higher than both (Table 2). This indicates that the longer exposure to predators significantly reduced aphid populations in comparison with those protected from predation during one week. Early predation, which showed an overall trend of higher suppression than late predation (**Fig. 4**), resulted more effective than late predation in 4 landscapes, indicating that in those landscapes arriving early was more effective to suppress aphids. However, we also found the opposite trend in two landscapes, where late predation was more effective than early predation (**Table 3**). These results suggests that in those landscapes there was a numerical response of predators, i.e. more predators attacked the aphids after their populations build up than during the initial week of the study, when aphids populations were smaller.

Table 2. Summary of model selection statistics and comparison of variable effects for evaluating predation of melon aphid by natural enemies in the Lockyer Valley, Queensland, Australia (in bold the best explanatory model).

Statistical Model	*df*	AICc	*Wi*	Log-lik.	test	*L* Ratio
1- Initial aphids (Null model)	504	5131.38	0.00	-5127.36		
2- Initial aphids + season	503	5133.40	0.00	-5127.35	1 vs 2	0.01
3- Initial aphids + predation	499	5093.46	0.04	-5079.23	1 vs 3	48.13
4- Initial aphids + predation x season	497	5092.56	0.06	-5074.19	3 vs 4	5.04
5- Initial aphids + landscape	486	5111.29	0.00	-5069.55	1 vs 5	57.81
6- Initial aphids + predation x landscape	**429**	**5087.04**	**0.91**	**-4904.91**	**3 vs 6**	**174.32**

References: *df* = degrees of freedom; AICc = Akaike's Information Criterion adjusted for sample size; *Wi* = Akaike's weights; Log-lik. = Log-likelihood; L Ratio = ratio of Log-likelihood tests; initial aphids = effect of the initial number of aphids on final population number (null model); season = early versus late season trial; predation = effects of predator manipulations; landscape = effects of the landscapes used in the study.

Table 3. Final number of aphids / plant (mean + SE, back-transformed data) after predator manipulations in each landscape studied. Different letters in each row indicate significant differences among treatments (*P* < 0.05, pre-planned t-test contrasts, significant suppression is indicated in bold).

Trial	**landscape**	**Pred. Exclusion**				**Late Predation**				**Early Predation**				**Continuous Pred.**			
Early season	1	33.4	+	20.5	a	31.3	+	24.8	a	20.3	+	16.1	a	43.4	+	26.7	a
	2	63.8	+	32.6	a	**19.9**	**+**	**13.1**	**b**	**26.1**	**+**	**17.4**	**b**	**2.0**	**+**	**1.2**	**c**
	3	97.0	+	45.1	a	**24.3**	**+**	**14.6**	**b**	**22.4**	**+**	**13.9**	**b**	**1.1**	**+**	**0.7**	**c**
	4	191.5	+	91.1	a	89.3	+	54.1	ab	**75.4**	**+**	**45.7**	**b**	**55.5**	**+**	**26.6**	**b**
	5	69.5	+	33.6	a	80.7	+	49.6	a	114.6	+	70.4	a	62.8	+	30.3	a
	6	50.3	+	24.8	a	50.6	+	31.8	a	39.9	+	25.2	ab	**20.3**	**+**	**10.1**	**b**
	7	92.8	+	77.3	a	62.6	+	68.4	a	68.3	+	74.6	a	23.6	+	19.8	a
	8	214.5	+	101.4	a	164.7	+	99.1	a	**16.2**	**+**	**10.0**	**b**	**10.9**	**+**	**5.4**	**b**
	9	59.6	+	21.3	a	69.7	+	31.3	a	93.5	+	42.0	a	**34.0**	**+**	**12.3**	**b**
	10	63.6	+	40.9	a	28.2	+	23.4	ab	**5.6**	**+**	**4.9**	**c**	**13.1**	**+**	**8.6**	**bc**
	11	150.3	+	67.5	a	87.9	+	50.2	ab	**51.3**	**+**	**29.5**	**b**	**61.6**	**+**	**27.9**	**b**
	12	101.6	+	60.6	a	83.7	+	52.1	a	99.6	+	61.7	a	**12.1**	**+**	**6.1**	**b**
Late season	13	99.0	+	36.2	a	**34.0**	**+**	**11.3**	**b**	80.4	+	26.0	a	**33.2**	**+**	**11.0**	**b**
	14	76.0	+	35.2	a	**22.7**	**+**	**12.9**	**b**	43.4	+	17.8	ab	33.0	+	15.5	ab
	15	127.0	+	27.3	a	**74.5**	**+**	**18.4**	**b**	**74.5**	**+**	**18.4**	**b**	**37.8**	**+**	**8.6**	**c**
	16	109.6	+	27.0	a	105.4	+	25.9	a	**85.3**	**+**	**23.9**	**b**	**91.8**	**+**	**22.6**	**b**
	17	75.2	+	24.0	b	66.0	+	21.2	b	95.0	+	30.2	a	**52.6**	**+**	**16.9**	**c**
	18	97.7	+	38.5	a	74.0	+	21.9	a	**53.8**	**+**	**16.0**	**b**	88.8	+	29.6	a
	19	84.0	+	24.2	a	**51.3**	**+**	**17.0**	**b**	68.5	+	22.6	ab	**59.8**	**+**	**17.4**	**b**
Landscapes with aphid suppression								6				9				14	
Landscapes with late > early suppression								2									
Landscapes with early > late suppression												4					
Landscapes with continuous > late or early suppression																10	
Landscapes with continuous > late & early suppression																5	

Landscape composition effects on pest suppression

A total of 4,670 land cover areas were mapped across the 19 landscapes analysed (245.8 ± 66.2 areas / landscape, mean ± SD, **Table 4**). Landscape composition was very variable, but in general it was dominated by grasslands and pastures (25.9% of the total area, range 5.5 – 44.8%), fallow fields (21.9%, 3.6 – 48.3%), and non-crop bushland (21.1%, 3.0 – 55.9%). The only single crop type that represented more than 3% of the landscape was Lucerne (5.8%, 0.4 – 11.8%). Cucurbits accounted for 1.6% (0.0 – 4.0%), and all other crops combined represented 8.6% (1.2 -20.0%) of the landscape area. Finally, we observed small percentages of the landscape with houses (4.4%), major paved roads (1.8%) and natural or artificial water reservoirs (1.9%).

Table 4. Land cover types identified in the landscapes studies in the Lockyer Valley, during the experiments of November 2009 and March 2010. Major land categories represent areas > 4%, with the exception of Cucurbit crops, which was considered separately as it was the focal crop under study. Major land categories were used in multiple regression analysis to test their influence on aphid suppression, diversity categories were considered to estimate habitat diversity.

Major land categories	Diversity land cover categories	% area	# areas
Grassland	Grassland (pasture)	25.920	828
---	Fallow land (stubble or bare-soil)	21.863	935
Non-crop (bushland)	Non-crop (remnant bushland) [1]	21.088	210
Lucerne	Lucerne	5.833	275
Non-crop (riparian)	Non-crop (remnant riparian) [1]	4.540	26
Cucurbits	Cucurbits (melon, watermelon)	1.644	132
Other crops[2]	Sorghum	2.194	112
	Weedy fields	1.670	88
	Corn	1.011	34
	Beans	0.993	39
	Brassicas	0.794	44
	Turf	0.603	53
	Tomato	0.252	18
	Onion	0.244	16
	Spring onions	0.182	13
	Carrots	0.124	4
	Orchards	0.118	11
	Potato	0.113	7
	Capsicum	0.096	6
	Cereal grains	0.081	8
	Lettuce	0.055	6
	Sunflower	0.038	6
	Celery	0.025	5
	Hay	0.022	1
	Beetroot	0.016	1
	Silver beet	0.014	2
	Sweet potato	0.003	1
---	Houses and urban[3]	4.359	949
---	Roads[3]	1.803	136
---	Water (lakes, water storage ponds)[3]	1.892	465

[1] Non-crop (remnant bushland) represents uncultivated and sometimes grazed land containing a mix of native and exotic plant species. Non-crop (remnant riparian) is similar to non-crop (bushland), but along water courses such as creek banks.

[2] Other crops include all crops representing < 4% of area (except cucurbits)

[3] Fallow fields, houses, roads, and water bodies were not considered in the multiple regression analysis as they are not a significant source of insects.

Aphid survival on the continuous and early predation treatments was completely independent of their potential for population growth in each landscape, measured by predator exclusion treatments (the control treatment, **Table 5**), indicating that predation during the first week completely disrupted aphid population growth. By contrast, aphids survival in the late predation treatment was highly correlated with their potential population growth in each landscape (partial correlation coefficients ranging from 0.70 to 0.82, **Table 5**), indicating that predation was not as strong as when it was delayed for a week (**Table 5**). Therefore, potential of population growth was the main predictor in all significant models of aphid survival on the late predation treatment.

At most scales investigated, predation was significantly higher in landscapes with a higher proportion of Lucerne (**Table 5, Fig. 5**). This is indicated by significant negative effects of the area of Lucerne observed at most models at various scales and for all predator manipulations, with partial correlations ranging from -0.40 to -0.68 (**Table 5**). The proportion of cucurbits and other crops were also associated with aphid decrease, but only in a reduced number of models and with minor effects. Habitat diversity also decrease aphid populations, but this effect was significant in only one model. By contrast, the percentages of grassland and native vegetation were consistently associated with higher aphid populations, suggesting that these habitats may interfere with predation.

Continuous and early predation responded to landscape composition at large scale, with the two best models explaining predation occurring at 1.5 km radius from the experimental fields (adjusted r^2 =0.45, and r^2 = 0.48; **Table 5**, models in bold, **Fig. 5 and 6,** respectively). For both predator treatments Lucerne increased aphid suppression significantly at that scale (partial correlations of -0.63 and -0.48, respectively).

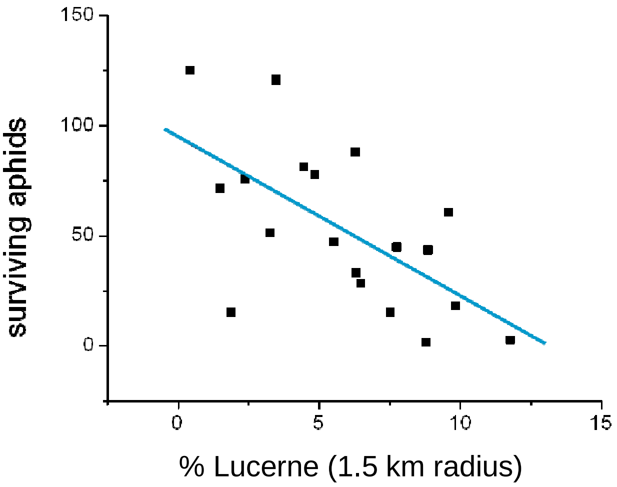


Fig. 5. Relation between the number of aphids surviving in the continuous predation treatment and the areas of Lucerne at a scale of 1km radius or 2km diameter. The higher the Lucerne area, the lower the number of aphids surviving. (see **Table 5** for the statistics of the model).

For continuous predation, grassland had a disruptive effect on suppression (partial correlation = 0.48), whereas for early predation the disruptive effect was associated with the area of native vegetation (partial correlation = 0.55). By contrast, the best model to explain late predation occurred at a smaller spatial scale, 0.5 km radius from the experimental field (adjusted r^2 =0.65, **Table 5, in bold, Fig. 7**). In addition of a large effect of aphid potential population growth (partial correlation = 0.82), there was a positive association between the area of non-crop bushland and aphid increase (partial correlation = 0.54), suggesting again a disruptive effect of non-crop habitat on aphid suppression. However, models at wider scales had also considerable support from the data, suggesting that at a scale of 2 km radius the area of Lucerne significantly increased aphid suppression (adjusted r^2 = 0.62, partial correlation = 0.63, **Table 5**, *model in italics*, **Fig. 8**)

Table 5. Summary of multiple regression models statistics for evaluating the relation between landscape land cover types and melon aphid suppression at different spatial scales in the Lockyer Valley, Australia.

Radius (km)	Model	Log-lik.	AICc	Δi	*Wi*	Adj. r^2	*P*	Partial correlations
	Continuous Predation							
	Intercept (I) + Aphid Potential Growth (A)	-88.85	185.30	10.15	---	-0.05	0.7366	
0.25	I + Riparian*	-86.69	180.98	25.74	0.00	0.16	0.0492	
0.50	---[1]	---	---	---	---	---	---	
1.00	I + Grassland* - Lucerne(*)	-84.15	179.16	4.00	0.05	0.32	0.0181	G: 0.48; L: -0.44
	I + Grassland*	-86.18	179.96	4.80	0.03	0.21	0.0291	
	I – Lucerne*	-86.66	180.92	5.77	0.02	0.17	0.0476	
1.50	**I + Grassland* - Lucerne****	**-82.15**	**175.16**	**0.00**	**0.35**	**0.45**	**0.0033**	**G: 0.48;L: -0.63**
	I + Grassland* - Lucerne** - Native Vegetation	-80.90	176.41	1.26	0.19	0.48	0.0046	G: 0.56; L: -0.68; NV: -0.35
	I - Lucerne**	-84.67	176.95	1.79	0.14	0.32	0.0066	
2.00	I - Lucerne**	-84.21	176.02	0.87	0.23	0.35	0.0042	

Table 5. (Continuation)

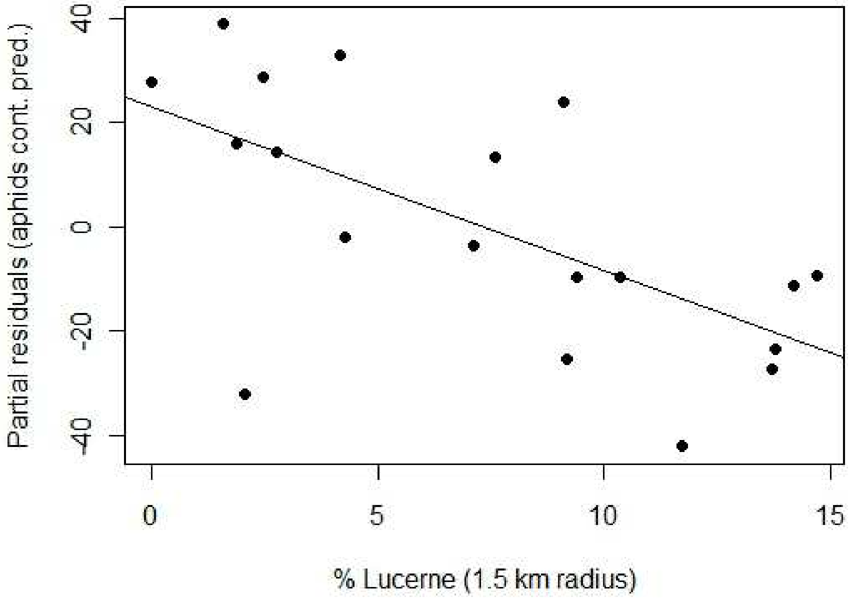
Radius (km)	Model	Log-lik.	AICc	Δi	*Wi*	Adj. r^2	*P*	Partial correlations
	Early Predation							
	Intercept (I) + Aphid Potential Growth (A)	-88.85	185.30	7.76	0.01	-0.05	0.7366	
0.25	I + Grassland	-90.93	189.46	8.92	0.00	0.08	0.1300	
0.50	I + Native Vegetation**	-86.89	181.38	0.84	0.19	0.40	0.0023	
1.00	I + Native Vegetation* - Lucerne$^{(*)}$	-85.82	182.50	1.96	0.11	0.43	0.0045	NV: 0.56; L: -0.43
	I + Native Vegetation***	-87.74	183.08	2.54	0.08	0.34	0.0051	
1.50	**I + Native Vegetation* - Lucerne***	**-84.84**	**180.54**	**0.00**	**0.30**	**0.48**	**0.0020**	**NV: 0.55; L: -0.48**
	I + Native Vegetation**	-87.34	182.27	1.74	0.12	0.37	0.0035	
2.00	I - Lucerne**	-87.34	182.28	1.74	0.12	0.37	0.0035	
	I + Native Vegetation**	-88.11	183.82	3.28	0.06	0.32	0.0073	

Table 5. (Continuation)

Radius (km)	Model	Log-lik.	AICc	Δi	Wi	Adj. r^2	P	Partial correlations
	Late Predation							
	Intercept (I) + Aphid Potential Growth (A)	-86.60	180.80	3.26	0.05	0.53	0.0003	
0.25	I + A*** + Grassland$^{(*)}$	-84.92	180.69	3.15	0.05	0.58	0.0004	A: 0.78; G: 0.37
0.50	**I + A *** + Native Vegetation***	**-83.34**	**177.54**	**0.00**	**0.25**	**0.65**	**< 0.0001**	**A: 0.82; NV: 0.54**
1.00	I + A *** - Cucurbits$^{(*)}$ - Lucerne* - OC$^{(*)}$	-80.84	180.69	3.15	0.05	0.69	0.0003	A: 0.77; C: -0.45; L: -0.58; OC: -0.49
	I + A *** - Lucerne	-84.95	180.76	3.22	0.05	0.58	0.0004	A: 0.73; L:-0.40
1.50	I + A *** - Lucerne* - OC$^{(*)}$	-82.44	179.49	1.95	0.09	0.66	0.0002	A: 0.74; L: -0.61; OC: -0.07
	I + A *** - Lucerne$^{(*)}$	-84.55	179.95	2.41	0.08	0.60	0.0003	A: 0.70; L: -0.61
	I + A *** - Habitat Diversity$^{(*)}$	-84.65	180.17	2.63	0.07	0.59	0.0003	A: 0.73; HD: -0.48
2.00	I + A *** - Lucerne* - OC$^{(*)}$	-81.86	178.34	0.80	0.17	0.68	0.0002	A: 0.77; L: -0.63; OC: -0.06
	*I + A *** - Lucerne**	*-83.92*	*178.70*	*1.16*	*0.14*	*0.62*	*0.0002*	*A: 0.73; L: -0.63*

Notes: At each spatial scale we present first the model with the minimum AICc, and indicate all competing models ($\Delta i < 2$) within each scale below, however, the values Δi column are calculated for all models within each predator manipulation treatment; models in bold indicate best model for each predation treatment. For details about summary statistics see notes under **Table 1** and data analysis section in material and methods. OC = Other crops. Significant predictors are indicating as: *** $P < 0.001$, ** $P < 0.01$, $P < 0.05$, and $^{(*)}$ $P < 0.10$. Partial correlations indicated by the initials of each predictor.

[1] none of the models fitted at this scale were significant.



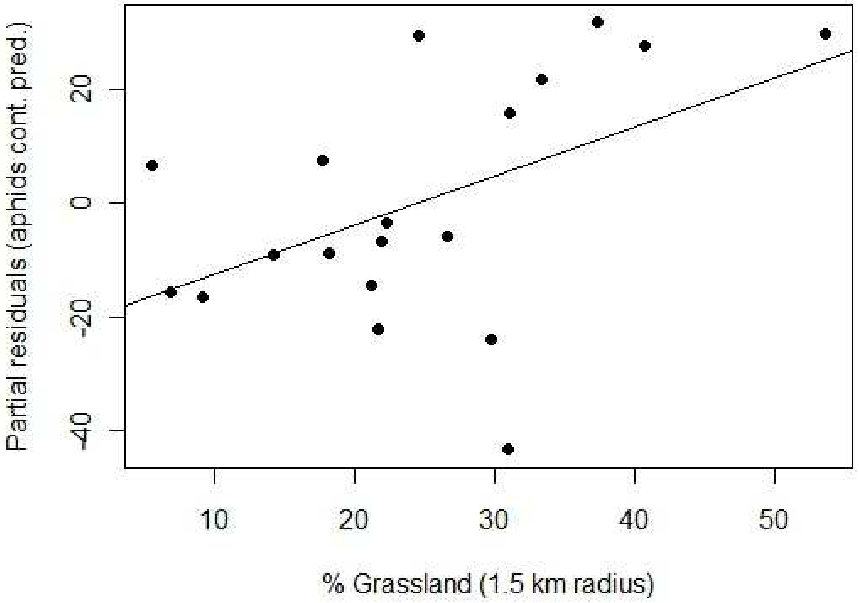


Fig. 6. Relation between the number of aphids surviving in the continuous predation treatment (represented by the partial residuals of the model), and the areas of Lucerne and grassland at a scale of 1.5 km radius. The higher the Lucerne area, the lower the number of aphids surviving predation, whereas the opposite effect was observed for the area of grassland (see **Table 5** for the statistics of the model).

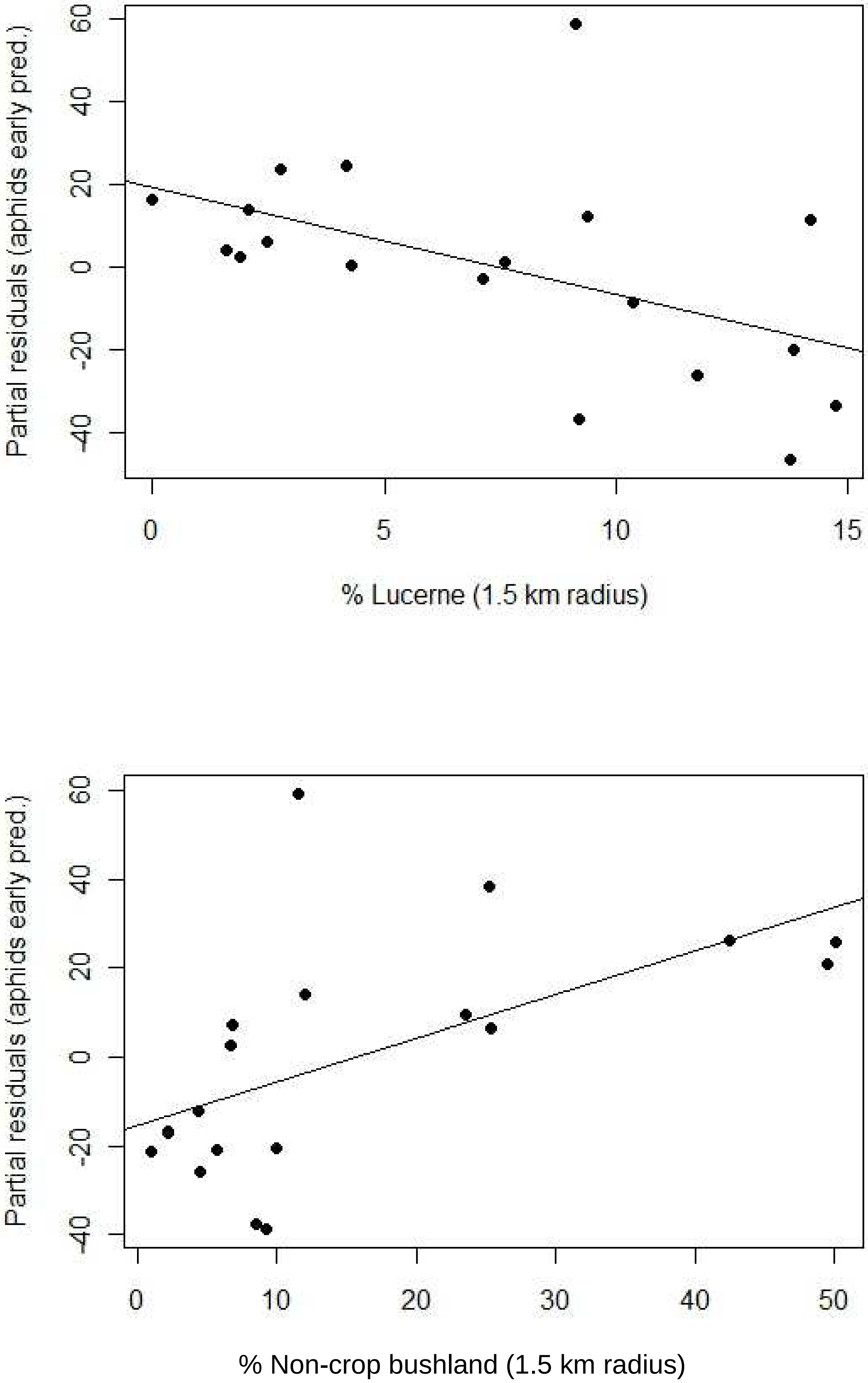


Fig. 7. Relation between the number of aphids surviving in the early predation treatment (represented by the partial residuals of the model), and the areas of Lucerne and non-crop bushland at a scale of 1.5 km radius. The higher the Lucerne area, the lower the number of aphids surviving predation, whereas the opposite effect was observed for the area of non-crop bushland (see **Table 5** for the statistics of the model).

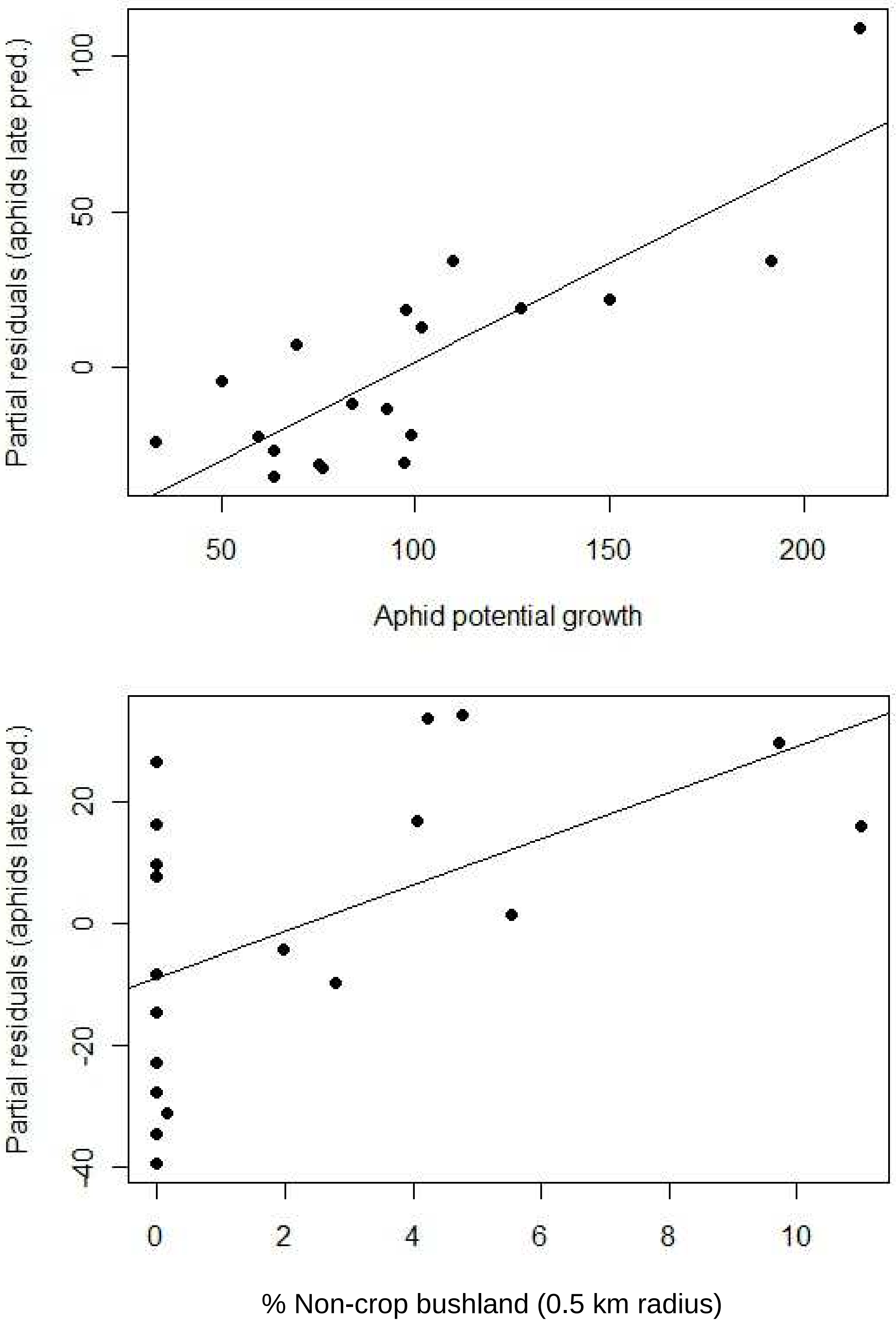


Fig. 8. Relation between the number of aphids surviving in the late predation treatment (represented by the partial residuals of the model), and the aphid potential growth and areas of non-crop bushland at a scale of 0.5 km radius. Aphid potential growth is estimated for each landscape by aphid population size in the predator exclusion treatment, the higher positive correlation, the less aphid populations were disrupted by predation. Similarly, the higher the non-crop bushland area, the higher the number of aphids surviving predation (see **Table 5** for the statistics of the model).

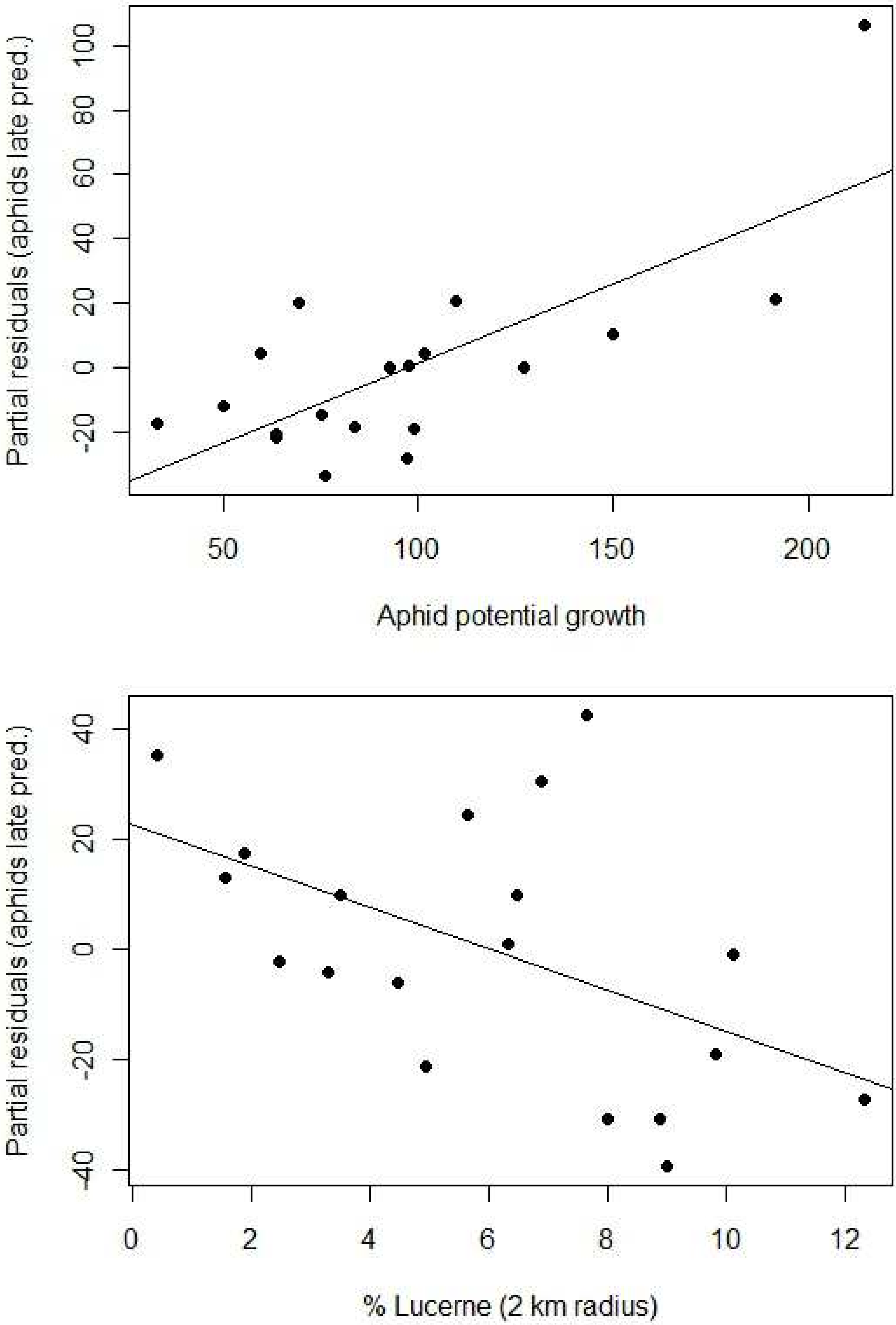


Fig. 9. Relation between the number of aphids surviving in the late predation treatment (represented by the partial residuals of the model), and the aphid potential growth (see caption of Fig. 8 for explanation) and areas of Lucerne at a scale of 2 km radius. Higher percentage of Lucerne in the landscape resulted in higher aphid suppression (see **Table 5** for the statistics of the model).

Landscape functional effects on pest suppression

We sampled a total of 2,554 predators with the sticky traps (ST) located at 1 km radius from the experimental field (**Table 6**). Most of the predators were spiders, occurring in 75.9% of the samples, followed in importance by several species of aphidophagous ladybird beetles (9.2% of the samples), brown and green lacewing (5.6%), hoverflies (3.2%), and predatory bugs (2.9%). Only eight aphid parasitoid specimens were detected by ST, confirming the null levels of parasitism observed in the experimental manipulations of aphids. Mobile predators varied significantly in abundance across the major land type covers sampled ($F_{5,581}$=6.49, $P <$ 0.0001), being more abundant in Lucerne (L), other crops (OC) and cucurbits (CU), with lower abundances in grasslands (G) (**Fig. 10a**). The lowest numbers were collected from non-crop bushland (NV) and non-crop riparian (R) (**Fig. 10a**). Spiders were more abundant and homogeneously distributed across cover types, although we observed significantly lower abundance in the non-crop riparian habitat ($F_{5,581}$=2.74, P = 0.0187; **Fig. 10b**).

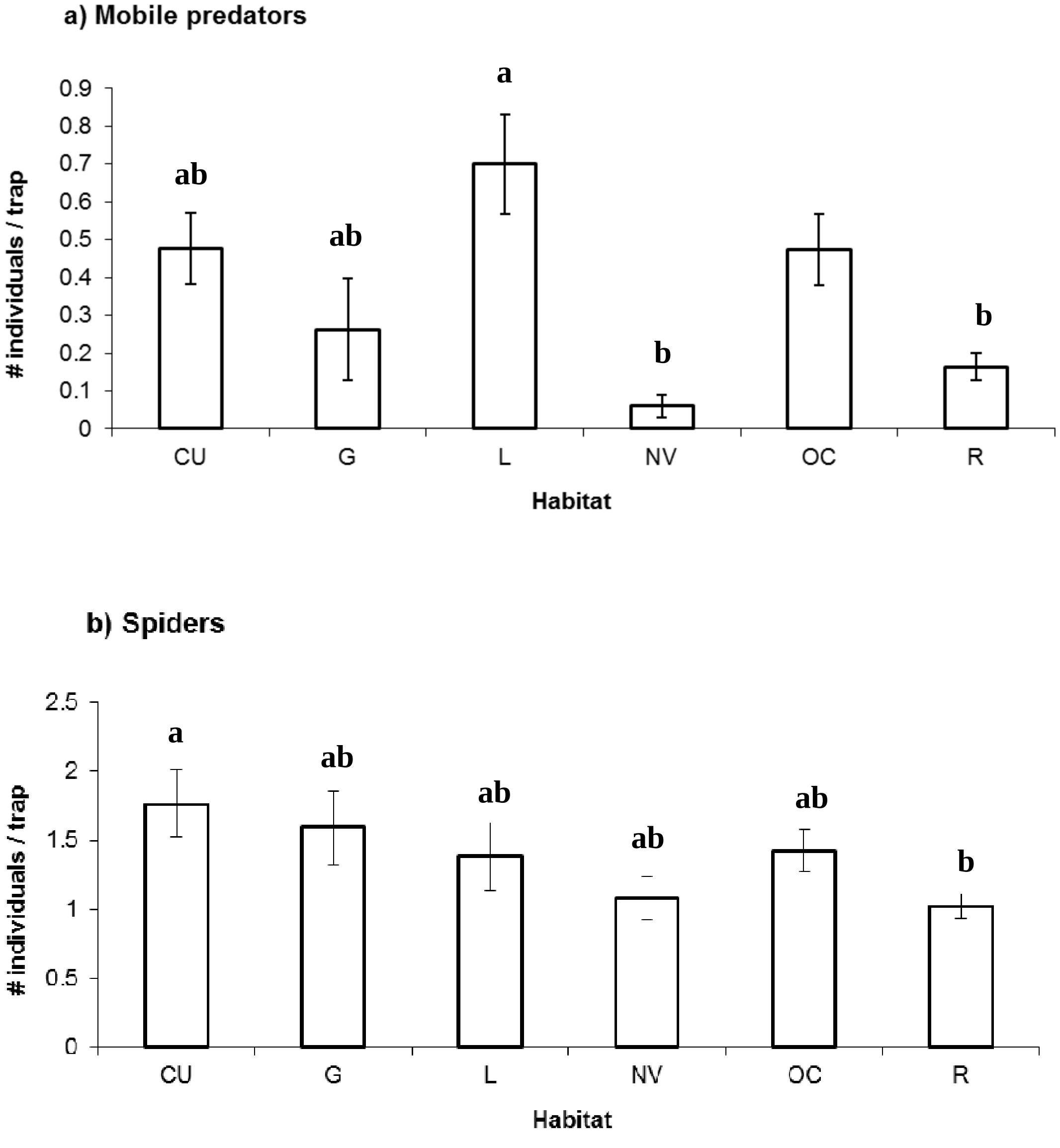


Fig. 10. Natural enemy abundance per major land cover types. Mobile predators include all predators with flying adult stages. Different letters among cover types indicate significant differences ($P < 0.05$, *t*-tests adjusted by the Bonferroni method for multiple comparisons).

Table 6. Natural enemies of melon aphids collected by sticky traps in the Lockyer Valley, Australia, during the two field experiments in November 2009 and March 2010.

Order / Family	**Species**	**Common name**	**Total ind.**	**Total samples**	**% samples**
Aranae		Spiders	2280	698	75.9
Neuroptera					
Hemerobiidae	*Micromus* sp.	Brown Lacewing	71	50	5.4
Chrysopidae		Green Lacewing	2	2	0.2
Diptera					
Syrphidae		Hoverfly	52	29	3.2
Coleoptera					
Coccinellidae	*Diomus notescens*	Two-spotted Ladybird	30	28	3.0
	Coccinella transversalis	Transverse Ladybird	26	25	2.7
	Hippodamia variegata	White Collared Ladybird	25	22	2.4
	Micraspis frenata	Stripped Ladybird	4	4	0.4
	Coelophora inaequalis	Variable Ladybird	3	3	0.3
	Harmonia conformis	Common Spotted Ladybird	2	2	0.2
	Cryptolaemus montrouzieri,	Mealybug Ladybird	1	1	0.1
		unidentified Ladybird	1	1	0.1
Melyridae	*Dicranolaius bellulus*	Red and Blue Beetle	22	21	2.3
Hemiptera					
Anthocoridae	*Orius* sp.		18	18	2.0
Geocoridae	*Geocoris* sp.	Big eye bug	5	5	0.5
Nabidae		Damsel bugs	4	4	0.4
Hymenoptera					
Braconidae	Subfamily: Aphidiinidae	parasitoids	8	7	0.8
		Total	**2554**	**920**	**100**

We found that 23 of the predictors measuring landscape functionality correlated aphid suppression (**Appendix I**). With those predictors we fitted 29 MLR models that had combinations of all independent predictors in the initial full model, and were subject to stepwise backward regression, as in the previous section analysis (**Appendix II**). This analysis yielded five models that were significant (**Table 7**). The best predictors for aphid suppression combining all land covers were either the number of all predators combined or of mobile predators present within 1 km radius from the experimental fields, explaining 21-25% of the variation of the data (**Fig. 11 and 12**). Adding the potential population growth of the aphids only add a modest increase in the predictive power of the model (**Fig. 13**). A better fit to the data was obtained by predictors that incorporated both the information of the area covered by each vegetation type and the abundance of natural enemies (**Table 7**). The best model explained 48% of the variation of the data and suggested significant aphid suppression associated with increased number of all predators in other crops, but a decrease in aphid suppression associated with higher numbers of predators in Lucerne, in contrast with our expectations (**Fig. 14**). Measures of distance from patches with predators were not correlated with aphid suppression, and all other predictors that showed marginally significant correlations were not significant in any of the models investigated.

Table 7. Summary of multiple regression models statistics for evaluating the relation between landscape functional predictors and melon aphid suppression at different spatial scales in the Lockyer Valley, Australia.

Radius (km)	Model	Log-lik.	AICc	*Δi*	*Wi*	Adj. r^2	*P*	Partial correlations
	Predictors combining all land covers							
1.00	**Intercept (I) - Mean load all predators (AP)**	**-85.67**	**178.94**	**0.0**	**0.52**	**0.25**	**0.01745**	
	I - Mean load mobile predators (MP)	-86.19	179.97	1.0	0.31	0.21	0.02935	
	I + Aphid Pot. Growth (A) - MP*	-85.10	181.06	2.1	0.18	0.25	0.04015	A: 0.33; MP: -0.57
	Predictors for individual land covers							
1.00	**I + Mean AP $_{\mathbf{(Lucerne)}}$ – Mean AP $_{\mathbf{(OC)}}$**	**-60.25**	**132.50**	**0.0**	**0.997**	**0.48**	**0.00751**	**AP$_{\mathbf{L}}$: 0.73; AP$_{\mathbf{OC}}$: -0.45**
	I + Mean Spiders $_{(OC)}$	-68.11	144.21	11.7	0.003	0.24	0.03136	

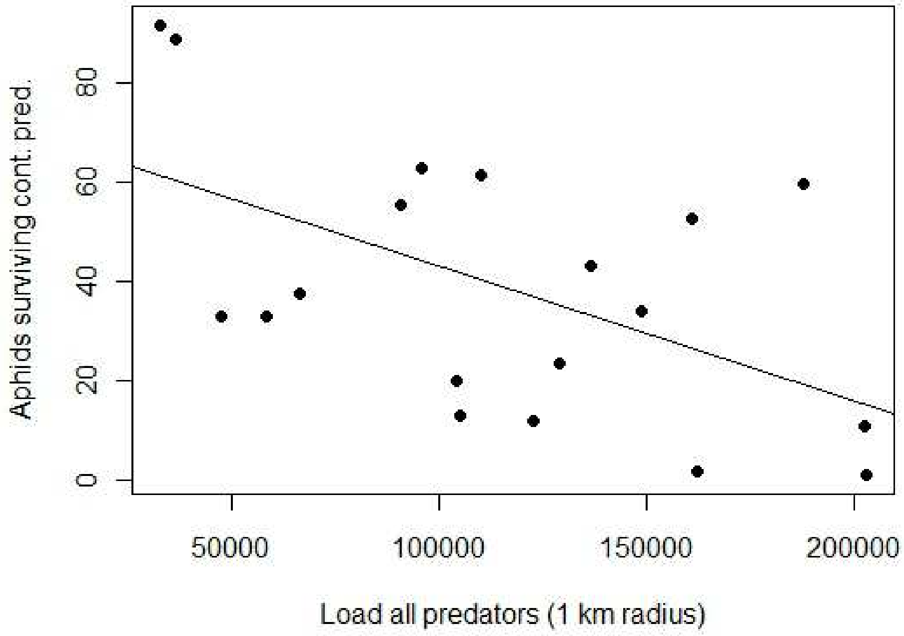


Fig. 11. Relation between the number of aphids surviving in the continuous predation treatment and the load of all predators at 1km radius. Mean load of all predators (AP) represent a measure of the total abundance of predators in the landscape, adjusted by sampling effort, and was calculated as: Σ (area$_{(AP)}$ x AP) /# areas sampled with sticky traps. Higher predator abundance in the landscape resulted in lower aphid populations (see **Table 7** for the statistics of the model)

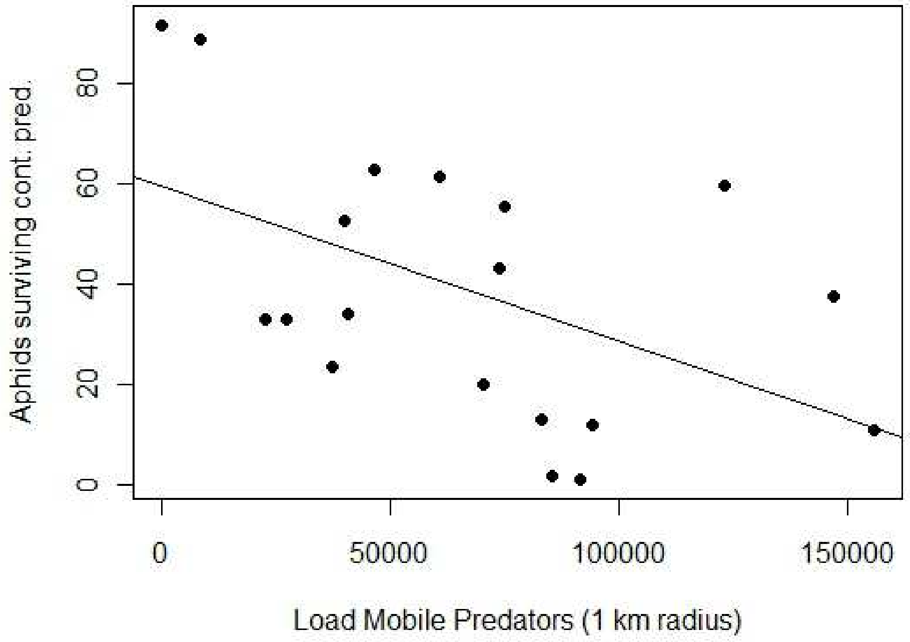
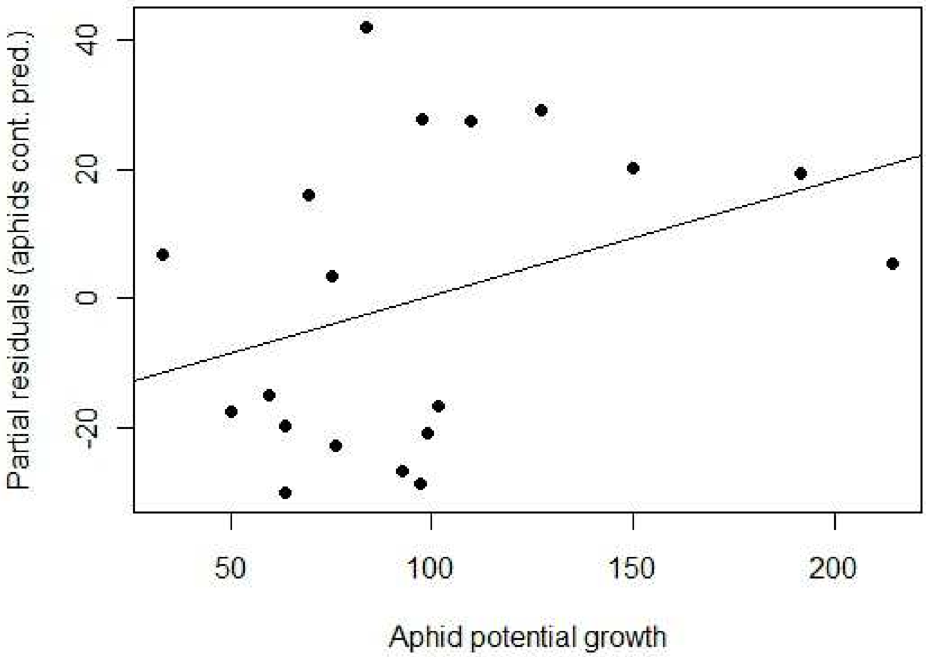


Fig. 12. Relation between the number of aphids surviving in the continuous predation treatment and load of mobile predators at 1km radius (calculated as in figure 10, but using only mobile predators). Higher mobile predator abundance in the landscape resulted in lower aphid populations (see **Table 7** for the statistics of the model).



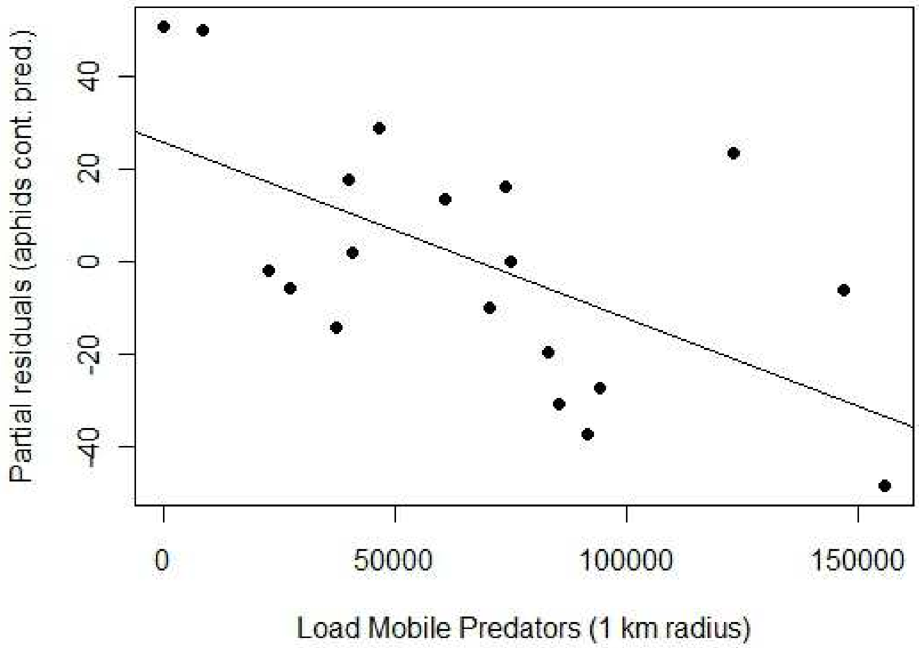


Fig. 13 (top). Relation between the number of aphids surviving in the continuous predation treatment (represented by the partial residuals of the model), and the aphid potential growth (**Fig. 14** botton; see caption of Fig. 7 for explanation) and load of mobile predators at 1km radius (calculated as in figure 10, but using only mobile predators). Higher mobile predator abundance in the landscape resulted in lower aphid populations (see **Table 7** for the statistics of the model).

Discussion

Our results demonstrated dramatic increases in the pest suppression by predators when they arrive immediately after pest colonization on the field. This confirms previous theoretical predictions that suggest that generalist predators arriving early to crop fields in low numbers can exert the same or even more suppression than larger number of specialist natural enemies, that typically arrive later than the pest and sometimes too late to prevent outbreak populations (Landis and Van der Werf 1997; Chang and Kareiva 1999; Symondson *et al.* 2002; Gardiner *et al.* 2009). The proposed mechanism for this highly effective pest suppression is the pest mortality produced by predators when pest numbers are low, before they reach threshold densities that lead to outbreak populations under exponential growth.

Previous studies have provided empirical evidence that suggest that relatively small number of generalist predators present early in the season, after crop emergence, are highly effective to suppress pest populations (Landis and Van der Werf 1997; Fox, Landis *et al.* 2004; Fox *et al.* 2005; Costamagna and Landis 2006). However, those studies could not distinguish the impact of predators arriving early from the impact of increased time exerting predation, i.e. the accumulated effect of more days of predation on the same pest population. Our experimental design is unique because we manipulated separately predator arrival (by delaying predation using cages) and length of predation (by maintaining the same time interval predation in the early and late predation treatments). Comparing the early with the late predation treatments suggests that there is an overall trend of higher suppression of aphids in populations under early predation. However, this general trend varied across landscapes, with only four landscapes where predation was significantly higher in the early than in the late predation treatment. Moreover, we observed in two cases the opposite effect, higher suppression of predators arriving late than those acting during the first week of the study. At least two mechanisms can explain this unexpected result. First, local environmental conditions may have varied between the two weeks, resulting in lower populations of predators available to suppress the aphids. These may have included abiotic factors (i.e. temperature, rain, humidity) or the dynamics of other pests in nearby fields that may have moved away predation from our experimental fields. Alternatively, predation may have been more effective during the second week of the experiment due to a numerical response of predators, i.e. aphid populations that become attractive to more predators when they reach a population level above a certain threshold (Hemptinne *et al.* 1993; Elliott, Kieckhefer et al. 2002; Evans and Toler 2007). In most cases (14 landscapes) we observed significant suppression by natural enemies, with similar (and nearly additive) effects of predation in the first and second week.

At the landscape scale, we did not observed a positive association between the area of non-crop bushland and riparian vegetation, and the levels of aphid suppression in our manipulations. Moreover, the area of native vegetation was positively associated with higher aphid populations at various scales, being the most significant predictor of late predation. This result contradicts the theoretical expectation for the role of native vegetation and most of the empirical work previously conducted on the landscape ecology of biological control overseas (Kruess and Tscharntke 1994; Marino and Landis 1996; Thies and Tscharntke 1999; Menalled *et al.* 2003; Thies *et al.* 2003; Costamagna *et al.* 2004; Roschewitz *et al.* 2005; Bianchi *et al.* 2006; Gardiner *et al.* 2009; Gardiner *et al.* 2009; Gardiner *et al.* 2009; Holzschuh *et al.* 2010; Werling and Gratton 2010), and from the Lockyer Valley, VG 05014 and VG06024. These studies showed natural enemies on native plants, and net immigration from the riparian remnant to the crop in large numbers in spring, but movement back and forth throughout the year. However, at least two important features of our study system may explain this apparent contradiction between our results and previous findings. First, almost all previous studies have been conducted in temperate to cold regions, where natural enemies need to go through an overwintering period. In most of those regions, woodlots and forests are therefore crucial as overwintering habitats to sustain natural enemy populations (Landis *et al.* 2000). By contrast, the subtropical coastal climate on the Lockyer Valley allow natural enemy populations to move year-round through crop habitats, since there is no period without at least some crops covering a portion of the landscape. Therefore, the role of non-crop bushland and native vegetation as an overwintering site is minimal in our system.

A second difference between our study system and previous studies refers to the level of disturbance of the non-crop remnant habitat. An important role assigned to non-crop habitat in other systems is to serve as a refuge from disturbance effects on natural enemies, including extreme temperatures, unfavourable humidity conditions and general activities associated with cropping (i.e. cultivation, pesticide application, etc) (Landis *et al.* 2000). However, the native vegetation in the Lockyer Valley is to a great extent under grazing by cows, and is very open (i.e. tree canopies are typically separated) and with a low diversity of plant species in the understory, suggesting a less favourable habitat in comparison with the typical temperate forests where most other studies were conducted. A similar reasoning can also be applied for the role of grasslands, since they were also associated with higher aphid populations. The results of our sampling with sticky traps corroborate these hypotheses, since both native and riparian vegetation, as well as grasslands, registered the lowest levels of natural enemies observed. However, our sampling was limited for the periods under study (less than four weeks combining both experiments) and we cannot rule out that native vegetation may harbor higher natural enemy population at different times of the year as has been shown in VG05014 and VG06024, and recent findings from a GRDC project on the Darling Downs. Native remnant vegetation harboured natural enemies during the time when few crops were in the ground (April-June).

Our results indicate that the area with Lucerne is the most influential in increasing aphid suppression. This result is consistent at several scales, although it is most significant at larger spatial scales (i.e. > 1 km). This results is not unexpected, as Lucerne has been shown as an important reservoir of natural enemy populations, as it is not typically sprayed with insecticides (Hossain *et al.* 2001; Elliott, Kieckhefer *et al.* 2002; Hossain *et al.* 2002; Snyder and Ives 2003; Pearce and Zalucki 2005; Pearce and Zalucki 2006). In addition, our sampling with sticky traps suggests it was the habitat with high number of natural enemies during the period of our studies. Thus, Lucerne can also be a refuge for aphidophagous natural enemies. It provides prey and is typically under minimal chemical disturbance (although is sprayed for Jassids Jan-Feb), and may be amenable to a push pull system due to somewhat regular cutting and baling.

Classifying habitats as sources using the information of natural enemy abundance provided by the sticky traps and disregarding the actual vegetation cover present on them, was less effective to explain our data. As we expected, increased abundance of natural enemies combined with the size of those areas resulted in higher aphid suppression, a result that was consistent for all predators combined or mobile predators separately and explained 21-25% of the variability in the data. However, a more effective method to predict aphid suppression was to combine the mean number of predators found in each vegetation type with the total area of coverage in the landscape, which resulted in a model that explains 48% of the data. This model indicated a significant increase in aphid suppression with higher number of predators in other crops, but, in contrast with our expectations, a decrease in aphid suppression associated with higher number of predators in Lucerne. This result is difficult to explain, as we would have expected that the higher number of predators in Lucerne spill over to other crops. However, it is possible that Lucerne has a dual, more dynamic role than previously thought. During cutting or periods of regrowth, Lucerne may act mostly as a source of natural enemies, therefore forcing natural enemies to forage in other habitats. By contrast, if pest populations are high in Lucerne fields, they may act as sinks of natural enemies, pulling them into the Lucerne and off of other fields, thereby decreasing biological control. If these assumptions are correct, we can then re-interpret our results as follows. First, when we look at the area of Lucerne without information about their natural enemy populations, we are actually capturing most of its role as a source. In this scenario we are assuming that most Lucerne fields are indeed sources of natural enemies most of the time. Second, when we refine our models and incorporate information about natural enemy abundance in those Lucerne fields, we are giving more weight to areas that have high natural enemy populations, that are most likely to act as sinks, resulting in an a negative association between Lucerne and aphid suppression. Further research is needed to fully understand the role of Lucerne and how management can play a key driver in area-wide biological control.

In summary, we observed strong effects of natural enemies suppressing aphid populations, which were more effective if they arrive immediately after the pest population. We found that most of the natural enemies were present in managed habitats particularly in Lucerne, suggesting that it is crucial to preserve biological control to minimize insecticide applications on these crops. Riparian and non-riparian bushland remnant vegetation has relatively lower populations of natural enemies, but also low variability, making it a consistent low source of natural enemies.

II. Crop colonisation: the role of on-farm refuges in high beneficial landscapes versus low beneficial landscapes

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Introduction

The movement of beneficial insects into agricultural crops may be facilitated through the provision of "on-farm" refuges such as wildflower strips, perennial forage crops or strips of native vegetation that provide resources for the predatory and parasitic species sought for pest control (Brewer *et al*. 2008; Werling and Gratton 2008; Haenke *et al*. 2009; Tscharntke *et al*. 2002). In addition, vegetable growers are often asking what should they plant where to encourage beneficial insects. To optimally design and place these on-farm refuges requires that we first understand the contribution that these on-farm or established habitats in relation to other sources of beneficial insects (namely environmental or landscape sources). If there is a large "landscape source" of beneficial insects nearby is there any value in maintaining an on-farm refuge?

Tscharntke *et al.* (2005) hypothesized that agri-environment schemes (eg. revegetation and environmental plantings) will be most effective in enhancing biodiversity in simple landscapes. In cleared landscapes there may be not enough species diversity to effectively colonize the managed habitat. In complex landscapes there is already high species diversity and adding on-farm habitat for natural enemies will not add much. Therefore, what is the benefit of maintaining an on-farm refuge when the landscape contribution is small? How does this change for beneficial insects with different dispersal capacities?

Here, we explore these issues initially using spatially explicit modelling and then test some of the predictions of these models in a local-scale controlled field study to examine critically whether these predictions hold up under farm conditions. This section is split into two subsections, firstly the model rationale, methods, and results (its predictions) are described, then we show how we designed and implemented the field study to address the predictions of the model. Next, we describe the field experiment methods, and results. The findings of these two studies are then discussed in relation to management implications, and areas that could benefit from further research are highlighted.

Material & Methods - *Model – Simulation of crop colonisation processes from multiple source habitat types.*

Research questions:

- How does the presence of natural enemy source habitat at the landscape scale influence the benefit of established on-farm predator refuges near crop fields (e.g. flower strips, perennial forage, native vegetation)?
- How does the dispersal capacity of natural enemies influence this process?

This model considers a 64 by 64 grid "designed" landscape, containing "Landscape Source" (LS) background predator habitat, "Refuge Source" (RS) established predator habitat, crop and matrix (unsuitable habitat). Predators are initially only present in LS or RS and colonise the landscape from these habitats. The landscape has a toroidal structure so predators that move from the map on one side reappear at the other side of the map. Predator dispersal is described with a Laplace (negative exponential) kernel. Predators that arrive in the crop stay there (i.e. sticky crop), predators arriving in all other habitats continue to move (for example natural enemies that lay eggs/parasitise). No predator mortality or reproduction takes place.

Scenarios: Landscapes contain 39%, 10% or 4% LS, and 0.1% RS that can be established next to the crop or far away (**Fig. 1**). We further consider 3 types of predators: mobile (mean dispersal distance approx 30 m), intermediate (mean dispersal distance approx 20 m) and poorly dispersing (mean dispersal distance approx 7 m). Thus, we have a 3 (39%, 10% or 4% LS) x 2 (RS close and far) x 3 (mobile, intermediate and poorly dispersing predator) factorial design.

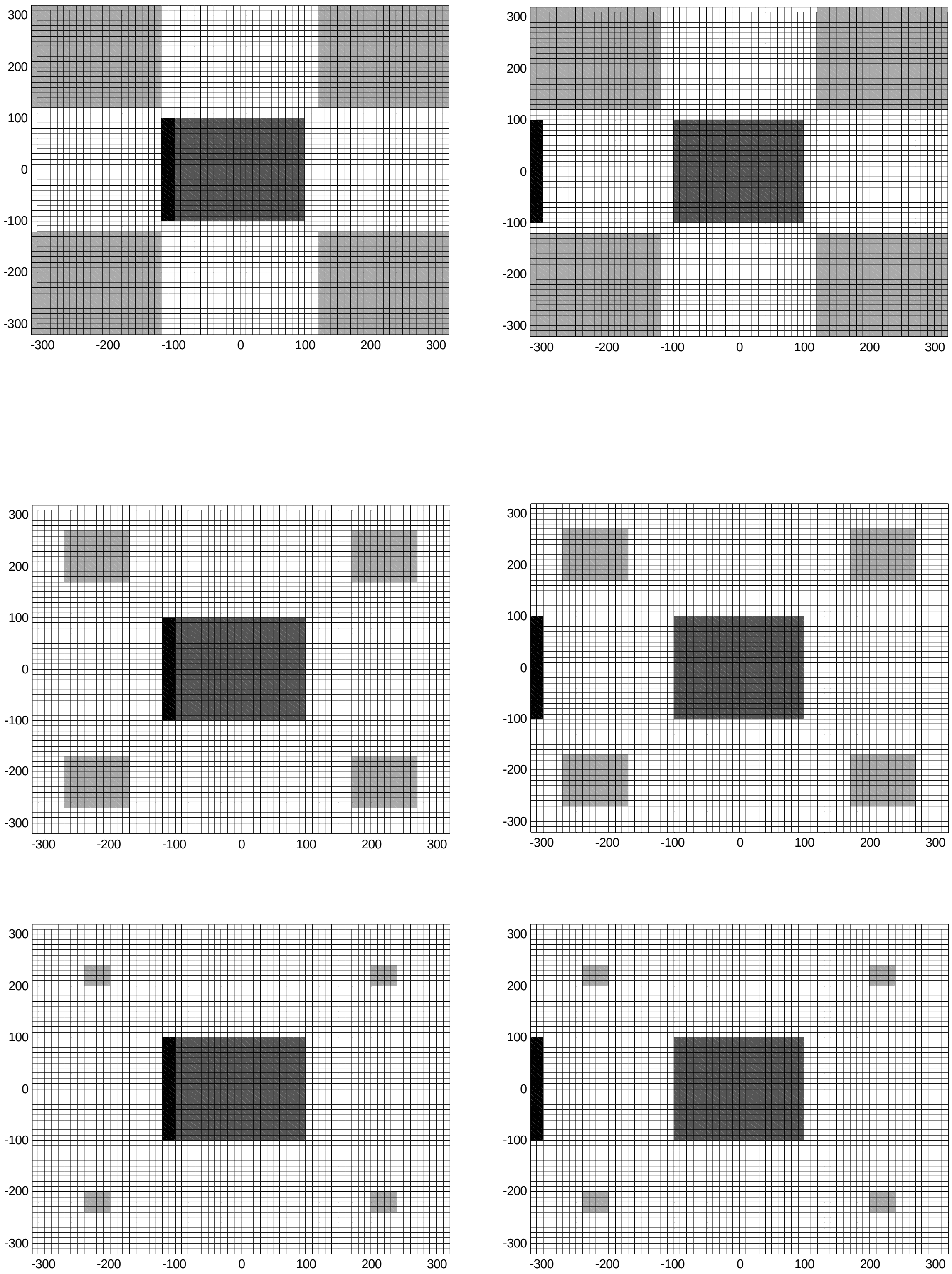

Fig. 1. Landscapes with 3 levels of Landscape Source (light grey), a crop (dark grey), Refuge Source (black; far and close) and matrix (white).

Results - *Model*

Establishing “Refuge Sources” (either near or far from crops) in high “Landscape Source” landscapes has a negligible effect on the accumulation of predators in the crop (**Fig. 2A** and **3A**). This is true for mobile, intermediate and poorly dispersing predators. The contribution of predators from “Refuge Sources” gets swamped by the large numbers of predators colonising the crop from the abundant “Landscape Source”.

In medium “Landscape Source” landscapes, establishing “Refuge Source” (either near or far from crops) has only a small effect on the accumulation of mobile and intermediate dispersing predators in the crop. However, for poorly dispersing predators, “Refuge Source” near the crop leads to faster crop colonization by predators. For instance, it takes 380 time steps to accumulate 20% of the predators in the crop when “Refuge Source” is near and 506 time steps when “Refuge Source” is far (**Fig. 2B**).

In low “Landscape Source” landscapes, establishing “Refuge Source” near or far from crops does not lead to major differences in the accumulation of mobile predators in the crop (**Fig. 2C**), even though “Refuge Source” delivers a substantial percentage of predators in the landscape (**Fig. 3C**). For mobile predators in low “Landscape Source” landscapes it doesn’t matter so much *where* “Refuge Source” is established, it matters *that* “Refuge Source” is established. For poorly dispersing predators in low “Landscape Source” landscapes, establishing “Refuge Source” near or far matters a lot for the accumulation of predators in crops. For instance, it takes 14 time steps to accumulate 20% of the predators in the crop when “Refuge Source” is near and 479 time steps when “Refuge Source” is far (**Fig. 2C**). Thus, because the number of predators colonizing the crop in low “Landscape Source” treatment are fewer than in medium and high “Landscape Source” treatment (and the proportion of predators coming from “Refuge Source” is relatively high) the location of “Refuge Source” relative to the crop becomes more important. This is most pronounced for poorly (and intermediate) dispersing predators.

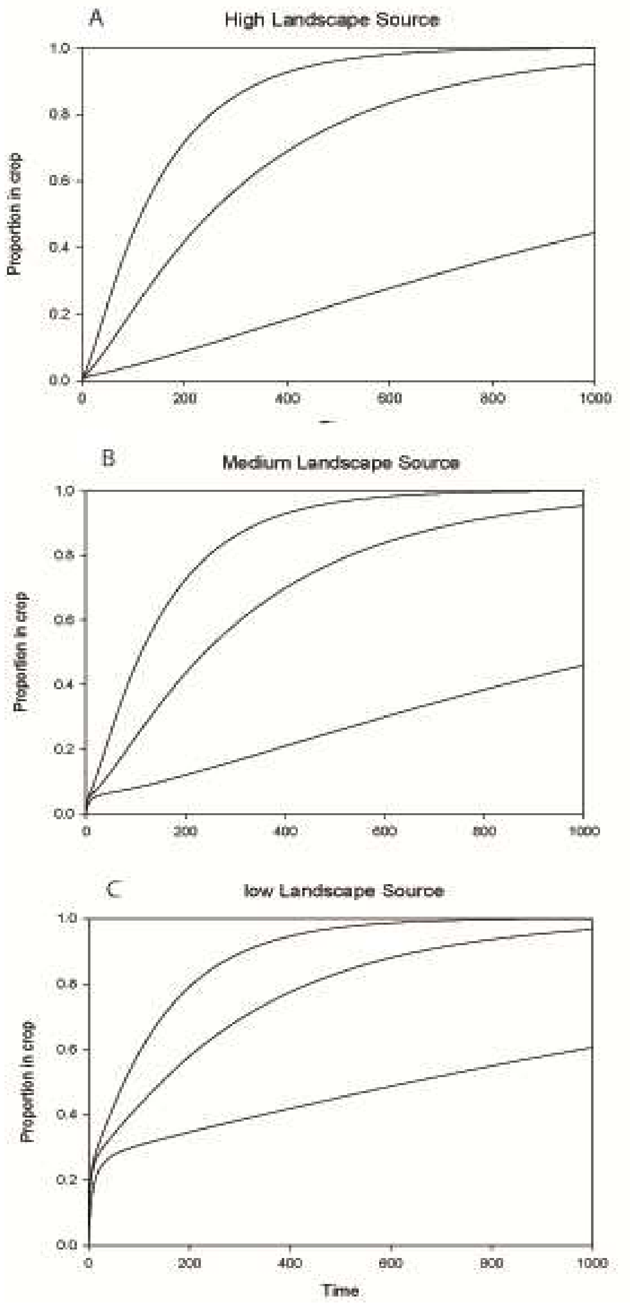

Fig. 2A-C. Proportion of predators accumulated in the crop for “Refuge Source” near (solid line) and far (dotted line) for high (top), medium (middle) and low “Landscape Source” landscapes (bottom). Each graph shows good, intermediate and poor dispersing predators.

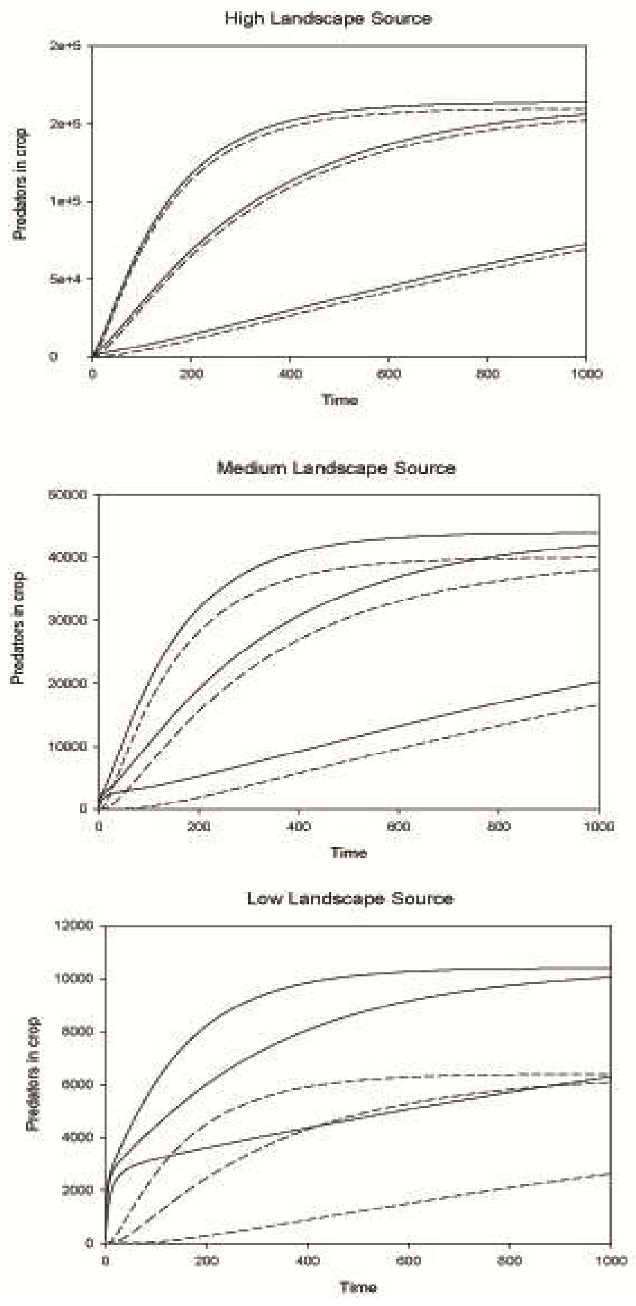

Fig. 3A-C. Number of predators accumulated in the crop for “Refuge Source” near (solid line), far (dotted line) and “Refuge Source” absent (dashed line) for high (top), medium (middle) and low “Landscape Source” landscapes (bottom). Each graph shows good, intermediate and poor dispersing predators.

From the results of this spatially explicit model one would predict that when there is a high landscape source of beneficial insects the establishment of on-farm refuges has negligible impact on the accumulation of beneficial insects in crops. When there is a low landscape source of beneficial insects, however, the presence of on-farm refuges has a dramatic effect on the accumulation of beneficial insects in crops. Under this scenario refuges provide much faster colonisation and therefore earlier control of pests before they can reach outbreak densities. These results may be used to design better refuges, when the landscape contribution of beneficial insects in any given area has been quantified. However, several assumptions are made by the model, and to test whether these predictions are robust under natural conditions it is necessary to evaluate these predictions experimentally in the field. We therefore designed a manipulative experiment to test the effect of having refuges near a crop in the presence of high landscape sources of beneficial insects and low landscape sources.

Material & Methods - *Field Experiment – Linking model predictions with field situations.*

Trichogramma are egg parasitoid wasps that target the eggs of lepidopterous pests such as *Helicoverpa armigera*. Many experiments in the published literature report relatively slow rates of spread of these wasps when released in agricultural crops. For example: egg parasitism only 10% at 15m from release site (Bueno *et al*. 2011).

We chose *Trichogramma* wasps as the beneficial insect for use in our manipulative experiment as: 1) they are frequently used by growers in the Lockyer Valley and elsewhere as part of IPM of *Helicoverpa* spp., 2) the literature suggests that these wasps tend to disperse relatively slowly in crops and 3) the model predicted that a larger effect would be expected for beneficial insects with slower rates of dispersal.

Field Trials were conducted at the University of Queensland and CSIRO field stations at Gatton, SE Queensland, Australia. Two fallow, bare-soil fields were selected, separated by approximately 2km, each field had been completely cleared of weeds prior to the start of the field trials. Temperature and weather data was collected from the Bureau of Meteorology Gatton weather station (Lat -27.54, Long 152.34) situated approximately 1km from each site. For each trial one field was designated "high release" and one "low release" representing "high landscape predator sources" and "low landscape predator sources", respectively, and these fields were cleared and alternated between trials. In each field experimental plots were set up with a central release point, and six plots arranged in a circular design around the central point (**Fig. 4**). The six plots were designed to simulate a field and a refuge, for each trial 3 of these refuges had parasitoid releases, and three were controls with no release. Wind speed affects the dispersal of *T. pretiosum*, with dispersal reduced at higher wind speeds, and wind direction also affects the pattern of dispersal (Fournier and Boivin 2000). Our experimental design controls for the effect of wind direction, as each treatment is replicated in any one wind direction. Further, the treatments were rotated by 60^{o} each replicate to control for prevailing wind direction (see example result **Appendix III**).

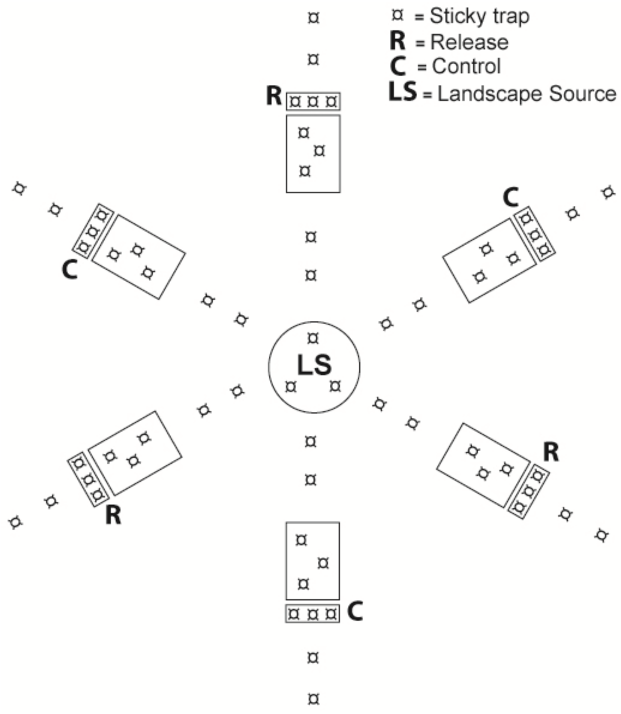

Fig. 4. Experimental design for the field experiment, this design was implemented in two fallow, bare-soil fields, for each experiment one field was designated High Landscape Source, and one Low Landscape Source.

Sentinel egg cards and sticky traps were placed at the site one week prior to the commencement of each trial to assess background levels of *Trichogramma* abundance. For each trial 1,200 sweet corn (*Zea mays*) Hybrid H5 (Pacific seeds, Australia) plants were grown to stage V6 (approx 45cm tall) in pots, and transferred to the field site where they were arranged in containers treated with Fluon™, to prevent ants from accessing the plants. Egg cards were prepared from *Helicoverpa armigera* obtained from a culture held at the Australian Cotton Research Institute, Narrabri. *Trichogramma* were obtained from Bugs for Bugs (Australia), a commercial supplier of biocontrol agents, and supplied as release cards of approximately 1000 wasps. For each release, emergence controls were set (2 per field) these comprised a single release card placed in a cage at the release point. Emerging wasps were removed daily to monitor emergence. These were stored in Ethanol and subsequently counted using a scanner and ImageJ image analysis software (see result in **Appendix IV**). For each trial a subset of these wasps (200 per trial) were sexed to ensure that the sex ratio was similar across trials as the relationship between the number of wasps released and the resulting level of parasitism would be affected by strong sex biases. At each field temperature loggers (HOBO) were placed with the emergence controls to ensure that the temperature at the release sites did not diverge greatly form ambient conditions. For each trial, corn plants were placed in the field on day zero. On day one egg cards were attached to the underside of corn leaves in the outer plots, 10 egg cards per plot (60 per field). Transparent sticky traps covered with Tanglefoot were placed as per figure 1 (63 sticky traps per field). *Trichogramma* release cards were attached to corn plants in the central plot at approximately noon. On day two and day three all sticky traps and egg cards were replaced at noon and on day four they were collected and the fields were cleared to remain fallow before the next trial.

The egg cards retrieved from the field were photographed to record the number of intact eggs returned (following low levels of predation), they were then maintained at 20^{oc} for four days and emerging *H. armigera* were removed twice daily to avoid the consumption of parasitised eggs. The egg cards were then placed in emergence vials to allow *Trichogramma* to emerge. After emergence the number of parasitised eggs was scored, based on the characteristic blackening of the egg chorion, and the number of emerged *Trichogramma* was also recorded. Sticky traps were examined under a microscope and the number of *Trichogramma* recorded for each trap.

In trial one (12/04/2011-15/04/2011) 175,000 *Trichogramma* were released in the high release field, 55,000 in the low release field, and 1,000 at each of the release plots. These numbers were based on an analysis of published studies on *Trichogramma* dispersal in crops (Fournier & Boivin 1999 & 2000, Bueno *et. al.* 2012, Stinner *et. al.* 1974, Wright *et. al.* 2001) and the relatively low rates of recapture recorded by these studies. In our trial levels of parasitism were very high on day one of the experiment, so for subsequent trials we reduced the number of *Trichogramma* released. In trial two (19/04/2011 – 22/04/2011) and trial three (12/05/2011 – 15/05/2011) 5,000 *Trichogramma* were released in the high release field, 1,000 in the low release field, and 110 in the release plots. For Trials one and two each egg card held 8-10 *H. armigera* eggs, for trial three, however, egg production was low and egg cards were prepared with 6-8 eggs per card.

Results - *Field Experiment*

Weather data

Throughout the three experiments (T1 - T3) temperatures were within a similar range, although night temperatures were lower for T3. Temperatures at the release points and the emergence controls were consistent with ambient temperatures (**Fig. 5**).

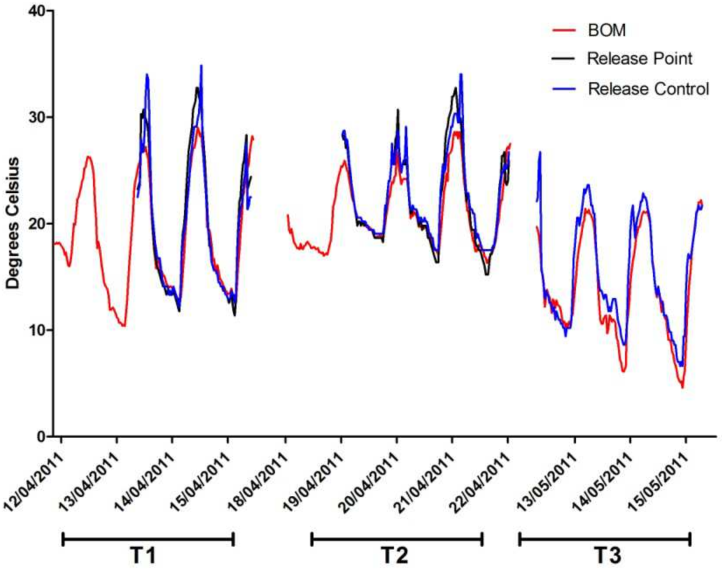

Fig. 5. Temperature recorded at 30 minute intervals, taken from the Bureau of Meteorology, and data loggers (HOBO) placed at the “Landscape Source” release point and next to the emergence control cages.

The average wind speed was much higher on the first two days of T3, this allowed us to examine the effect of elevated wind speed on beneficial insect movement during this trial (**Fig. 6**).

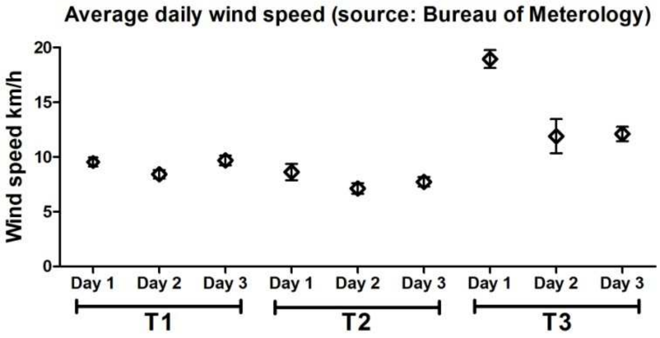

Fig. 6. Average daily wind speed across the three experiments.

Throughout the three trials the sex ratio of wasps released was close to 50:50 (**Fig. 7**), meaning that the parasitism response variable was not affected by skewed sex ratios in any of the releases.

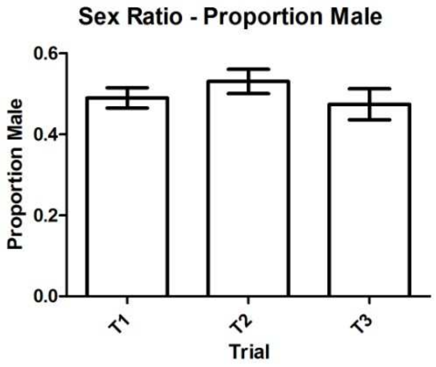

Fig. 7. The sex ratio was close to 50:50 across trials, T1 n = 350, T2 n = 330, T3 n = 120.

Trial 1

175,000 *Trichogramma* were released in the high release field, 55,000 in the low release field, and 1,000 at each of the release plots. Twently egg cards, each holding 10 eggs were placed at each of the six plots (3 release plots and 3 control plots) and replaced daily, sticky traps were also replaced daily. **Figure 8** shows results of the emergence controls (one emergence cage per field).

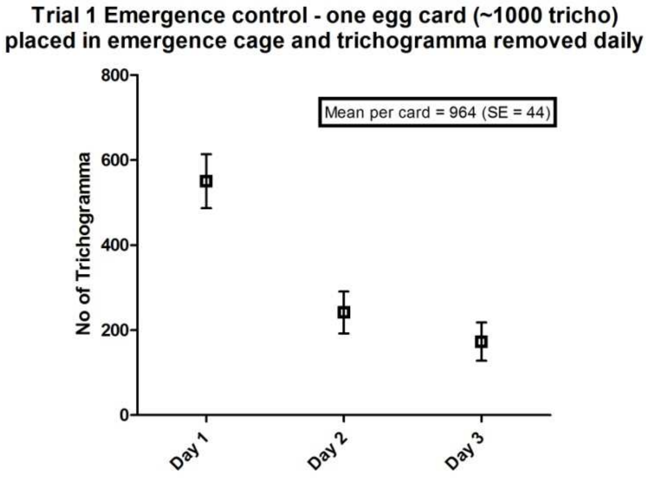

Fig. 8. *Trichogramma* emergence per day at the release point.

Our treatment was met (**Fig. 9**), refuges with *Trichogramma* releases had a higher number of wasps returned in sticky traps. The on-farm refuges had a greater effect on parasitoid accumulation than landscape sources; with low landscape release even surpassing the high landscape release (**Fig. 10**). This higher accumulation of parasitoid wasps translated directly into a higher parasitism of *Helicoverpa* eggs (**Fig. 11**).

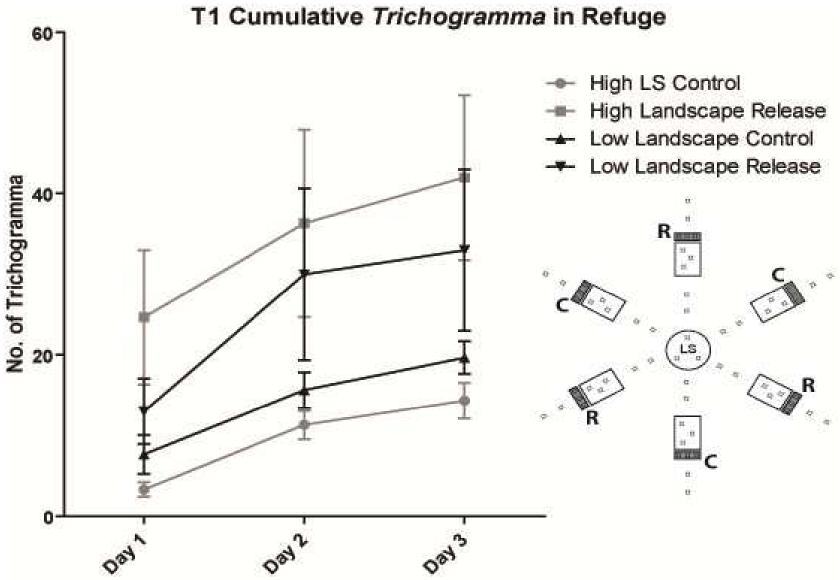

Fig. 9. Cumulative total number of *Trichogramma* individuals retrieved from the sticky traps in the refuges (control or release) each day. The refuges are where the release points were situated, this graph shows that our treatment was achieved, in that there were more wasps in the refuge release plots than the controls.

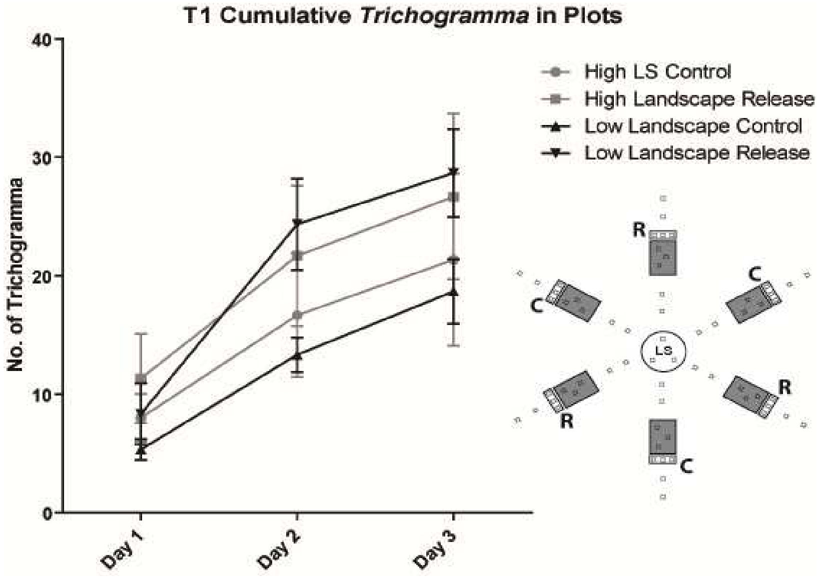

Fig. 10. Cumulative mean of each of the three plots (3x Release, 3x control).

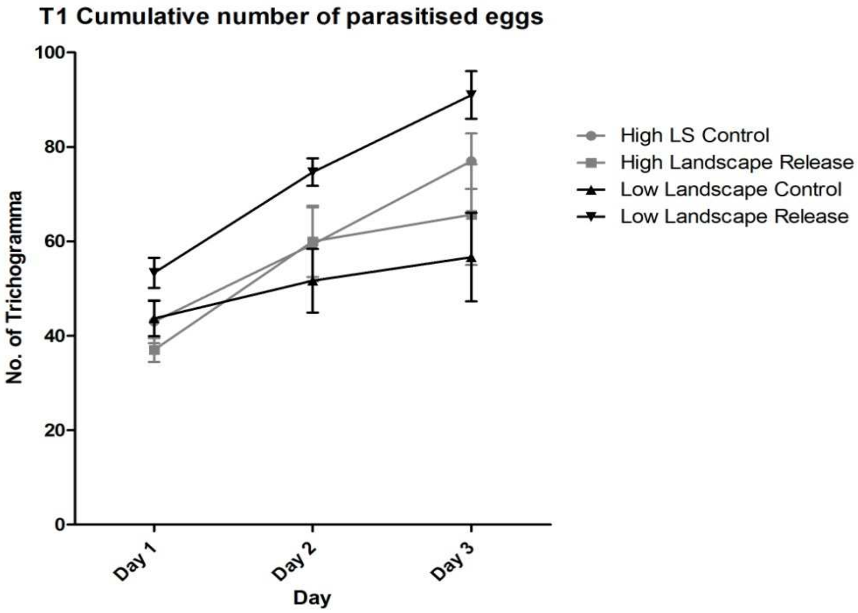

Fig. 11. Mean and SEM of the three plots for each treatment.

Trial 2

5,000 *Trichogramma* were released in the high release field, 1,000 in the low release field, and 110 in the release plots. 20 egg cards, each holding 10 eggs were placed at each of the six plots (3 release plots and 3 control plots) and replaced daily, sticky traps were also replaced daily. Emergence from the release points was more consistent across days than for T1 (**Fig. 12**).

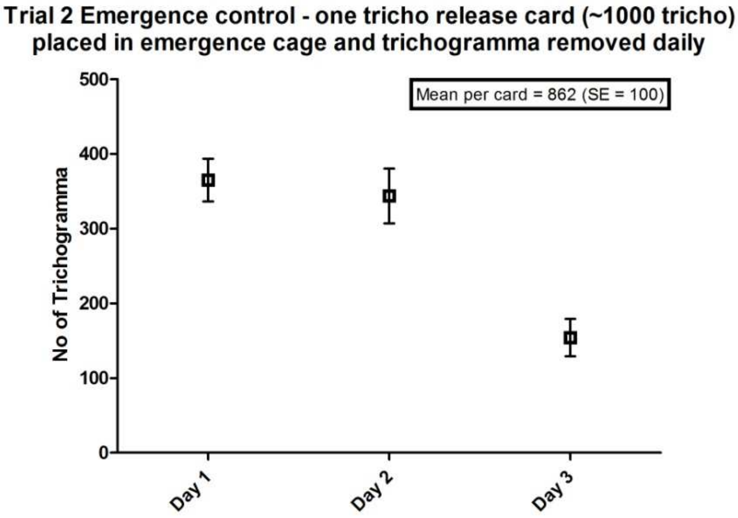

Fig. 12. *Trichogramma* emergence per day at the release point.

As the number of *Trichogramma* released in this trial was lower than for T1, the number caught in sticky traps was much lower, and hence the error around the estimate of wasp accumulation in each of the refuges and plots was higher (**Figs. 13** & **14**). In this trial, Landscape had a higher effect than on-farm refuges, although the difference was not statistically significant (**Figs. 14** & **15**).

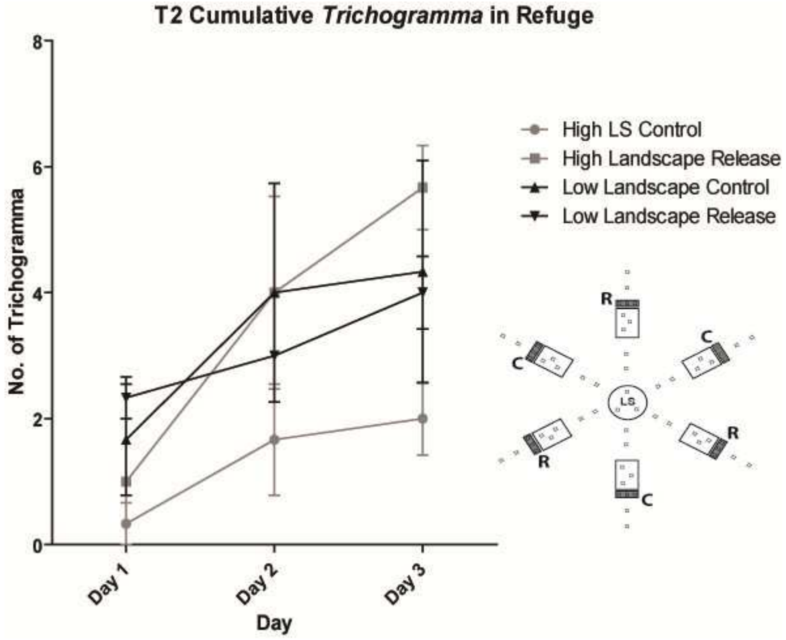

Fig. 13. Cumulative total number of *Trichogramma* individuals retrieved from the sticky traps in the refuges (control or release) each day.

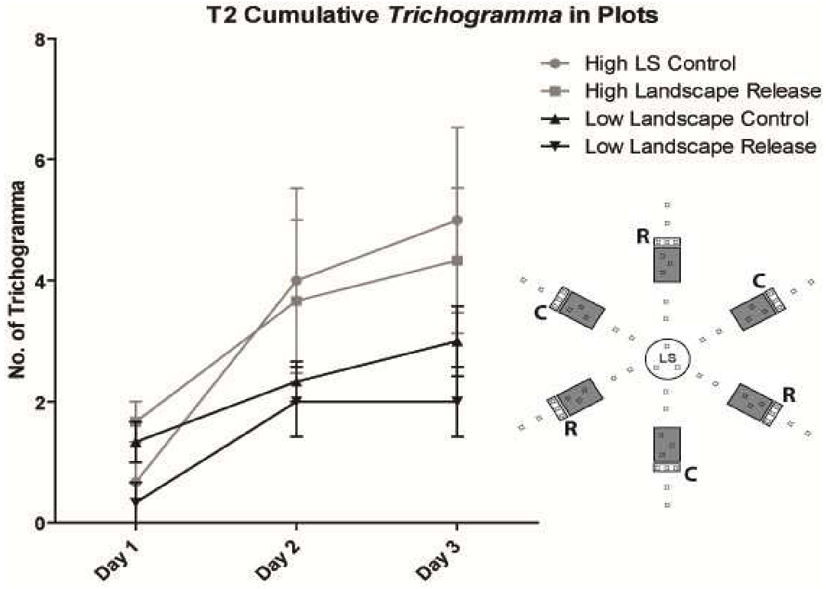

Fig. 14. Mean and SEM of *Trichogramma* retrieved from the plots (n = 3 for each treatment), shown in grey in the map.

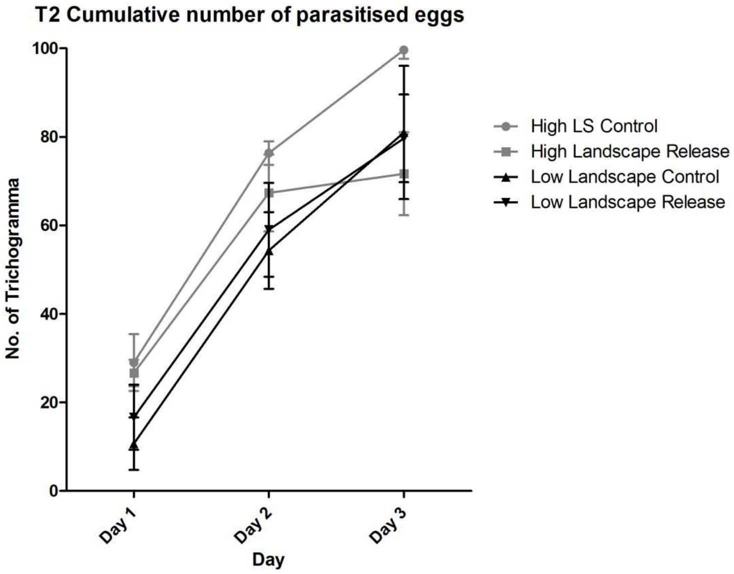

Fig. 15. Cumulative parasitised eggs returned from each of the plots (n=3 per treatment).

Trial 3

In trial three *Trichogramma* emergence in the field release was lower than for the previous two trials (**Fig. 16**), and had not reached peak emergence by the end of the trial.

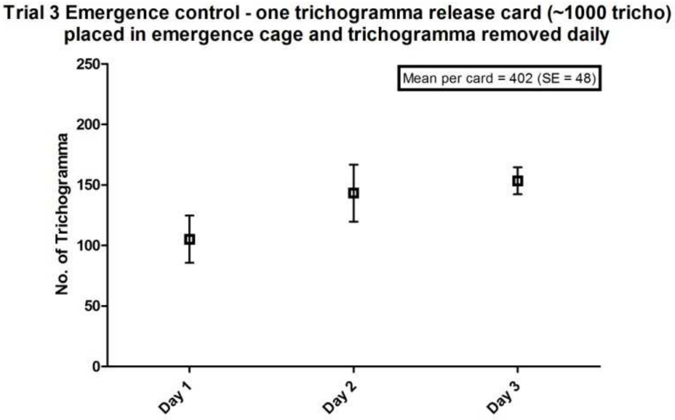

Fig. 16. Wasps returned from emergence controls during T3.

During trial 3 the higher wind speeds (**Fig. 6**) reduced *Trichogramma* movement to effectively nothing, there was almost no activity on days one and two (**Figs. 17,18** & **19**). On day 3 the wind was calmer, and some activity was recorded, but there was no discernible pattern in the accumulation of wasps, or the parasitism of eggs, as a result of the reduced activity in the previous two days.

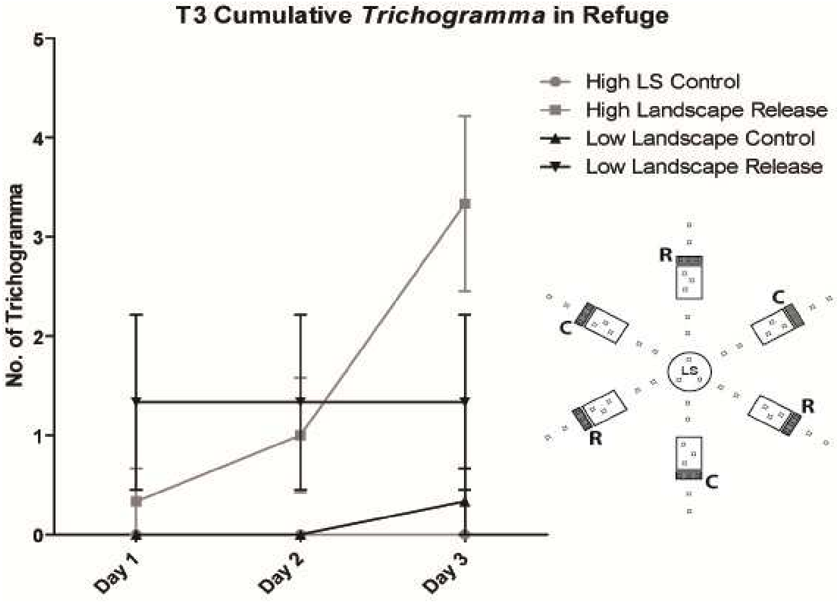

Fig. 17. Cumulative total number of *Trichogramma* individuals retrieved from the sticky traps in the refuges (control or release) each day.

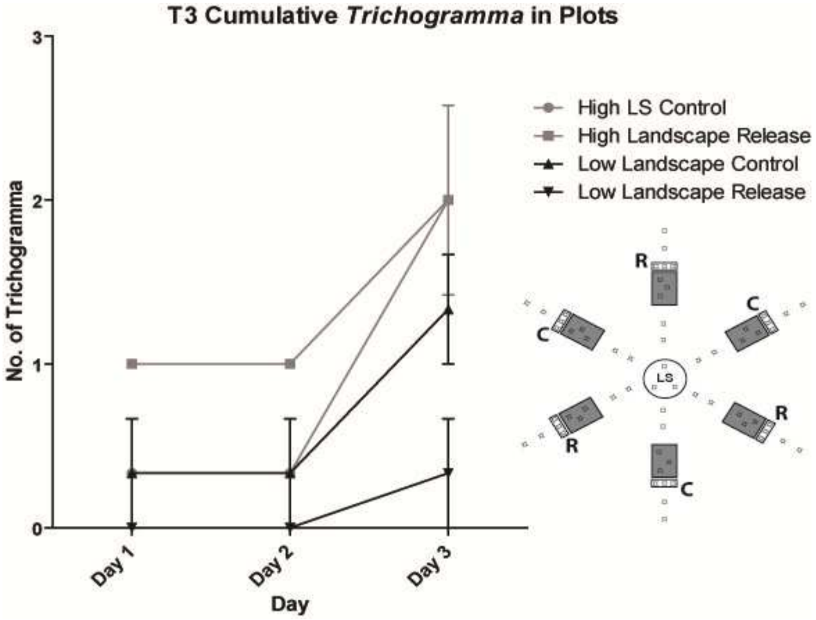

Fig. 18. Mean and SEM of *Trichogramma* retrieved from the plots (n = 3 for each treatment), shown in grey in the map.

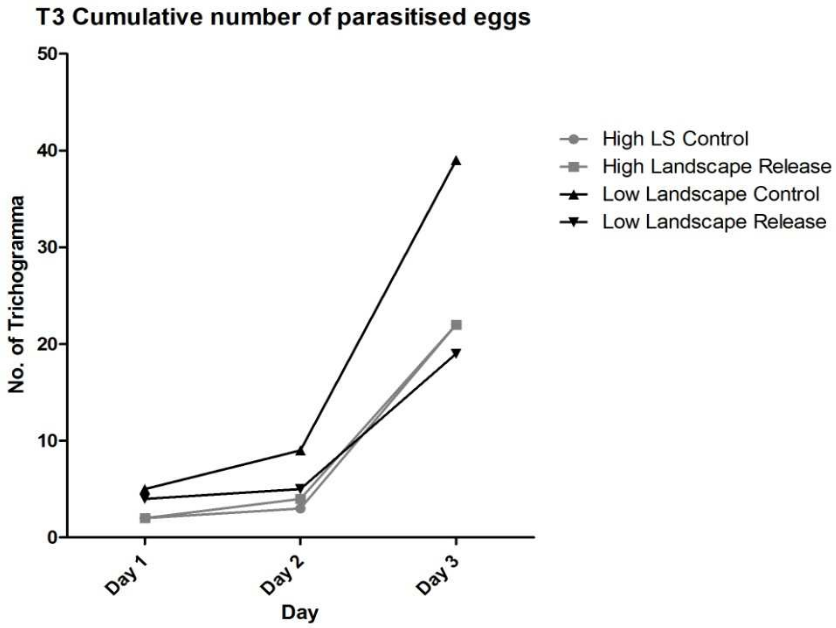

Fig. 19. Cumulative parasitised eggs returned from each of the plots (n=3 per treatment).

Discussion

Field testing spatially explicit models

Our approach to the problem of beneficial pest movement into crops from on-farm refuges and landscape sources has been to combine spatially explicit modelling with a field test of the predictions of the model. Mathematical models provide a means to explore the relative contribution of multiple factors to a process of interest. It also allows for generalizations that can be extended more broadly to several vegetable systems across regions. In the construction of simplified models various assumptions are made, and a multitude of environmental factors that have not been incorporated into the model may also affect the process of interest. It is therefore critical that predictions made by a model are tested so that the applicability of the predictions to real-world situations can be evaluated. There are several possible approaches to model testing in ecology, including but not limited to: 1. controlled laboratory experiments, 2. manipulative field experiments, 3. large scale field studies. Each approach has benefits and limitations; controlled laboratory experiments might yield better model fitting, but exclude environmental factors that have not been explicitly incorporated into the model. Manipulative field experiments match natural conditions more closely, but the natural behaviour of the organism used may be affected by the conditions of the experiment. Large scale field studies may provide the closest fit to natural conditions, but the practical considerations of maintaining relatively controlled conditions and monitoring insect movement in such large scale studies make them particularly difficult to implement for a question such as this. We took the approach of a small scale field-based manipulative experiment as the best compromise for this study, and the best chance of extending results to many growers in many regions. Even at this scale, field tests of ecological models are logistically complex, but our research highlights the value of model testing to the application of knowledge gained through modelling exercises as explained below.

Role of on-farm refuges for beneficial recruitment to crops

The results of our manipulative field experiment show that placing refuges near a crop has a positive effect on the accumulation of beneficial insects within a crop, and that this effect is more pronounced when the landscape contribution of beneficial insects is low. This finding fits with the predictions of the theoretical exploration of this issue in our spatially explicit model. This effect was, however, more pronounced in our first trial (T1) where the number of beneficial insects released was higher, and in line with commercial release rates. In the second trial (T2) the release rate was lower, and at these beneficial insect densities the effect of landscape contribution was greater than that due to the presence of refuges, although not statistically significant. In our third trial (T3) beneficial insect dispersal was heavily repressed by the presence of above average wind speed, and this highlights the importance of environmental factors that were not considered in the theoretical model to beneficial insect dispersal under field conditions.

Dispersal of Trichogramma wasps

In our trials, using plots of sweet-corn in fallow field matrix, *Trichogramma* wasps dispersed much more rapidly and further than the published literature suggests (Fournier and Boivin 1999 & 2000; Bueno *et al.* 2012; Stinner *et al.* 1974; Wright *et al.* 2001). In trial one and two the wasps had reached the furthest point of our experimental plots (50m from the release point) on day one. This finding is significant because the dispersal of *Trichogramma* wasps across fallow fields has received little attention prior to this study. It also adds weight to our findings, as our model shows that the effects of the refuge-landscape interaction will be weaker in highly dispersing predators, and wasps in this case.

Future research priorities

Our research highlights a knowledge gap in the dispersal capacity of beneficial insects, and across fallow fields. Whereas there is a large body of literature on *Trichogramma* dispersal in planted fields, prior to our work nothing was published on their dispersal capacity across open space. This is perhaps understandable, as long range dispersal and host searching are difficult to test under field conditions but it is critical to do so, because the results of laboratory experiments can be difficult to extrapolate to insect behaviour in the field. Further, many beneficial insects are studied within the context of their efficacy within a crop. When the focus is to boost the recruitment of beneficial insects into a crop from external sources, dispersal across open landscapes is critical. Our model and results indicate that the ability of a beneficial insect to disperse across open landscapes has a strong effect on the relevance of establishing on-farm refuges in comparison to maintaining landscape refuges. For many key insect pests “major effect” of beneficial insects has been established. In order to prioritise the provision of refuges, and optimise their positioning, the dispersal capacities of these key beneficial insects from an on-farm refuge into the crop of interest, and across open space warrants further investigation.

Additional research is required to evaluate the role of on-farm refuges for poorly dispersing beneficial insects; our model shows that the effect of on farm refuges will be greater for beneficial insects with low dispersal capacity. We have also showed that it can have a positive effect even for beneficial insects with high dispersal capacity, but further testing of low-dispersing beneficial insects was beyond the scope of this study. The key question arising from this finding is; “If no on-farm refuge is provided, how well are beneficial insects with low dispersal capacity recruited into the crop?”

III. How many aphids can the striped ladybird beetle and the red & blue beetle eat?

CSIRO hosted a student intern from France Agrocampus Ouest, Mr. Barthelemy Chenaux. As part of his internship requirements he conducted a study on two native predators that are abundant in many vegetable cropping systems, the striped ladybird beetle and the red and blue beetle. For copyright reasons, the full article is not included. The main finding is that two common predators of vegetable pests consume 39 and 60 aphids per day, respectively, and the more aphids available the more they eat. This aphid has been recorded to feed on over 200 host plants from Australia. These two predators can play an important role in aphid suppression in Australian agro-ecosystems and specifically vegetables production systems.

The article titled ‘Functional response of two common Australian predators, *Dicranolaius bellulus* (Guerin-Meneville) (Coleoptera: Melyridae) and *Micraspis frenata* (Erichson) (Coleoptera: Coccinellidae), attacking *Aphis gossypii* Glover (Hemiptera: Aphididae), can be found in the Australian Journal of Entomology, 2011, 50:453-459.

AUSTRALIAN JOURNAL of ENTOMOLOGY

Australian Journal of Entomology (2011) **50**, 453–459

Functional response of two common Australian predators, *Dicranolaius bellulus* (Guérin-Méneville) (Coleoptera: Melyridae) and *Micraspis frenata* (Erichson) (Coleoptera: Coccinellidae), attacking *Aphis gossypii* Glover (Hemiptera: Aphididae)

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TECHNOLOGY TRANSFER

Grower and Community Group Engagement

There were many different types of activities throughout the project to engage and communicate the concept of 'Revegetation by Design', 'early predator arrival', 'Ecosystem Services' and integrating native vegetation and habitat management with pest control. First, Dr. Costamagna and a team of eight worked with 19 growers and their families across the Lockyer Valley, QLD. Second, Drs. Costamagna and Schellhorn presented two talks at grower workshops lead by David Carey DPI&F held at Gatton on 6 May 2011, 27 March 2012. A total of 35 people attended. The first year results were to be presented in late 2010, but rescheduled due to the flood. Quizzes were given at the end of workshops to assess knowledge uptake. Third, Dr. Costamagna sent letters to all grower collaborators, Jan 2010, thanking them for their participation and providing information about preliminary results. Fourth, Dr. Schellhorn presented two talks at grower workshops on the Darling Downs, Dalby and Brookstead, QLD, 28 July 2011. A total of 62 people attended. Although the majority of growers in the area produce cotton and grain, some are vegetable growers and the messages cut across industry. This workshop was featured in the Rural weekly, Friday 19 August 2011. Fifth, at the International Ecology Congress meetings (an international symposium held once every four years) in Brisbane in August 2009, CSIRO show-cased the 'Revegetation by Design' project in a brochure, and Dr. Schellhorn gave a presentation. Sixth, Dr. Schellhorn gave two nationally invited talks, at the DEEDI Science Review Highlights, and The University of QLD. Seventh, two international talks were given, Dr. Schellhorn presented at CIRAD, Montpellier France (funded invitation), 3-4 Oct 2011, and Dr. Costamagna (post-departure from CSIRO) presented at Entomological Society of America Reno, NV, USA Nov 2011. Eight, two articles were published in peer reviewed journals, 'The risk of exotic and native plants as hosts for four pest thrips (Thysanoptera: Thripinae),' *Bulletin of Entomological Research* 2010, and 'Functional response of two common Australian predators, *Dicranolaius bellulus* (Guerin-Meneville) (Coleoptera: Melyridae) and *Micraspis frenata* (Erichson) (Coleoptera: Coccinellidae), attacking *Aphis gossypii* Glover (Hemiptera: Aphididae),' *Australian Journal of Entomology* 2011. In addition, two additional manuscripts have been drafted as evidenced by the detail in the first two research reports that appeared in this report. It is hoped that both of these are submitted by mid-year. They have been delayed due to the early departure of Dr. Costamagna. Finally, articles appeared in *Vegetables Australia* May 2009, 'Revegetation by Design: The Role of Native Vegetation in Horticulture Systems', February 2011, 'Beetle Allies for Vegetable Growers'. This last article also appeared in the international industry publication *Outlooks on Pest Management* in February 2011. Two additional articles are in development, working with CSIRO communications, to be circulated to HAL prior to submitting mid-year 2012.

After our presentations at workshops we discussed with growers the options for creating on-farm refuges for beneficials. Many growers were keen to trial different options. However they all said that they need to know which plants to select, where to locate the planting, how many metres apart and how to manage the refuge to get the most out of the pest control services, and other co-benefits such as income from hay or in the case of environmental plantings, income from carbon capture.

RECOMMENDATIONS

The key recommendations to continue moving towards integration and adoption of 'Revegetation by Design' and 'Ecosystem Services' concepts as part of an IPM strategy include recognizing that the landscape context of a farm matters. Some fields/farms in some landscapes are getting free pest control services where natural enemies are responding quickly, colonizing the crop, and suppressing the pests, while other landscapes are not. Early response by predators leads to lower pest populations. Therefore, on-farm refuges to support beneficial insects are a critical component for better capture of pest control services. Recommendations to move towards on-farm management of beneficial insects include:

1) Trialling the best-bet on-farm beneficial-refuge options for vegetable production systems in the different regions. Early and continuous predator access kept pest populations low. These refuges would have to be managed and pest relationships would need to be understood. The on-farm trials would include: a) first developing a simple cost-benefit analysis of the different planting options, including farm constraints (space, current production system), markets (demand for native vegetation seed, and hay), and seed or seedling availability; b) next working with growers who are keen to plant on-farm trials in different spacing arrangements; c) developing 'simple measures of effectiveness' in a monitoring program such as earliness of predator arrival, number of days pest populations stay below threshold, co-benefit payment of refuge (eg. Hay or seeds for native plant industry). We have now shown that there are many options for hosting beneficials, both native plants and perennial forages. Further, we have created an extensive data base on native plants (specific to three major vegetable production regions Lockyer Valley, Fassifern Valley, Northern Adelaide Plains), and their traits including information such as growth habit (eg. Low growing shrubby), flowering time, attractiveness to beneficials, risk score for pests of vegetable crops, and locations where to source seed and tubestock. This information combined with results from our past research could be used to trial refuge options and develop a decision support tool.

2) Developing a decision-support tool to assist growers with plant selection (both native and agronomic), sourcing seed and tube stock, and implementation. Growers frequently ask what should they plant where to encourage beneficial insects. A decision support tool may also include environmental plantings that link with carbon capture.

3) Investigating how the condition of native remnant vegetation affects the pest load and habitat for beneficial insects. Some remnants contained mostly native plants, while others were overgrazed, or full of broad-leaf weeds known to harbour pests and disease of vegetable crops. A project by a PhD student could focus on the link between native remnant condition and production based ecosystem services.

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APPENDICES

Appendix I. Variables for landscape analysis, with information from sticky traps and area, that correlated significantly with aphid suppression**:**

Variables combining all crops:
1- Mean number of all predators combined / number of areas sampled with sticky traps at the 1 km scale (combining all the crops in the landscape)
2- Proportion of the number of areas sampled that had all predators (i.e. all predators > 0) at the 250 meters scale
3- Mean area with mobile natural enemies x number of natural enemies / number of areas sampled with sticky traps at the 1 km scale (combining all the crops in the landscape)
4- Mean area with all predators x number of all predators / number of areas sampled with sticky traps at the 1 km scale (combining all the crops in the landscape)

Variables calculated per crop:
5- Mean number of all predators combined / sticky trap in Lucerne at the 1 km scale
6- Mean number of spiders / sticky trap in Lucerne at the 1 km scale
7- Mean number of mobile Natural Enemies / sticky trap in Other Crops at the 1 km scale
8- Mean number of all predators combined / sticky trap in Other Crops at the 1 km scale
9- Mean (Cucurbit area with all predators x number of all predators in Cucurbits / number of areas sampled with sticky traps) at the 1 km scale
10- Mean (Other Crops area with mobile Natural Enemies x number of mobile Natural Enemies in Other Crops/ number of areas sampled with sticky traps) at the 0.5 km scale
11- Mean (Other Crops area with all predators x number of all predators in Other Crops/ number of areas sampled with sticky traps) at the 0.5 km scale
12- Mean (Other Crops area with spiders x number of spiders in Other Crops/ number of areas sampled with sticky traps) at the 0.5 km scale
13- Mean (Other Crops area with mobile Natural Enemies x number of mobile Natural Enemies in Other Crops/ number of areas sampled with sticky traps) at the 250 m scale
14- Mean (Other Crops area with all predators x number of all predators in Other Crops/ number of areas sampled with sticky traps) at the 250 m scale
15- Mean mean (Other Crops area with spiders x number of spiders in Other Crops/ number of areas sampled with sticky traps) at the 250 m scale
1- Mean (Cucurbit area with all predators x number of all predators in Cucurbits / number of areas sampled with sticky traps) at the 1.5 km scale
16- Mean (Cucurbit area with spiders x number of spiders in Cucurbits / number of areas sampled with sticky traps) at the 1.5 km scale
17- Mean (Cucurbit area with all predators x number of all predators in Cucurbits / number of areas sampled with sticky traps) at the 2.0 km scale
18- Mean (Cucurbit area with spiders x number of spiders in Cucurbits / number of areas sampled with sticky traps) at the 2.0 km scale

Appendix II. Full MLR models fitted combining all independent predictors that correlate with aphid suppression:

Variables combining all landscape covers:

model	*Scale*	*variable*	*Area in predictors*
OO = EE + 1 + 2	Mixed	AP	yes
OO = EE + 3	1 km	MP	yes
OO = EE + 4	1 km	AP	yes

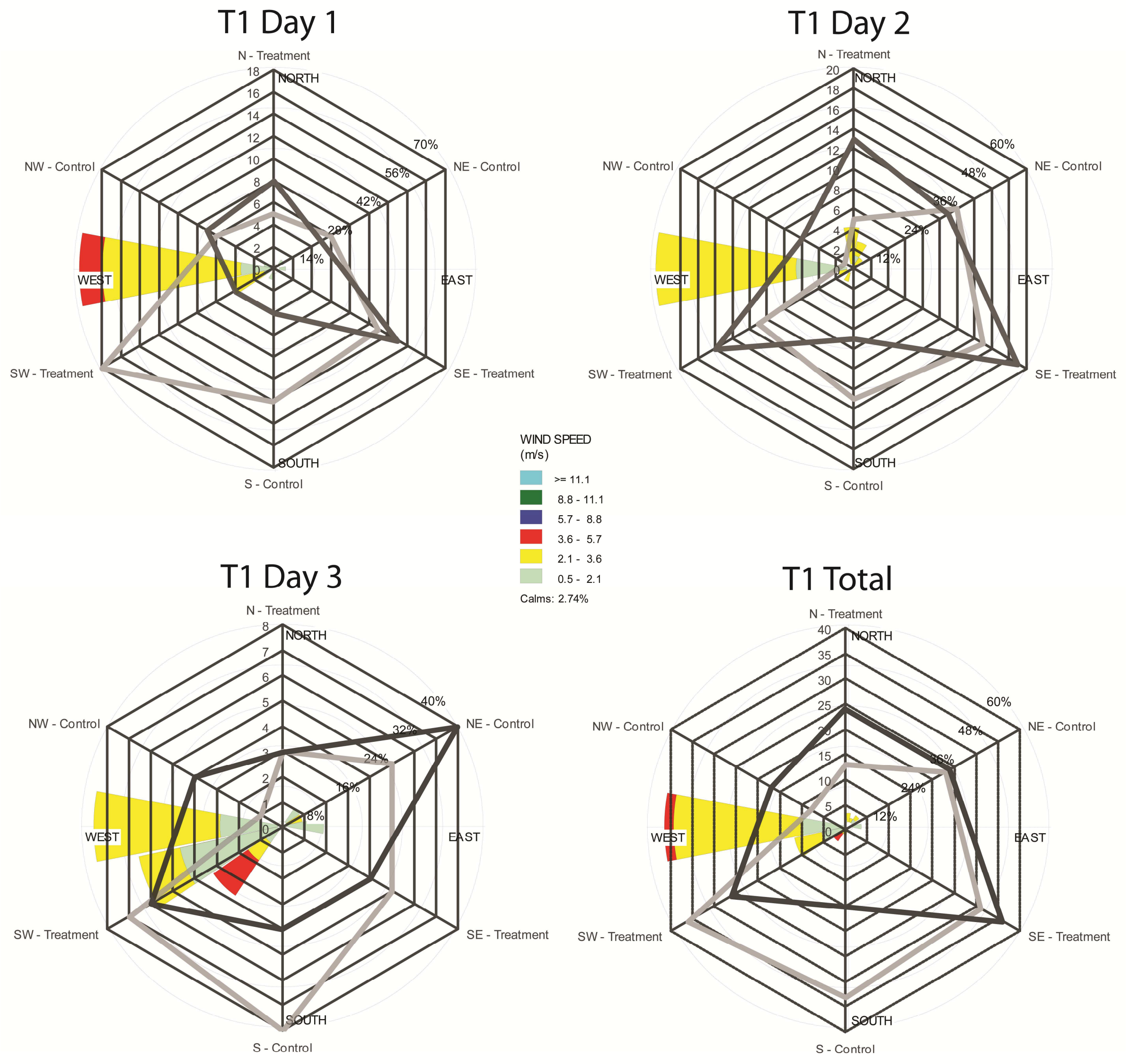
Variables calculated per landscape cover:

model	*Scale*	*variable*	*Area in predictors*
OO = EE + 5 + 6	1 km	AP	no
OO = EE + 3	1 km	SPI	no
OO = EE + 7	1 km	MP	no
OO = EE + 9 + 11	Mixed	AP	yes
OO = EE + 9 + 14	Mixed	AP	yes
OO = EE + 10	0.5 km	MP	yes
OO = EE + 11 + 16	Mixed	AP	yes
OO = EE + 11 + 18	Mixed	AP	yes
OO = EE + 12 + 17	Mixed	SPI	yes
OO = EE + 12 + 19	Mixed	SPI	yes
OO = EE + 13	0.25 km	MP	yes
OO = EE + 14 + 16	Mixed	AP	yes
OO = EE + 14 + 18	Mixed	AP	yes
OO = EE + 15 + 17	Mixed	SPI	yes
OO = EE + 15 + 19	Mixed	SPI	yes
Combining mobile predators and spiders			
OO = EE + 6 + 7	1 km	SPI MP	No
OO = EE + 6 + 10	Mixed	SPI MP	yes
OO = EE + 6 + 13	Mixed	SPI MP	yes
OO = EE + 7 + 12 + 17	Mixed	MP SPI SPI	yes
OO = EE + 7 + 15 + 17	Mixed	MP SPI SPI	yes
OO = EE + 7 + 12 + 19	Mixed	MP SPI SPI	yes
OO = EE + 7 + 15 + 19	Mixed	MP SPI SPI	yes
OO = EE + 10 + 12 + 17	Mixed	MP SPI SPI	yes
OO = EE + 10 + 15 + 17	Mixed	MP SPI SPI	yes
OO = EE + 10 + 12 + 19	Mixed	MP SPI SPI	yes
OO = EE + 10 + 15 + 19	Mixed	MP SPI SPI	yes

OO = continuos predation treatment
EE = predator exclusion treatment
AP = all predators
MP = mobile predators
SPI = spiders

Appendix III.

Number of wasps collected in sticky traps plotted against direction of the traps, combined with windrose displaying the wind direction and strength for each day. Gray represents wasp dispersal pattern in high landscape, and black represents low landscape. The experimental design allowed us to confirm that wind is not a key driver in local foraging and dispersal.



Appendix IV

Automatic *Trichogramma* counting using a high resolution transmission scanner and ImageJ software, adaptive local threshold was used to identify wasps from other particles (top, white bar = 1mm), this allowed many thousands of *Trichogramma* to be counted accurately by the software (below).