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Biological Control

Vegetation increases the abundance of natural enemies in vineyards

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ABSTRACT

Non-crop areas can increase the abundance of natural invertebrate enemies on farmland and assist in invertebrate pest control, but the relative benefits of different types of vegetation are often unclear. Here, we investigated abundance of natural enemies in vineyards with edges consisting of different types of vegetation: remnant native forests, wooded margins planted after establishment of the crop (hereafter called shelterbelts), or pasture. Invertebrates were sampled four times using canopy sticky traps and ground level pitfall traps, replicated across two seasons at one of the sites. The distribution and abundance of natural enemies in relation to edges with adjacent vegetation or pasture were mapped by distance indices (SADIE) and compared with ANOVAs. There was a positive influence of adjacent wooded vegetation on staphylinids, predatory thrips, predatory mites, spiders, ladybird beetles and hymenopteran parasitoids including *Trichogramma* egg parasitoids in the canopy and/or at ground level, although there were significant differences among sites and groups of organisms. In contrast, pasture edges had no effect or a negative effect on numbers of natural enemies in vineyards. To directly assess potential beneficial effects of adjacent vegetation, predation and parasitism of eggs of a vineyard insect pest, *Epiphyas postvittana* Walker (Lepidoptera: Tortricidae), was measured. Parasitism by *Trichogramma* was higher adjacent to remnant vegetation while predation was not affected. These results indicate that the abundance and distribution of vineyard natural enemies and parasitism of pest moth eggs is increased adjacent to edges with wooded vegetation, leading to beneficial effects for pest control. The conservation of remnant woodland and planting of shelterbelts around vineyards may therefore have direct economic benefits in terms of pest control, whereas non-crop pasture may not produce such benefits.

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1. Introduction

As more arable land comes under cultivation, there are potential consequences for agricultural pest control, because a decrease in non-crop habitat in a landscape can reduce the abundance and effectiveness of natural enemies of pests (Bianchi et al., 2006). Many studies have demonstrated that the activity of natural enemies and other beneficial invertebrates in agricultural ecosystems is reduced as diverse habitat is lost (Schmidt et al., 2004). These effects have been detected for a variety of enemies including parasitoids, spiders, beetles and predatory mites (Symondson et al., 2002; Thorbek and Bilde, 2004; Tsitsilas et al., 2006). Non-crop vegetation may provide resources for enemies not found in crops such as shelter, overwintering sites and food sources particularly for a wide range of arthropods with primarily carnivorous feeding habits that need plants for pollen or nectar to complement prey. However, maintaining or even increasing non-crop habitat comes at a cost to farmers in terms of a reduction in the area available for production.

By understanding characteristics of vegetation that promote natural enemies, this potential cost could be decreased (Gurr et al., 2004). For instance, vegetation that provides nectar resources can increase activity of predators and parasitoids (Landis et al., 2000; Hooks et al., 2006; Winkler et al., 2006). This increased activity at field edges can translate into decreased crop damage in adjacent crops and therefore could provide direct benefits to offset costs (Landis et al., 2000; Tscharntke et al., 2002; Bianchi et al., 2006; Tsitsilas et al., 2006). However the connection between natural enemy activity and pest control is not always clear (Gurr et al., 2000). For instance Olson and Wäckers (2007) found no change in cotton boll damage with decreasing distance from a field margin, despite an increased abundance of natural enemies. Pest damage can even be higher at the edge of fields bordered by trees despite an increase in natural enemies (Holland and Fahrig, 2000).

Sustainable pest control usually involves many enemy species that have an impact on a particular prey and whose importance may change over time (Rosenheim, 1998; Memmott et al., 2000; Symondson et al., 2002; Cardinale et al., 2003). For instance, control of aphids involves different natural enemies in particular years and regions (Thies et al., 2005) and the key controlling agent might switch between different groups (Schmidt et al., 2003). When assessing the overall benefits of adjacent vegetation on decreasing

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crop damage, the impact of a range of host/parasitoid and predator/prey interactions therefore needs to be assessed.

In this study, we evaluate the impact of vegetation adjacent to vineyards in south-eastern Australia on natural enemy abundance. The most significant insect pest in Australian vineyards is light brown apple moth, *Epiphyas postvittana* Walker (Lepidoptera: Tortricidae) (LBAM). LBAM is known to be parasitised by 25 species of Hymenoptera (Paull and Austin, 2006) and attacked by predators including spiders, predatory Hemiptera and neuropteran larvae (Thomson and Hoffmann, 2006a). A host of pests other than LBAM also attack vines including eriophyoid mites, weevils, scale, mealybugs and Rutherglen bugs (Buchanan and Amos, 1992). These vary in importance depending on region and season, and are all potentially controlled by natural enemies including parasitoids and predatory mites.

In many parts of Australia, there is increasing interest in understanding the impact of non-crop vegetation within agricultural landscapes on production. The vegetation might consist of remnant woodland that has never been used for cropping, or new plantings aimed at providing shelter from wind or chemical drift, corridors for wildlife, removal of waste water or meeting regulatory requirements. At present, vegetation is not specifically maintained or planted for promoting invertebrate natural enemies, and we are unaware of studies that investigate this issue within a vineyard context.

To address the potential impact of vegetation on pest control in vineyards, data were collected over two grape growing seasons using two trapping methods (canopy and ground level) at multiple sites. Spatially explicit sampling and mapping techniques were used to establish patterns of natural enemy abundance throughout one vineyard with two wooded and two pasture edges. At other sites we examined invertebrate diversity and abundance in different types of vegetation and within the adjacent vineyards. Finally, we investigated whether spatial patterns in natural enemies could be linked to predation and parasitism of eggs near adjacent vegetation.

2. Materials and methods

2.1. Sites

Sampling was undertaken at 10 sites in commercial vineyards at Yarra Glen (37°43′S, 145°24′E) in two grape growing seasons, 2004–2005 and 2005–2006. Each site consisted of a block of the same grape variety (Chardonnay) with 3 m between rows, and rows consisting of vines 2 m apart planted to trellis with poles 5 m apart and of similar size (5–8 ha). Vine size and vigour were similar throughout the blocks. Undervine and interrow management practices were similar: soil under the vines was bare earth following application of herbicides, and between the vines was mown grass (mainly perennial rye grass *Lolium perenne* and phalaris *Phalaris* sp., with varying amounts of capeweed *Arctotheca calendula* and clover *Trifolium repens*). Only chemicals of low toxicity to beneficials (based on IOBC ratings – http://www.koppert.nl – and related data – see Thomson and Hoffmann, 2006b) were used, including sulphur (Thiovit®) (at 200 g/100L) and tebufenozide (Mimic®). We selected vineyards with three different edges: remnant, complex shelterbelts (*sensu* Tsitsilas et al., 2006) or cleared (pasture). Remnant refers to vegetation which is presumed to predate the establishment of agriculture in the region and thus may be representative of the original landscape. There was only limited remnant vegetation with a complex understory in the region considered. The term shelterbelt refers to planted trees with an understory consisting of shrubs and grasses.

In the first season (2004–2005), intensive sampling was carried out throughout an entire vineyard (site 1) with remnant (REM1),

shelterbelt (SB1) and pasture edges for spatial analysis of the distribution of natural enemies relative to the edges. Sampling points were established at 100 points located randomly throughout the vineyard. In the second season (2005–2006), sampling was repeated at site 1 in woody vegetation and in the vines 5 and 50 m into the vineyard at both woody (e.g., SB and REM) vegetation edges to compare consistency between seasons. We also sampled at five additional vineyards with adjacent SB vegetation, one site with REM vegetation and two sites with pasture edges.

At each site with woody vegetation we sampled in the vegetation and in vine rows 5 and 50 m from vegetation (REM1–2 and SB1–6), again with five replicate sampling points at each distance. Vegetation at each site is given in Appendix A. We also further assessed the effects of edges at two other sites where the vines had pasture edges, sampling points extended at 10 m intervals from the center of each vineyard to the pasture edges. Sampling points for pasture edges extended 50 m into the vineyard, again with five replicate sampling points at each distance.

2.2. Sampling

At each sampling point we placed a pitfall trap to sample ground level invertebrates and a yellow sticky trap to sample canopy invertebrates. Pitfall traps consisted of an outer sleeve and an inner container with 4 cm of ethylene glycol. For the spatial collection, pitfall traps consisted of two plastic cups (Charnol Australia), 70 mm diameter × 80 mm deep. For all other collections each pitfall trap consisted of a glass test tube, 20 mm diameter × 150 mm deep, inserted into a plastic sleeve, 22 mm diameter × 150 mm deep, inserted so that the top was flush with the surface. The yellow sticky traps were 240 mm × 100 mm (Agrisense) sheets suspended from the lower wire of a vertical two-wire trellis system 1 m above the ground. Sampling in both seasons was repeated over 4 months (November–February), with traps placed and collected the first week of each month. Previous work has shown the importance of repeated temporal sampling to obtain a range of organisms in vineyards (Thomson et al., 2004). Invertebrates collected on yellow sticky traps were assessed *in situ*, the contents of pitfall traps were sieved and transferred to a 10 cm Petri dish. Collections were sorted using a microscope (Leica MS5) at magnification 20× to 100×: insects (CSIRO, 1991), spiders (Hawkeswood, 2003) and parasitoids (Stevens et al., 2007) were sorted to family and mites to functional group (Krantz, 1978).

Yellow sticky traps collected Araneae, Hemiptera, Diptera, Coleoptera, Hymenoptera, Neuroptera, Odonata, Thysanoptera and Lepidoptera. Pitfall traps collected Coleoptera, Araneae, Hymenoptera, Diptera, Dermaptera, Acarina, Neuroptera, Isopoda, Lepidoptera and Hemiptera. Lacewings were predominantly brown *Micromus tasmaniae* (Walker) (Neuroptera: Hemerobiidae). Three families of predatory Hemiptera were found (Reduviidae, Nabidae and Anthocoridae) and numbers combined. The Diptera were sorted to family, the large number of Syrphidae analyzed separately and the other predatory/parasitic families (Empididae, Tachinidae and Cecidomyiidae) combined. There were 10 families of Hymenoptera: Formicidae, Braconidae, Ichneumonidae, Chalcididae, Encyrtidae, Pteromalidae, Aphelinidae, Mymaridae, Scelionidae and Trichogrammatidae. The last group was considered separately as it represents important egg parasitoids of LBAM (Glenn et al., 1997). Numbers of the other Hymenoptera, excluding Formicidae, were combined as 'parasitoids'. The role of ants in our vineyards is not fully known so their numbers were included in community analysis but not as predators.

Twelve families of Coleoptera were recorded: Carabidae, Staphylinidae, Anthicidae, Scarabidae, Curculionidae, Coccinellidae, Elateridae, Corylophidae, Byrrhidae, Bostrichidae, Lathridiidae and Tenebrionidae. Seven families were sufficiently numerous to be in-

cluded in community analyses and the three most abundant were predators and included in all analyses. These were the Carabidae, Coccinellidae (here *Stethorus* sp., *Cryptolaemus montrouzieri* Mulsant, four species of Scymninae *Diomus sydneyensis* (Blackburn), *D. notescens* (Blackburn) and two currently undescribed species (Ślipiński, personal communication), four species of Coccinellinae (*Coccinella transversalis* (Fabricius), *C. septempunctata* L. and *Micraspis frenata* (Erichson) and a *Harmonia* sp., predators of a range of pests including aphids, psyllids, leaf hoppers, chrysomelids, mites, mealybugs, scale and white flies (Ślipiński, 2007)), and five genera of Staphylinidae (*Blediotrogus*, *Tachinus*, *Leptacinus* and two Aleocharinae genera *Ocalea* and *Aleochara*, all predators (CSIRO, 1999), especially the Aleocharines which are known to be mite predators in vineyards). Predatory mites (including Phytoseiidae) were considered as a functional group. We also counted the most abundant of several Thysanoptera, including *Desmothrips* sp. (Aeolothripidae), a facultative predator usually of larvae of other thrips and potentially eggs of LBAM (Thomson, unpublished observation). Spiders are generally considered as contributing to pest control. Eighteen families were present (Agelenidae, Amaurobiidae, Clubionidae, Ctenidae, Dictynidae, Gnaphosidae, Heteropodidae, Linyphiidae, Lycosidae, Metidae, Micropholcommatidae, Miturgidae, Nemesiidae, Nicodamidae, Oxyopidae, Salticidae, Theridiidae, Zoridae). Dermaptera mainly consisted of the native common brown earwig, *Labidura truncata* Kirby (Dermaptera: Labiduridae). Because of applications of tebufenozide (Mimic®) (applied against LBAM), there were low numbers of all Lepidoptera and it was not possible to analyse naturally occurring LBAM. The analyses focused on organisms collected in sufficient numbers and that were likely to act as natural enemies of pests affecting grape production.

2.3. Predation and parasitism trials

We investigated natural predation and parasitism of LBAM eggs to directly assess the impact of vegetation on pest control. LBAM eggs were obtained from a colony originating in the Yarra Glen area (see Thomson et al., 2000). Emerged moths were placed for oviposition in plastic cups (Charnol, Australia) with horizontal ridges. The plastic cups were cut into strips with egg masses intact. Eggs laid in plastic cups were collected and stored at 4 °C until needed.

There are three flights of LBAM each year (Danthanarayana, 1975). In 2005, eggs were placed outside on 1 February for five days and a second batch placed outside on 6 February for five days to coincide with the predicted second flight. At each of the 100 sampling points in the vineyard on each occasion, we placed three LBAM egg cards (containing two egg masses of 20–70 eggs). LBAM egg masses form a raft which adheres to the cup and, although confirmation predation as the cause of egg loss would only be possible with direct observation, our previous experience suggests egg masses are not displaced by events such as rain or wind. Cards were scored for missing egg masses lost due to predation. They were placed at 25 °C for a further five days, then assessed for parasitism (eggs turning black), and returned to 25 °C until parasitoids emerged and were identified morphologically (Glenn et al., 1997). Percentage egg masses lost to predation or parasitism was calculated for each sampling point.

2.4. Analysis of collections

The mean numbers of each group collected per trap within a vineyard across the season were used in the analyses. We focused on groups which are commonly regarded as contributing to natural control of pests, and which occurred in most sites. Groups present in low numbers (means <5%) or not present at all sites were excluded.

Two types of analyses were undertaken on the data. We used Spatial Analysis by Distance IndicEs (SADIE) (http://www.rothamsted.bbsrc.ac.uk/pie/sadie: Perry et al., 1999) to detect and measure the degree of non-randomness of the distribution of natural enemies for the 100 points of season 1. We computed (I_a), the index of aggregation which equals 1 when the counts are arranged randomly in the grid, but >1 if counts are aggregated into clusters. I_a and its associated probability (P_a) measure the probability that the observed counts are arranged randomly among the given sample units. We computed V_i, the degree to which a unit contributes to clustering, and V_j, the extent to which a unit contributes a gap. Large values of V_i (>1.5) indicate patchiness, large negative values of V_j (<−1.5) indicate a gap, values close to one indicate random placement.

To determine if the distribution of non-random groups was related to the position of the field margins, cluster data files from the SADIE analyses were used to map distributions of the gaps (V_j) and patches (V_i) by importing the data files from SADIE to SURFER®.

For all other data, analysis of variance (ANOVA) was used to determine the effect of distance from the vineyard edge, site and sampling time (month) on the abundance of different predators. All analyses were undertaken with SPSS for Windows (version 15, SPSS Inc., Chicago, Illinois). Data were log-transformed prior to analysis and normality of the transformed data was confirmed with Kolmogorov–Smirnov tests. Seven groups – spiders, predatory thrips, Trichogrammatidae, Staphylinidae, Coccinellidae, parasitoids and lacewings – were included in canopy analysis, and five groups – Araneae, Staphylinidae, Carabidae, predatory mites and parasitoids – were considered at ground level. For site 1, which was sampled in both seasons, we extracted data for the 30 sampling points from season 1 corresponding to the points of the second season (SB1 and REM1) to directly compare results obtained across the two seasons. The ANOVAs considered the effects of distance into the vineyard and season. We also analyzed data for the eight sites examined in season 2 with wooded edges (SB1–6 and REM1–2). The ANOVAs included effects of distance, month and site, and were also repeated by averaging numbers across months and reanalyzing to test for site and distance effects. Because values at different distance classes in the same site might be autocorrelated in the landscape, we used REML to test for significant effects in the ANOVA, using the Mixed Model procedure in SPSS. Finally, we investigated edge effects at the two sites with pasture rather than wooded edges. In this case sampling was more intensive (six points rather than three points extending into the vineyard) and distance was therefore treated as a covariate in analyses of covariance (ANCOVAs) that also included site and month. The ANCOVAs were repeated after averaging data across months.

We tested similarity of community structure in the vegetation (V) and in the vineyard (50 m) at both ground and canopy levels across the eight sites with wooded edges sampled in season 2. Standardized Mantel statistics (r_m) were calculated based on the relative Sørensen distance measures of matrices. Randomization tests (1000 reps) were undertaken to test significance. For the canopy samples, 14 groups were included in this analysis while for the pitfall samples seven groups were included (see Results).

2.5. Analysis of predation/parasitism

The distributions of preyed upon egg masses and parasitised egg masses were investigated with SADIE (Perry, 1998). Distributions significantly different from random were mapped and associations between variables investigated. The overall spatial association between parasitised egg masses and *Trichogramma* distribution in February when the egg masses were in place was assessed by examining correlation between the clustering indices of each set. The degree of association between the two variables,

measured at the same location within the grid, was assessed with the QUICK ASSOCIATION ANALYSIS SHELL (version 1.5.2) program (Winder et al., 2001). A SADIE measure of local spatial pattern association (X_p) was calculated between the first set of cluster indices and the second set at one X, Y point. This measure of local association was mapped to graphically display patterns of association.

An overall measure of the spatial association between the two sets of cluster indices was obtained by averaging the X_p – values across the grid. The significance of X was tested against values X_{rand} using a randomization test. Allowance was made for small-scale autocorrelation in both sets of clustering indices which reduces the effective sample size using the method of Dutilleul et al. (1993). The effective size of the combined data sets was computed and degrees of freedom adjusted. Critical limits were inflated by a scale factor, and the significance of the randomization set adjusted. If $P < 0.025$ there was significant positive association, and if $P > 0.975$ there was significant negative association.

3. Results

3.1. Invertebrates collected

Over four months in the first year, 8183 individuals were retrieved from pitfalls: 4364 Formicidae (collected from 90% of traps), 1086 Araneae (68%), 548 parasitoids (61%), 339 Carabidae (43%), 224 Staphylinidae (27%), 256 predatory mites (25%), 197 larval Neuroptera (17%), 85 Curculionidae (17%) and 50 predatory Hemiptera (11%). For the canopy traps there were 26,195 organisms, including 2301 Trichogrammatidae (81%) and 9489 other parasitoids (94%), 2161 Syrphidae (30%), 771 Araneae (71%), 708 Coccinellidae (64%), 512 brown lacewings (44%), 453 predatory Diptera (49%), 259 Lepidoptera (33%), 51 predatory Hemiptera (10%) and 39 Staphylinidae (9%).

In the second year, 16,551 individuals were retrieved from pitfalls: 12,391 Formicidae (collected from 94% of traps), 2455 Isopoda (45%), 561 predatory mites (35%), 393 Araneae (49%), 256 Staphylinidae (36%), 240 parasitoids (28%), 152 Dermaptera (18%) and 100 Carabidae (20%). The canopy traps yielded 49,282 organisms: 4551 Trichogrammatidae (88%) and 33940 other parasitoids (99%), 8341 Coccinellidae (88%), 1060 Araneae (81%), 433 Lathridiidae (48%), 222 predatory thrips (23%), 359 Staphylinidae (44%), 152 Corylophidae (22%), 75 Anthicidae (9%), 79 Curculionidae (14%) and 50 brown lacewings (9%). Most families of spiders were collected both from pitfall traps and canopy traps, the exception being Lycosidae which was only found in pitfall traps. Lycosidae was the dominant family in pitfalls (79%) and Linyphiidae in the canopy (38%).

There were changes in the frequency of taxa in the two seasons and across collection months. Corylophidae, Anthicidae, Curculionidae were in much lower numbers in season 1 and there were few syrphids and other predatory Diptera in the second season. Predatory thrips were only common in the second season and brown lacewings relatively less abundant in this season. Brown lacewings showed strong temporal changes in abundance (72% were from the November collection). Trichogrammatidae and Coccinellidae were collected throughout the first season but were more abundant in November (*Trichogramma*) and February (coccinellids) in the second season.

3.2. Spatial patterns and association with edges

SADIE analyses were undertaken to test for non-random distribution patterns within the intensively sampled vineyard. For groups collected in low numbers throughout the season or predominantly in one month, we only analyzed data summed across collections. For the other taxa, we analyzed total numbers as well as those from monthly collections.

Spiders, lacewing larvae, predatory mites, staphylinids and parasitoids collected in pitfall traps all showed non-random spatial patterns, while carabids, predatory Diptera and Hemiptera did not (Table 1). Spiders, coccinellids, predatory Diptera and Hemiptera, Syrphidae and *Trichogramma* collected in the canopy showed spatial structure, parasitoids, staphylinids, Lepidoptera and lacewing adults did not (Table 1).

With two exceptions, coccinellids and spiders collected in the canopy, increased abundance in predator groups collected from pitfall and yellow sticky traps was associated with the wooded vineyard edges. Ground spiders were more abundant adjacent to remnant vegetation (Fig. 1), a pattern consistent across months (data not shown). The distributions of both larval lacewings (Fig. 1) and parasitoids (Fig. 2) were consistently associated with the shelterbelt. Predatory mites were associated with the shelterbelt overall, and also when most of them were collected in February (Fig. 1). The distribution of staphylinids was influenced by both edges (Fig. 1). Weevils (Curculionidae) were the only pests detected, and were present in low numbers in all months. While this group was distributed non-randomly (Table 1), it was not more abundant around the edges.

Spider numbers in the canopy showed spatial structure for most (3/4) months and overall (Table 1). The abundance of canopy spiders consistently increased away from the shelterbelt and abundance was relatively higher at the remnant edge (Fig. 3). The distribution of Coccinellidae collected in the canopy was significantly non-random in half (2/4) the months and overall (Table 1), with abundance increasing with distance from the shelterbelt. Predatory Diptera and Syrphidae from the canopy were distributed non-randomly (Table 1); Diptera and Syrphidae were associated with the remnant edge (Fig. 3). Diptera were common in November and February, and in each of these months the distribution was non-random and associated with the remnant. Predatory Hemiptera were collected in low numbers and showed spatial structure (Table 1) but this was unrelated to the edges.

Table 1
Summary of SADIE analysis results for taxa collected in a vineyard (site 1) when pooled across four monthly collections. The Index of aggregation (I_a) indicates the overall degree of clustering in the grid (>1 indicates aggregation), V_j indicates the presence of gaps (neighbourhoods of units with counts smaller than the overall grid mean), V_i indicates the presence of patches of high abundance (neighbourhoods of units with counts larger than the overall grid mean). P values provide tests of spatial structure and patches or gaps.

| Variable	I_a Index of aggregation (P)	Mean V_j (P)	Mean V_i (P)
Ground collections			
Araneae	2.038 (<0.001)	−2.101 (<0.001)	1.819 (0.002)
Carabidae	1.337 (0.072)	−1.262 (0.106)	1.226 (0.123)
Curculionidae	1.455 (0.032)	−1.560 (0.017)	1.395 (0.040)
Predatory Diptera	0.952 (0.533)	−0.963 (0.506)	0.840 (0.798)
Predatory Hemiptera	0.945 (0.536)	−0.925 (0.579)	0.854 (0.735)
Neuroptera larvae	1.757 (0.004)	−1.756 (0.003)	1.598 (0.008)
Parasitoids	2.573 (<0.001)	−2.314 (<0.001)	2.687 (<0. 001)
Predatory mites	2.487 (<0.001)	−2.468 (<0.001)	3.085 (<0.001)
Staphylinidae	1.956 (<0.001)	−1.909 (0.002)	1.752 (0.004)
Canopy collections			
Araneae	1.784 (0.003)	−2.030 (0.001)	1.644 (0.01)
Coccinellidae	1.648 (0.009)	−1.756 (0.004)	1.471 (0.022)
Predatory Diptera	1.728 (0.003)	−1.716 (0.006)	1.541 (0.015)
Predatory Hemiptera	1.431 (0.037)	−1.420 (0.042)	1.376 (0.05)
Lepidoptera	0.863 (0.735)	−0.951 (0.517)	0.846 (0.783)
Neuroptera adults	1.032 (0.363)	−1.097 (0.259)	1.024 (0.352)
Parasitoids	1.168 (0.170)	−1.237 (0.113)	1.123 (0.221)
Syrphidae	1.376 (0.047)	−1.526 (0.023)	1.281 (0.085)
Trichogrammatidae	2.300 (<0.001)	−1.845 (0.003)	2.460 (<0.001)
Staphylinidae	1.018 (0.383)	−1.057 (0.300)	0.984 (0.423)
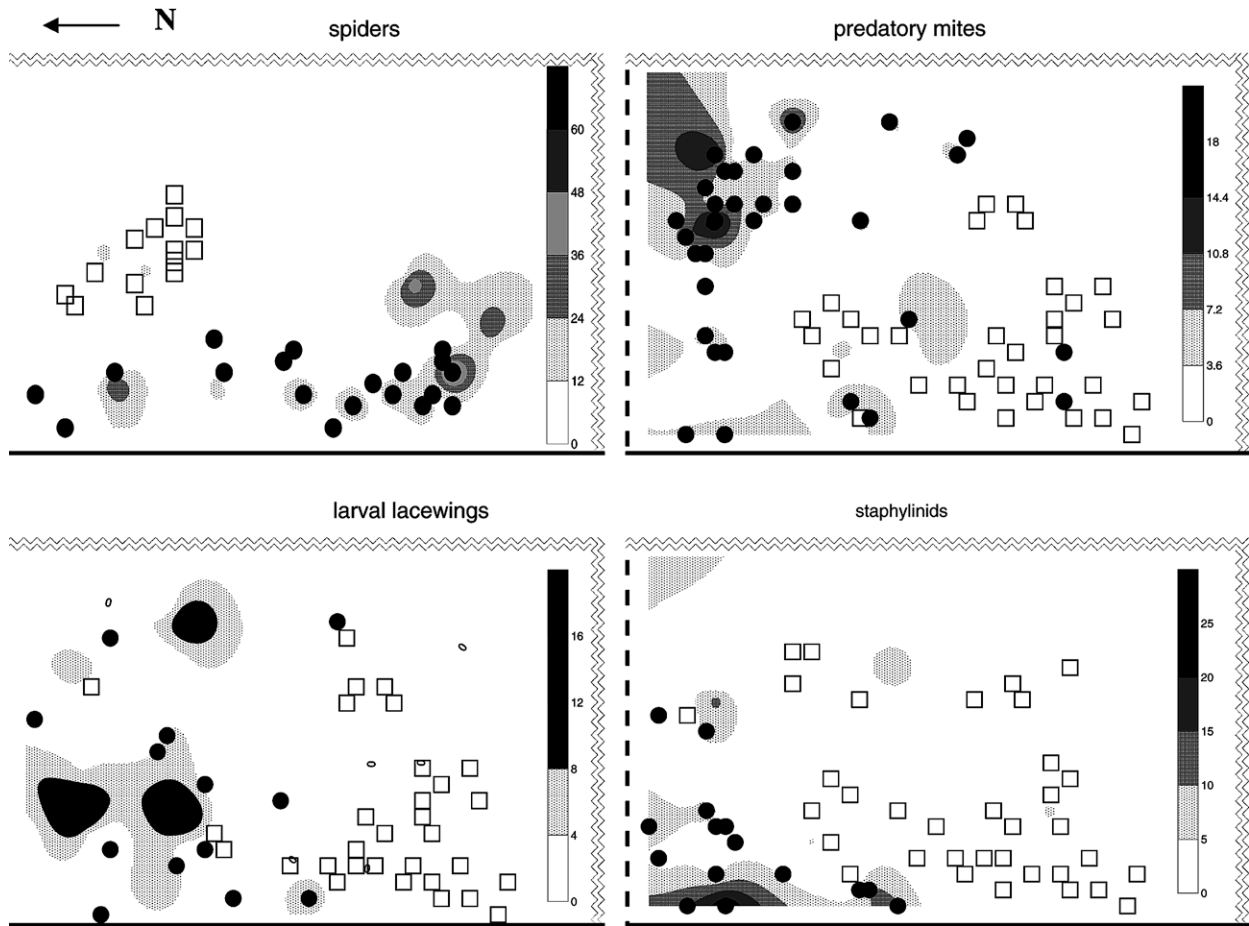
Fig. 1. Spatial distribution of predator groups collected from pitfall traps at site 1. Contour lines show total abundance collected at each sampling point for the four collections. Squares around sampling points indicate $V_j < -1.5$ (the presence of gaps), solid circles around sampling points indicate $V_i > 1.5$ (the presence of patches). The solid line shows the edge of the remnant vegetation (REM1), the dashed line shows the shelterbelt (SB1) and the double wavy line the two pasture edges.
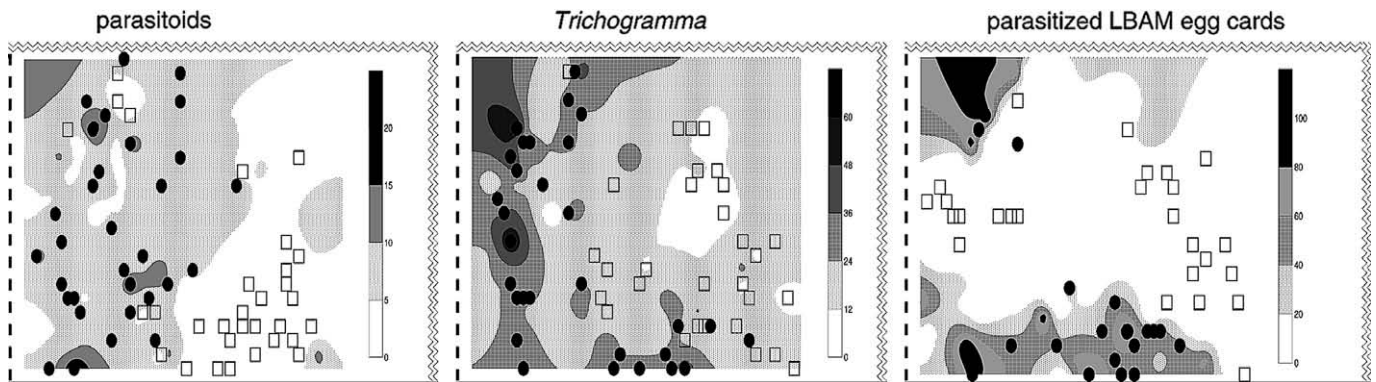

Fig. 2. Spatial distribution of *Trichogramma* and parasitised LBAM eggs at site 1 Contour lines show total abundance collected at each sampling point for the four collections. Squares around sampling points indicate $V_j < -1.5$, solid circles around sampling points indicate $V_i > 1.5$. The solid line shows the edge of the remnant vegetation (REM 1), the dashed line the shelterbelt (SB1) and the double wavy line the two pasture edges.

Finally, *Trichogramma* were distributed non-randomly overall (Table 2) and in three of the four months (all except January). In this group higher numbers were associated with both the shelterbelt and the remnant edges (Fig. 2).

In summary, the abundance of most groups of natural enemies was higher near the vegetated edges and declined further into the vineyard. The main exception to this pattern was for ladybird beetles and canopy spiders which were more abundant at this site away from the shelterbelt.

3.3. Comparison across seasons at site 1

The abundance of invertebrates in the second season at site 1 showed patterns that were consistent with those observed in the first season. Overall more invertebrates were collected in the vegetation than in the vine canopy (Fig. 4). In addition, the abundance of most groups of beneficials declined into the vineyard away from wooded vegetation with the exception of coccinellids and spiders. For the shelterbelt, as seen in season 1, there was an
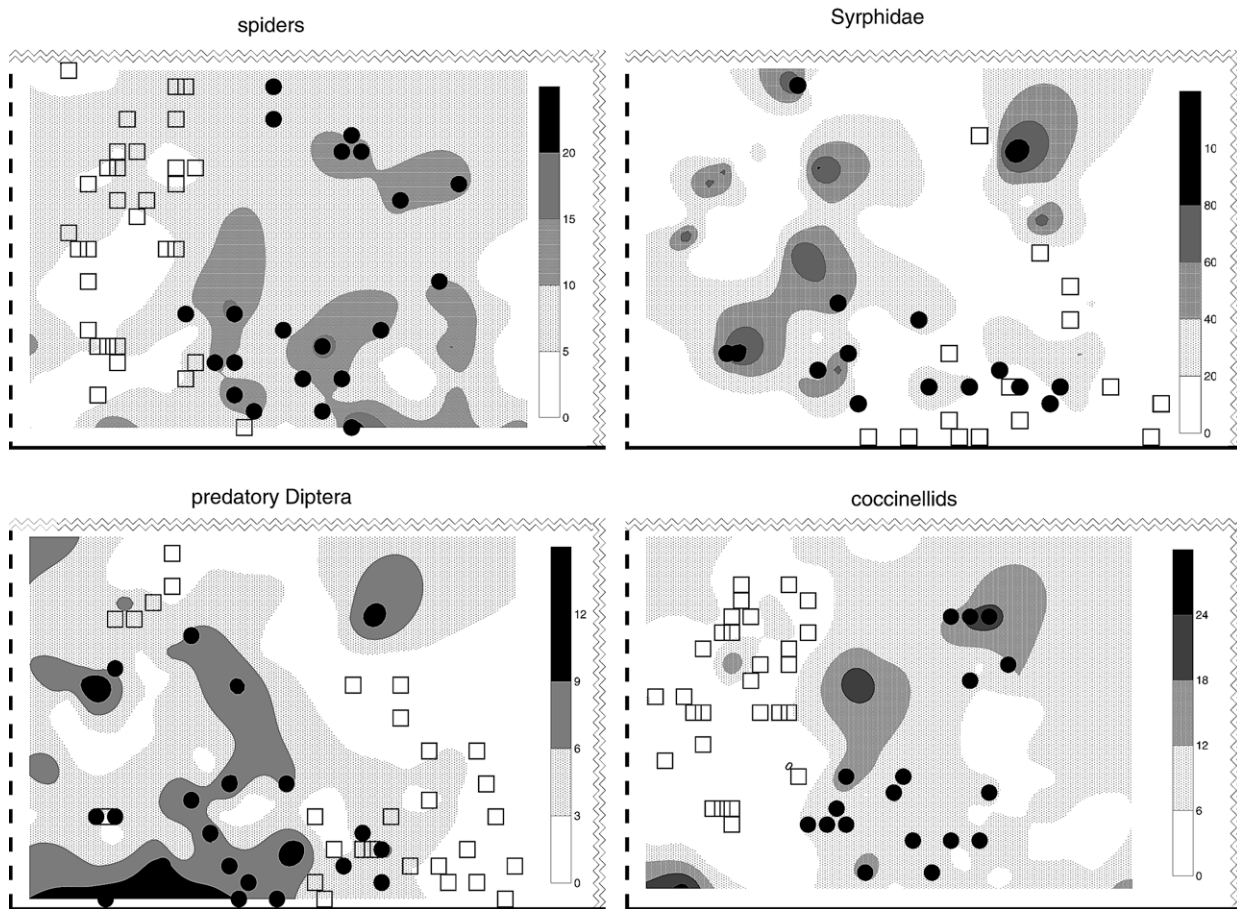
Fig. 3. Spatial distribution of predator groups collected in the vineyard canopy at site 1. Contour lines show total abundance collected at each sampling point for the four collections. Squares around sampling points indicate $V_j < -1.5$, solid circles around sampling points indicate $V_i < 1.5$. The solid line shows the edge of the remnant vegetation (REM 1), the dashed line the shelterbelt (SB1) and the double wavy line the two pasture edges.

Table 2
SADIE analysis results for February *Trichogramma* numbers and predation/parasitism levels in LBAM egg masses. The Index of aggregation (I_a) indicates the overall degree of clustering in the grid (>1 indicates aggregation), V_j indicates the presence of gaps (neighbourhoods of units with counts smaller than the overall grid mean), V_i indicates the presence of patches of high abundance (neighbourhoods of units with counts larger than the overall grid mean). *P* values provide tests of spatial structure and patches or gaps.

Variable	I_a Index of aggregation (P)	Mean V_j (P)	Mean V_i (P)
Trichogramma (February)	1.615 (0.01)	−1.573 (0.017)	1.575 (0.012)
Eggs lost to predation	0.988 (0.448)	−0.945 (0.55)	0.979 (0.475)
Eggs parasitised	1.523 (0.020)	−1.384 (0.045)	1.726 (0.006)

increase in canopy coccinellids and spiders away from the vegetation as well as a decrease in other taxa such as *Trichogramma* (Fig. 4). The response to the remnant was also consistent across season as evident from the decrease in the abundance of ground spiders, predatory mites and canopy *Trichogramma* (Fig. 4) with distance from the vegetation. ANOVAs testing the effects of distance and season on numbers of the different groups indicated significant effects of distance on canopy spider and coccinellid numbers in the shelterbelt transect, while numbers for predatory mites and ground spiders were significantly affected by distance in the remnant transect (Table 3). There were also interaction effects with month for *Trichogramma* from canopy samples at REM1 and SB1 (Table 3).

3.4. Site comparisons

ANOVAs on data for all eight sites collected in the second season showed significant responses in most groups to wooded edges, although site by distance interactions were also significant for several groups (Table 4). Overall in the canopy there were more parasitoids, staphylinids and predatory thrips (all eight sites), spiders and *Trichogramma* (6 of 8) and coccinellids (5 of 8) in the vegetation when compared to the vineyard, and numbers declined with increasing distance into the vineyard (Fig. 5). At ground level there were significantly more parasitoids, predatory mites and spiders (all 6 of 8) in the vegetation compared to the vineyard, with numbers again declining with distance into vineyard (Fig. 6) but differences depended on site and organism (Table 4). Significant effects of distance remained after Dunn–Sidak correction for multiple comparisons (number of groups considered) for all except canopy spiders and coccinellids, and ground collected parasitoids. When the ANOVAs were run on data averaged across months, significant distance effects were detected for all groups that exhibited these in the ANOVAs where month was included as a factor (results not presented). Site effects were not obviously related to whether vegetation consisted of remnants or shelterbelts (Figs. 5 and 6).

Mantel tests indicated that communities detected in the canopy from vegetation and vineyard were associated ($n = 8$, $r_m = 0.44$, $P = 0.012$) with a weaker association between communities at ground level ($n = 8$, $r_m = 0.39$, $P = 0.043$). This suggests that community structure in the vegetation at a site influences that in vine-
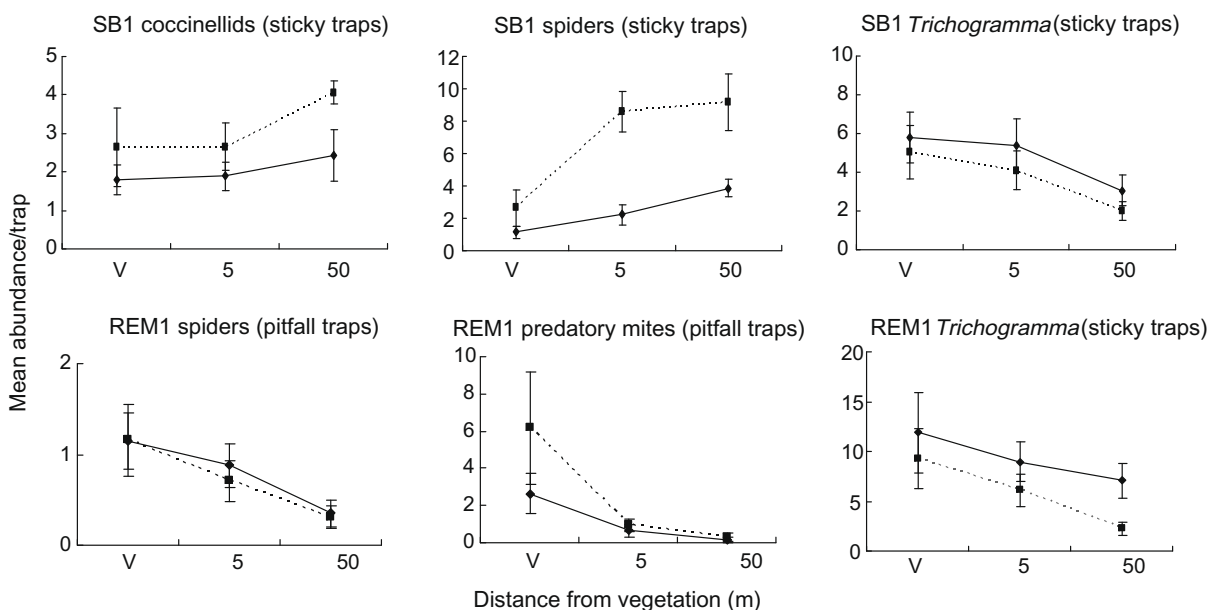
Fig. 4. Comparison of mean number of natural enemies collected in season 1 and season 2 for groups occurring in both seasons at SB1 and REM1. Solid lines represent season 1, dotted lines season 2. Error bars represent standard errors.

Table 3
ANOVAs testing the effects of distance and season on abundance of groups obtained from the canopy (sticky traps) and at ground level (pitfall traps) comparing results for season 1 and season 2 at replicated sites (SB1 and REM1).

	Distance (D)			Month (M)			Season (S)			Interactions (P values only)		
	MS	$F_{(2,6)}$	P	MS	$F_{(3,6)}$	P	MS	$F_{(1,6)}$	P	D × M	D × S	M × S
Shelterbelt (*SB1*)												
Araneae canopy	3.695	8.24	0.019	1.513	3.37	0.096	4.996	11.14	0.016	0.623	0.294	0.278
Coccinellidae canopy	50.227	13.56	0.006	26.756	7.22	0.020	122.853	33.16	0.001	0.570	0.092	0.015
Trichogramma canopy	0.739	23.51	0.001	2.310	73.52	<0.001	0.413	13.14	0.011	0.040	0.928	<0.001
Remnant (*REM1*)												
Araneae ground	2.122	11.61	0.009	0.648	3.54	0.088	0.000	0.00	1.00	0.755	1.00	0.028
Predatory mites	40.383	17.33	0.003	2.833	1.22	0.382	8.781	3.77	0.100	0.671	0.178	0.212
Trichogramma canopy	0.608	6.63	0.030	2.464	26.85	<0.001	0.561	6.11	0.048	0.359	0.920	0.002

yard and/or vice versa. In the canopy, higher numbers of groups in the vegetation were correlated with higher numbers in the vineyard (parasitoids, r = 0.905, N = 8, P = 0.002, coccinellids, r = 0.755, N = 8, P = 0.031).

3.5. Association with pasture edges

ANOVAs of the transect data from sites with pasture edges indicated no influence of distance on abundance of most invertebrates groups (Table 4). In the canopy, parasitoids, lacewings, spiders, ladybird beetles, *Trichogramma* and staphylinids and at ground level parasitoids, spiders and predatory mites all showed no increase as the pasture edge was approached at either site (Fig. 7). Spiders and parasitoids in the canopy showed significant changes with distance (Table 4) but this was due to reduced abundance at sample points closer to the edge (Fig. 7).

3.6. Parasitism and predation of light brown apple moth

On collection, 40% of egg masses were missing (almost certainly due to predation). Of the remaining egg masses, 57% were parasitised. Two species of *Trichogramma* were recovered from the parasitised eggs (*T. funiculatum* and *T.* sp. *x*).

Predation of LBAM eggs was randomly distributed throughout the vineyard, however there was a non-random distribution of parasitised eggs (Table 3 and Fig. 2). As mentioned above, *Trichogramma* showed a non-random distribution in February when the egg cards were present in the vineyard (see Table 2). The overall association between *Trichogramma* collected in February and LBAM parasitism (X_p) was 0.273, with a Dutilleul adjusted probability of 0.007. Egg parasitism and the numbers of *Trichogramma* were therefore correlated. The average number of *Trichogramma* per site over the entire season was also correlated with parasitism (data not shown).

4. Discussion

Landscape effects are commonly related to abundance of natural enemies (Bianchi et al., 2006). The proportion of non-crop land in an agricultural landscape has been shown to influence the abundance of a range of natural enemies such as parasitoids (Thies and Tscharnkte, 1999) and spiders (Schmidt et al., 2008). Landholders can most effectively alter landscapes at a local level, such as through cover crops and/or vegetation adjacent to their holdings (Gurr et al., 2004). It is for this reason that we investigated the effects of adjacent shelterbelts and remnants on beneficial inverte-

Table 4
ANOVAs/ANCOVAs testing the effects of distance, collection month and site on abundance of groups obtained from the canopy (sticky traps) and at ground level (pitfall traps) at vegetated and pasture edges. Mean squares (MS) are presented along with F ratios and P values. REML was used to test for significant effects in ANOVA to account for potential autocorrelation of site within landscape. Distance was treated as a covariate in the analyses on pasture edge data.

Wooded edges	Distance (D)			Month (M)			Site (S)			Interactions (P values only)		
	MS	$F_{(2,37)}$	P	MS	$F_{(3,37)}$	P	MS	$F_{(6,37)}$	P	D × M	D × S	M × S
Canopy												
Araneae	2.140	4.74	0.015	2.394	5.31	0.004*	0.876	4.23	0.002	0.10	0.169	0.065
Predatory thrips	6.848	10.65	<0.001*	3.486	5.43	0.003*	2.193	3.41	0.006*	0.005*	0.056	0.454
Coccinellidae	457.878	7.82	0.001*	1616.372	27.62	<0.001*	525.006	8.97	<0.001*	0.423	0.003*	0.001*
Parasitoids	7727.458	23.05	<0.001*	1582.149	4.72	0.007*	6700.546	19.98	<0.001*	0.074	0.001*	<0.001*
Staphylinidae	0.675	3.74	0.033	0.631	3.49	0.025	0.310	1.72	0.135	0.337	0.292	0.662
Trichogramma	257.007	11.35	<0.001*	480.590	21.23	<0.001*	55.497	2.45	0.036	0.682	0.001*	0.063
Lacewings[a]	0.258	1.90[b]	0.204									
Ground												
Araneae	8.729	11.49	<0.001*	1.665	2.19	0.088	0.829	1.09	0.369	0.128	0.029	<0.001*
Parasitoids	1.862	3.89	0.021	0.570	1.19	0.314	3.464	7.23	<0.001*	0.003*	0.433	<0.001*
Predatory mites	52.921	6.79	0.001*	5.180	0.67	0.574	25.122	3.23	0.003*	0.144	<0.001*	<0.001*
Pasture edges	MS	$F_{(1,53)}$	P	MS	$F_{(2,53)}$	P	MS	$F_{(1,53)}$	P	D × M	D × S	M × S
Canopy												
Araneae	2.001	8.52	0.005*	0.569	2.42	0.047	0.116	0.49	0.486	0.105	0.359	0.877
Coccinellidae	1.219	2.84	0.098	1.132	2.63	0.034	2.583	6.01	0.018	0.076	0.036	0.078
Parasitoids	542.411	21.02	<0.001*	338.479	13.12	<0.001*	214.383	8.31	0.006*	<0.001*	0.018	0.010*
Staphylinidae	0.657	1.27	0.265	2.722	5.26	<0.001*	0.225	0.43	0.513	0.004*	0.829	<0.001*
Trichogramma	0.386	0.26	0.610	3.315	2.26	0.062	0.040	0.03	0.869	0.930	0.692	0.030
Ground												
Araneae	0.055	0.56	0.462	0.063	0.63	0.539	0.232	2.34	0.138	0.497	0.182	0.766
Parasitoids	4.240	0.71	0.407	19.329	3.24	0.055	3.064	0.51	0.480	0.030	0.370	0.545
Predatory mites	4.003	1.59	0.219	1.631	0.65	0.532	0.601	0.24	0.630	0.789	0.594	0.070

* Significant values after Dunn–Sidak correction for number of groups compared.
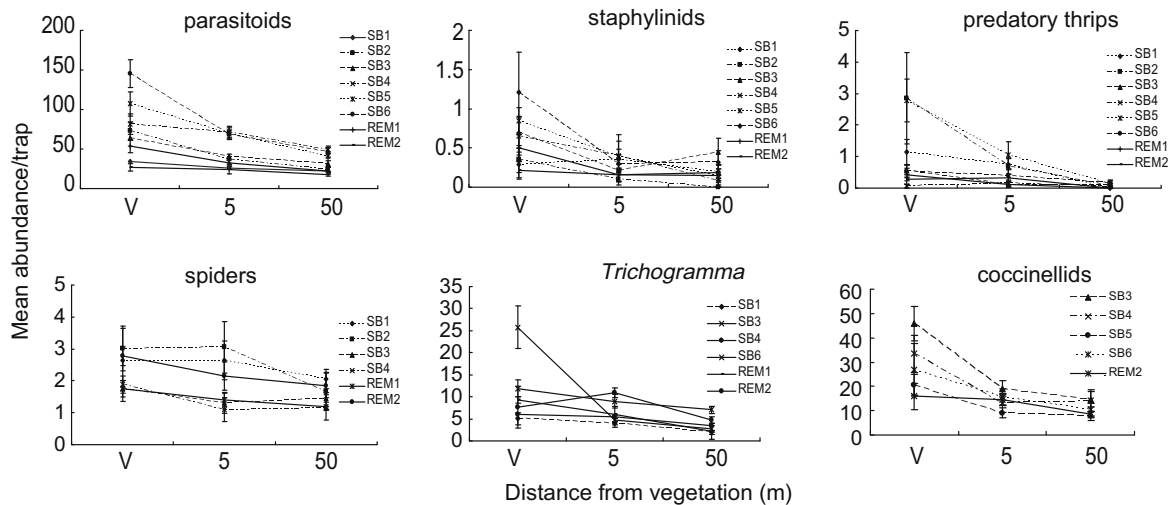[a] Analysis for December only when 72% collected.
[b] df 2, 9.

Fig. 5. Mean number of natural enemies for groups with significant decrease with increasing distance from the vegetation at the significant shelterbelt (SB) and remnant (REM) sites collected per trap with sticky traps in the vegetation (V), at the vineyard edge (5 m) and 50 m into the vineyard. Solid lines represent sites with adjacent remnant and dashed lines adjacent shelterbelts. Error bars represent standard errors.

brates inside vineyards. Overall we found that wooded vegetation adjacent to vineyards enhanced the abundance of natural enemies. Vines adjacent to vegetation tended to have higher numbers of *Trichogramma*, ground spiders, lacewing larvae, predatory mites, coccinellids, staphylinids, predatory thrips and parasitoids. These effects are unlikely to be a response to edges *per se* as they were not seen at the two sites where pasture edges were present; in fact pasture edges tended to decrease the relative abundance of two groups of beneficials.

However, arthropod responses to field margin vegetation were idiosyncratic. No site showed consistently high or low numbers of all groups in the vegetation or in the vineyard. We suspect that these inconsistent trends between sites reflected site characteristics rather than year-by-year variation. Our detailed sampling at one vineyard indicated that a negative effect of a shelterbelt on numbers of ladybird beetles and canopy spiders observed in one season was also detected with repeated sampling at this site in the second season, even though this pattern was not seen at other
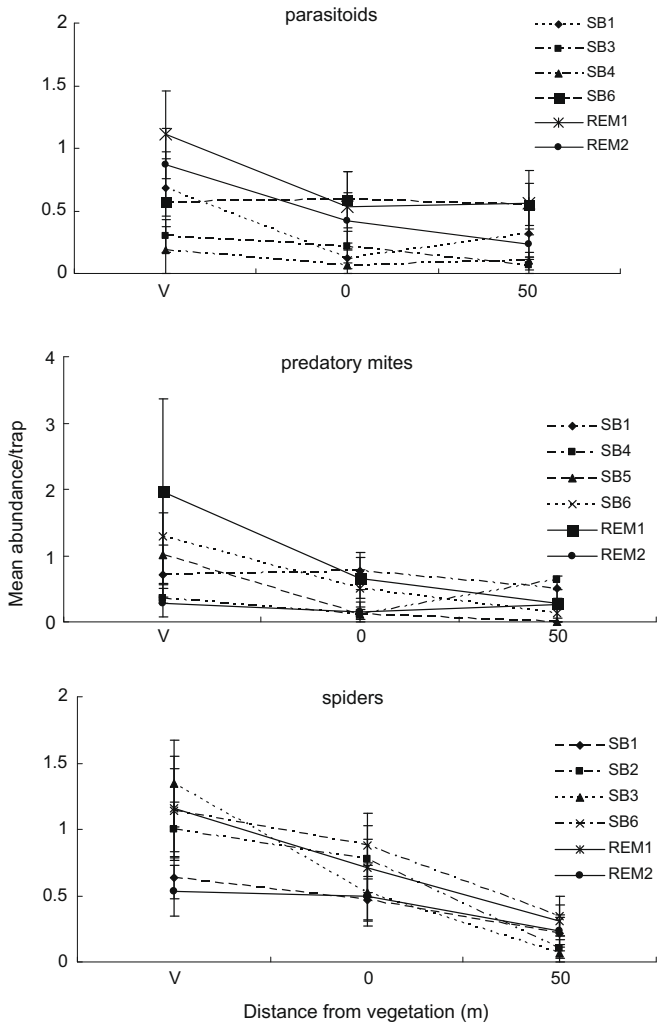
Fig. 6. Mean number (with the exception of predatory mite data which was log transformed to facilitate display of data from all sites on single set of axes) of natural enemies for groups with significant decrease with increasing distance from the vegetation for significant shelterbelt (SB) and remnant (REM) sites collected per trap with pitfall traps in the vegetation (V), at the vineyard edge (5 m) and 50 m into the vineyard. Solid lines represent sites with adjacent remnant and dashed lines adjacent shelterbelts. Error bars represent standard errors.

sites in the second season. The reasons for these inconsistent patterns between sites are unclear, particularly as they did not relate to whether vegetation was remnant or planted shelterbelt. Perhaps there are competitive interactions among generalist predators at some sites, or perhaps some field margins do not provide resources for particular taxa.

Changes in the relative abundance of beneficials extended well into the vineyard as evident from the figures. For the parasitoids from pitfall traps, for instance, numbers were still higher 100 m away from the shelterbelt. Similarly, for ground spiders, differences were detected 50 m from the remnant vegetation. These results suggest that wooded areas with understory can affect numbers of natural enemies well away from the vegetation.

The taxa increased by adjacent vegetation-predatory mites, spiders, staphylinids, lacewings, predatory flies (Tachinidae, Cecidomyiidae, Syrphidae) and a wide range of parasitoids including species of *Trichogramma* – are all potential natural enemies in vineyards. In addition to their importance as generalist predators (see Michaels, 2006), our collection of staphylinids included several species of Aleocharine staphylinids (genus Oligota), predators of agriculturally important phytophagous mites (Paoletti and Lorenzoni, 1989). Spiders have wide host ranges (Memmott et al., 2000) allowing adaptation to fluctuations in host availability (Nyffeler et al., 1992) and they are likely to be predators of multivoltine pests like LBAM. Lacewings are voracious predators of mites, mealybugs and LBAM eggs. A multispecies complex of parasitoids such as that seen here can improve control of various pests (Rodriguez and Hawkin, 2000) and a range of parasitoids attack vineyard pests (Thomson and Hoffmann, 2006a) including LBAM. Predatory mites contribute to control of eriophyoid mites, tachinids parasitise LBAM, while syrphids eat caterpillars, and Cecidomyiidae parasitise mealybugs and possibly scale (Waterhouse and Sands, 2001).

Direct evidence for a positive effect of vegetation on pests came from the parasitism of LBAM cards. The relatively higher parasitism rate near remnant vegetation and positive correlation between parasitism and numbers of *Trichogramma* responsible for parasitism suggests that high numbers of natural enemies have positive effects on pest control. On average, at sampling points close to the vegetation, the number of LBAM larvae would have been reduced from 1000 to 400 by *Trichogramma*. Parasitism levels were high and comparable to levels in releases of *Trichogramma* as well as background levels at some times of the year in this region
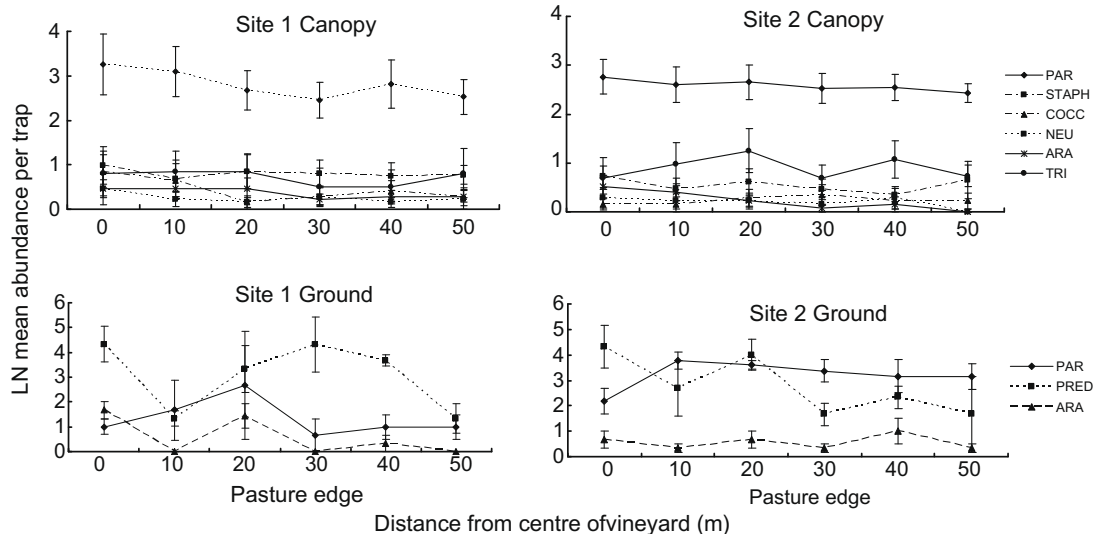

Fig. 7. Mean number (LN transformed to facilitate display of all taxa on a single set of axes) of predator groups collected at points across two vineyards with pasture edges, in the canopy and on the ground. Error bars represent standard errors.

(Thomson et al., 2000). Parasitism can be high in vineyards with low chemical use and particularly low sulphur inputs (Thomson et al., 2000). In contrast to the parasitism effects, we found no positive impact of vegetation on egg predation, which may reflect inconsistent effects of vegetation on generalist predators. Olson and Wäckers (2007) also found no effect of field margin type or distance from vegetation on predation of sentinel corn ear worm eggs despite increases in natural enemies.

Why did vegetation influence some groups but not others? Agroecosystems such as vineyards can be recolonized from perennial habitats by the groups represented here, including spiders, syrphids, staphylinids, parasitoids, predatory mites (e.g., Samu et al., 1999; Duelli and Obrist, 2003). Many spider species colonize crops by drifting through the air on threads of spider silk (ballooning) and responses to edges seen here are consistent with those reported elsewhere (Holland et al., 1999; Pearce and Zalucki, 2006). Staphylinids also possess a high movement rate (through flight or wind dispersal) (Bohac, 1999) and respond positively to field margins (Michaels, 2006) from where they appear to colonize fields (Olson and Wäckers, 2007). Shelterbelts in the vineyards tested here not only included many pollen and nectar producing plants, but also grasses, shrubs and tall trees. Remnant blocks are wider with more limited understorey but with overlap in species composition. Floral and extrafloral nectars are significant sources of nutrition for most adult predatory mites, lacewings, parasitoids, Cecidomyiidae, Tachinidae and syrphids, (Sommaggio, 1999; Wäckers, 2005).

The data collected here suggests that existing vegetation and revegetation contribute to pest control by natural enemies with the potential to reduce chemical applications, contributing to both increased economic and environmental sustainability of the wine industry. This is a step along the way to identify means to encourage environmentally sensitive crop protection measures. However, further work is required to discover aspects of vegetation important to the different groups. We are currently undertaking detailed spatial analyses of other vineyards and surveys of large numbers of vineyards with different adjoining vegetation.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocontrol.2009.01.009.

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