

The activities of generalist parasitoids can be segregated between crop and adjacent non-crop habitats

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Abstract Non-crop habitat adjacent to crops may be important for enhancing the activity of natural enemies in crops. However, it is not always clear whether natural enemies that are active in non-crop habitats actually contribute to pest suppression in adjacent crop habitats. We hypothesised that parasitic wasps that utilise the same hosts can be segregated between crop and non-crop habitats in an agro-ecosystem. We tested this hypothesis using the light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), in vineyards and adjacent native vegetation. We experimentally measured the parasitism rate of larval *E. postvittana* at six and eight sites in both vineyards and the adjacent native vegetation in two consecutive years. Wild larval Tortricidae were also collected

at each experimental site to assess their diversity and related parasitoids. Parasitised hosts were then identified using a PCR-based protocol to examine the parasitoids' host ranges. The parasitoid *Therophilus unimaculatus* (Turner) (Hymenoptera: Braconidae) was most active in non-crop native vegetation, whereas *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae) parasitised the most larvae in vineyards. Parasitism of *E. postvittana* by *D. tasmanica* was higher on grape than on plantain, which indicates that host plants influence activities in different habitat. Both species shared the same range of tortricid hosts. Overall, our results indicate the two key parasitoids that attack *E. postvittana* differ in their pattern of habitat use. The native vegetation adjacent to crops may not enhance the activity of some natural enemies for pest control in an agricultural ecosystem.

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Data accessibility Sequences deposited in GenBank (Accession Numbers: KF146183-KF146214; KM115588-KM115616).

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Key message

- There are several parasitoids associated with *Epiphyas postvittana* in Australia vineyards.
- Two parasitoids of *E. postvittana*, *D. tasmanica* and *T. unimaculatus*, differ in their pattern of habitat use, while both species shared the same range of tortricid hosts.
- Parasitism of *E. postvittana* by *D. tasmanica* was higher on grape than on *Plantago lanceolata*.
- In Australian vineyards, the vegetation adjacent to crop may not enhance the activity of parasitoids for pest control in the crop.

Introduction

Modern agriculture production has intensively reduced non-crop habitat areas and simplified agriculture landscapes. Therefore, most agricultural ecosystems occur as a fragmented mosaic of crop and non-crop habitats in which arthropod biodiversity and the efficiency of natural biological control are declining (Bianchi et al. 2006; Meehan et al. 2011). The remaining non-crop habitats, especially woody vegetation in agriculture landscapes, could be important to enhance the activities of natural enemies and their effectiveness in sustainable pest suppression (Landis et al. 2000). Non-crop habitats may provide natural enemies with resources such as overwintering shelter (Cortesero et al. 2000; Landis et al. 2000), alternative hosts (Williams and Martinson 2000) and food (Wratten et al. 2004; Begum et al. 2006; Berndt et al. 2006; Lee and Heimpel 2008). These resources are usually limited in highly disturbed and simplified crop habitats (van Emden 1965; DeBach and Rosen 1991; Landis et al. 2000). Therefore, non-crop habitats may enhance the abundance and activity of predatory species in crop habitats (Landis et al. 2000; Wilby and Thomas 2002; Rand et al. 2006). Moreover, the abundance, activity or impact of natural enemies at the boundary of crop and non-crop habitats, the so-called ‘edge effects’, is often higher than that in field interiors (Duelli et al. 1990; Dyer and Landis 1997; Thies and Tschardt 1999; Rand et al. 2006). This could be due to the proximity of alternative resources in the adjacent habitats (Rand et al. 2006). Predatory groups often move between adjacent habitats in agro-ecosystems. These movements could be driven by spatiotemporal variability in resource availability and resource utilisation patterns (Oksanen 1990; Holt and Hochberg 2001; Ries et al. 2004). However, the increase of natural enemy activity is not always linked to effective pest control (Gurr et al. 2000; Holland and Fahrig 2000; Olson and Wäckers 2007). Although many studies have put in evidence a positive relationship between landscape complexity and diversity/abundance of natural enemies, there is no clear evidence that higher abundance of natural enemies supports a more efficient biological control function (Chaplin-Kramer et al. 2011). Therefore, it is necessary to fill this gap and to explore a possible mechanism explaining compartmentalization of trophic networks in semi-natural and crop habitats.

Studies comparing communities of predator or parasitoid species in crop and non-crop habitats are typically performed by collecting data from insect traps (e.g. Miliczky and Horton 2005) or through direct sampling methods (e.g. Alhmedi et al. 2011). The abundance of relatively larger mobile parasitoids has been suggested to be unaffected by local vegetation when assessed using yellow

sticky traps in crops (e.g. Thomson and Hoffmann 2010). However, in practice, it is hard to accurately identify flying insects collected on yellow sticky traps. Moreover, the absence or presence of highly mobile adults may not be a good indicator of actual parasitism. Sampling of parasitoids using sentinel plants and host insects has been demonstrated to be an effective way to measure their activity in many studies (Suckling et al. 2001; Furlong and Zalucki 2007; Pfannenstiel et al. 2012). Therefore, controlled experiments are necessary to investigate thoroughly the direct interactions between natural enemies and their shared host species.

Host-parasitoid systems have long been used as model systems for studying ecological and evolutionary questions. The light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), and its larval parasitoids in vineyard ecosystems were the focal species. *E. postvittana* belongs to the family Tortricidae, which is one of the largest families of Lepidoptera, with over 10,000 described species. This family includes numerous major pests of crops, forests, and ornamental plants (Brown 2005). Hence, an understanding of factors that affect parasitism of *E. postvittana* is likely to be relevant to many other pest species and agro-ecosystems. Larval *E. postvittana* is a polyphagous leafroller that is known to feed on plants from 123 genera in 55 families (Suckling and Brockerhoff 2010). It is one of the most damaging insect pest species on grapes in Australian vineyards (Scholefield and Morison 2010). At least 26 species of parasitoids and hyperparasitoids are reported to be associated with *E. postvittana* in Australia (Paull 2007). *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae) is recorded as being the most abundant parasitoid of larval *E. postvittana* (Stephens et al. 1998; Suckling et al. 1998), accounting for 70 % or more of the observed parasitism in vineyards (Paull and Austin 2006). Another larval parasitoid, *Therophilus unimaculatus* (Turner) (Hymenoptera: Braconidae), has been documented as common in the least-disturbed native vegetation (Paull 2007). Both *D. tasmanica* and *T. unimaculatus* could attack *E. postvittana* that has already been parasitized by the other species, while larval *D. tasmanica* outcompete larval *T. unimaculatus* when they occur in the same host (Feng et al. 2015).

A number of leafroller species other than *E. postvittana* are present in vineyards and natural habitats. Little is known about the trophic links between parasitoids and their host leafroller in Australian vineyards and natural habitats, in part because there are no accurate morphological characters that can distinguish larvae of tortricid species, and parasitoids kill larvae before adults emerge. Molecular methods, especially DNA barcoding using short DNA sequences of a standardised region of the genome, have

become useful tools for identifying species (Hajibabaei et al. 2006; Smith et al. 2008) and detecting trophic links in complex food webs (Rubinoff et al. 2011). In addition, molecular operational taxonomic units (MOTUs) can be employed when undescribed species are encountered. These are groups of organisms that can be designated in taxonomic studies without necessarily being assigned a formal taxonomic rank. MOTUs based on DNA barcoding are widely used to investigate biological diversity and trophic links among poorly understood organisms (Floyd et al. 2002; Blaxter et al. 2005; Smith et al. 2005, 2009).

The main objective of this study was to explore a possible mechanism explaining the compartmentalization of trophic networks in vineyards and the adjacent semi-natural habitats. We investigated whether parasitoids attack the early larval stages of *E. postvittana* equally between vineyards and adjacent habitats. Field experiments were conducted in both vineyards and adjacent vegetation. Sentinel plants infested with young larval *E. postvittana* were used to determine the levels of parasitism. In addition, we tested whether host plants affect parasitism by comparing parasitism levels between two sentinel host plant species. To complement our field experiments, leafrollers and related parasitoids were sampled twice per month in both the vineyards and adjacent native vegetation during the experimental periods. A PCR-based protocol was used to determine the trophic links between indigenous leafrollers and related larval parasitoids. A phylogenetic tree-based method was used to identify leafroller MOTUs that are attacked by the two major parasitoids, *D. tasmanica* and *T. unimaculatus*.

Materials and methods

Study site

To examine the parasitism of *E. postvittana* in both vineyards and the adjacent woody habitats, two series of field experiments were conducted at six and eight vineyards in Adelaide Hills, South Australia over 2 years (for details, see supplemental material). Naturally occurring leafrollers and their associated parasitoids were also surveyed at an additional natural conservation site. The eight vineyards were all located in the Adelaide Hills region in South Australia. The closest and farthest distances between two sites were 5.6 and 51 km, respectively. Pesticides of low toxicity to natural enemies including sulphur, tebufenozide and chlorothalonil were used at some sites.

Plants and insects

To investigate parasitism of *E. postvittana* by indigenous parasitoids, two sentinel plant species were used, the

grapevine, *Vitis vinifera* L., and plantain, *Plantago lanceolata* L. *Plantago lanceolata* is a common host plant for *E. postvittana* in south Australia (Paull 2007). Potted plantain was grown from seed, several plants per pot, in a glasshouse three months before the experiment. Both grape and *P. lanceolata* are easy to grow so that sentinel potted plants could be standardised for age and quality.

Shiraz was used for the 2011 experiment and Chardonnay for the 2012 experiment. Chardonnay was chosen because population density of *E. postvittana* on this variety was observed to be relatively higher than on others (Paull 2007). Shiraz was chosen due to their availability and the shortage of Chardonnay in 2011. Both the plantain and grape plants were planted in nursery pots (300 mm × 120 mm × 150 mm) in a glasshouse and were moved to a field cage to acclimatise to natural conditions 4 weeks before the field experiments.

The culture of *E. postvittana* was maintained at 22 ± 2 °C under a 12 : 12 light-dark cycle (for details, see Yazdani et al. 2014). To obtain eggs of *E. postvittana*, six female and six male moths were held in a plastic cup with vertical ridges for mating and oviposition. A dental wick soaked in a 10 % honey solution was placed in each cup to provide water and food for the moths. The cups were maintained under natural light at room temperature. The moths laid their eggs in masses of 30–40 on the cup ridges, which were cut into small pieces (3 × 1 cm) to transfer them to plants.

Field experiment

General methods Each plant was infested with approximately 30 *E. postvittana* eggs. We covered these inoculated plants with perforated plastic bread bags to prevent the neonate *E. postvittana* from escaping. The larvae were allowed to settle on the plants for 3 days before moving them to the field. Plastic bags were removed once the plants were placed in the field. A 4 l plastic bottle provided water for the plants through two 10 mm siphoning ropes that were buried in the soil. Previous experiments showed that this construction maintains a water supply for the plants for up to two weeks. Due to the hot and dry weather, the bottle was refilled with water once per week during the experiments. To prevent the plants from falling over, the potted plants were tied together with the water bottle. The plants were collected after two weeks in the field. Next, larvae from the same plant were transferred to labelled plastic rearing cups (440 ml, 64 mm × 118 mm diam) containing fresh grape or plantain leaves and a piece of dry tissue paper. The larvae were reared at 22 ± 2 °C under a 14 l: 10 day light/dark cycle to determine the parasitism rate. The state of each larva was monitored until it produced a parasitoid, pupated, or died. **The 2011 parasitism experiment** A field experiment was conducted at six

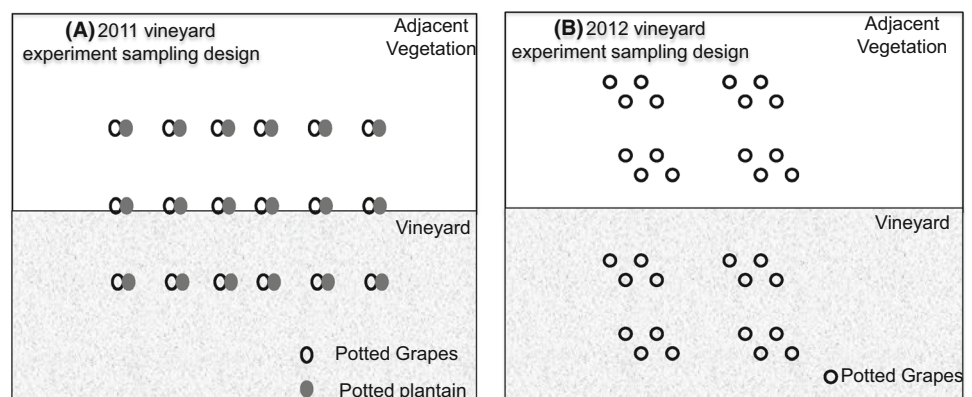
vineyards in the Adelaide Hills, in South Australia. The experiments were conducted twice. Plants infested with first instar *E. postvittana* were added to the field over three consecutive days at a rate of two vineyards per day on 7–9 November and 2–4 December 2011 for the first and second sample periods, respectively. In each vineyard, potted plants were placed at three locations on one border of the field: in the vineyard interior (40 m from the border), the vineyard edge (along the border row of vines) and in the native vegetation adjacent to the vineyard (20 m from the border). We placed six pots of grape and plantain in pairs at a distance of six metres between the pairs in the middle of each type of location. Therefore, 36 plants were placed in each vineyard during each experiment (Fig. 1a). **The 2012 parasitism experiment** A field experiment was performed in eight vineyards, of which six were those visited in 2011 and two additional vineyards. The experiment was set up over four consecutive days at a rate of two vineyards per day on 12–15 November and 4–7 December for the first and second sampling periods, respectively. We changed the experimental design from the previous year to increase statistical power. The border location was eliminated, and grape was the only host plant. At each sampling point, we placed pots with grape in quadruplets in the vineyard and adjacent vegetation. The pots were placed three metres apart in a square arrangement at each sampling point (across two rows of vines within vineyards), and four groups of four pots were spaced 12 m apart. Thus, 16 plants were assessed at each type of location, with a total of 32 plants being assessed at each vineyard during each visit (Fig. 1b). **Statistical analysis** To analyse the factors affecting parasitism of the experimentally introduced *E. postvittana*, the data from the 2011 and 2012 field experiments were modelled with the orthogonal split–split-plot and a split-plot general linear models, respectively, with the GLM procedure in the statistical package GenStat for Windows, 15th Edition (VSN International, Hemel Hempstead, UK). The vineyards were considered random

blocks. For the 2011 experiment, the three habitat locations within each site (the vineyard, the border and the adjacent vegetation) were the main plot factor, the type of host plant was the split-plot factor and the two repeated visits during the experiment constituted the split–split-plot factor. For the 2012 experiment, the habitat locations were the main plot factor, and the repeated visits were the split-plot factor. For all experiments, the proportion of larvae that were parasitised by (1) any species (overall), (2) *D. tasmanica* and (3) *T. unimaculatus* were calculated from the pooled numbers; these numbers were treated as the dependent variables. A modified Freeman and Tukey transformation (Zar 1999) was used to analyse the parasitism data to conservatively deal with the heterogeneity of variance in the presence of zero inflation. The level of significance was set at 5 % ($P < 0.05$). To determine if vineyard and adjacent vegetation habitats have significant effects on the activity of parasitoids, a one-degree contrast was conducted in both the years.

Parasitoid-host trophic links

To determine the trophic links between leafrollers and parasitoids, leafrollers were sampled in both the vineyards and adjacent vegetation every 2 weeks during the field experiments. Leafrollers were also sampled once every 3 months from August 2012 till March 2013 in each experimental site. In each site, a scanning sampling method was used to maximise the number of plants and grape leaf shoots sampled. Damaged leaves were the main plant parts sampled. We searched for leafroller larvae or pupae for 2 h at each sampling time. In addition, to more broadly survey the naturally occurring leafrollers and related parasitoids in the Adelaide Hills region, a regular monthly survey was carried out on plants in a non-agricultural area, the Waite Conservation Reserve, Adelaide, South Australia from February 2011 to July 2012. The collected leafrollers were reared in small plastic cups (100 ml) with host plant leaves,

Fig. 1 Scheme of field experiment sampling design: **a** 2011 sampling design and **b** 2012 sampling design



and parasitism rates were recorded. The leafroller cadavers after parasitoids emerged and the adult moths that emerged were preserved in 95 % ethanol for identification through DNA analysis. Total DNA was extracted from leafroller cadavers using QIAGEN DNeasy Blood and Tissue Kits following the manufacturer's protocol.

To determine the trophic links between the naturally occurring leafrollers and parasitoids, the hosts associated to each parasitoids were characterised through partially sequencing the mitochondrial cytochrome oxidase 1 (MT-CO1) gene using a PCR-based protocol. The PCR amplifications were performed using an MJ Research PTC-200 Thermo Cycler PCR system (MJ Research, Inc., Waltham, Massachusetts, USA). Partial COI sequences for the leafrollers were amplified using the Lepidoptera-specific primers LepF (5'-ATTCAACCAATCATAAAGA TATTGG-3') and MH-MR1 (5'-CCTGTTCCAGCTCC-ATTTTC-3') (Hajibabaei et al. 2006; Rougerie et al. 2011). PCR was carried out in a 50 μ L reaction volume, and contained 10 \times buffer, 10 mM MgCl₂, 2.5 pM each primer, 200 μ M dNTPs, 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 10–20 ng (1–2 μ l) of genomic DNA and 1 U of Taq DNA polymerase (Platinum Taq DNA polymerase; Invitrogen). The thermal profile was as follows: 1 min at 94 °C, followed by five cycles of 40 s at 94 °C, 40 s at 45 °C and 1 min at 72 °C, followed by 35 cycles of 40 s at 94 °C, 40 s at 51 °C and 1 min at 72 °C, with a final extension step at 72 °C for 5 min. The PCR products were visualised using 2 % agarose. Purified samples showing weak-to-strong bands were purified with a PCR product purification kit (Promega, Madison, Wisconsin, USA) and sent to the Australian Genomic Research Facility, Adelaide, South Australia for sequencing. The purified PCR products were unidirectionally sequenced using the primer LepF1 in 10 μ l reaction volumes.

The partial MT-CO1 sequences obtained from host tissue remains were then BLAST matched with GenBank database on homology. These sequences together with two partial leafroller MT-CO1 sequences from GenBank (accession numbers KF395763.1, KF404142.1) and three partial MT-CO1 sequences of *Epiphyas* species provided by Dr Roberta Hitchcock (sequence ID ww09288, ww09286, ww04414) were aligned using the program ClustalX (Thompson et al. 1997). To calculate the genetic distances between each sequence pair, we employed MEGA 5.2 (Tamura et al. 2011) with the Kimura 2-parameter model. A neighbour-joining (NJ) tree based on the K2P distances was constructed using MEGA 5.2, and 1000 bootstrap replicates were employed to calculate branch support. Sequences assigned to the same node were considered to belong to the same MOTU.

Results

The 2011 parasitism experiment

A total of 2112 and 2076 larval *E. postvittana* were recovered from the first and second sampling periods, respectively. The number of larvae varied because eggs are laid in masses that naturally vary in size and not all larvae survived. Thus, the total number recovered was less than the number placed in the field. More larvae were recovered from plantain than grape ($df = 35$, $t = 2.03$, $P < 0.001$). Three parasitoid species were recovered from the larvae placed on plants: *D. tasmanica*, *T. unimaculatus* and *Phytodietus celsissimus* (Turner) (Hymenoptera, Ichneumonidae).

Dolichogenidea tasmanica parasitised the most larvae in the vineyards and was either absent or parasitised only a few larvae in the native vegetation (Fig. 2). The contrast for parasitism by *D. tasmanica* between vineyard and adjacent vegetation was statistically significant in the split-split-plot analysis ($F_{1, 10} = 6.67$, $P = 0.027$). Parasitism by *D. tasmanica* at the border did not differ significantly from that in either adjacent vegetation or vineyards (post hoc Fisher test with the Bonferroni adjustment, $P > 0.05$). Parasitism by *D. tasmanica* was significantly higher on grape than on plantain ($F_{1, 15} = 6.38$; $P = 0.023$).

Parasitism by *T. unimaculatus* was significantly higher in adjacent vegetation than in vineyards ($F_{1, 10} = 17.2$, $P = 0.002$). At the border, the parasitism rate was lower than in adjacent vegetation ($P < 0.05$), but not different from that in the vineyards (post hoc directional Fisher test with the Bonferroni adjustment). Parasitism by *T. unimaculatus* was significantly higher in December 2011 than in November 2011 ($F_{1, 15} = 5.26$; $P < 0.05$). There was no significant statistical effect of host plant or any other interaction effects on parasitism by *T. unimaculatus*.

Total parasitism was only significantly higher in adjacent vegetation than vineyards and the borders (ANOVA, followed by multiple comparisons with a Bonferroni test, $F_{2, 10} = 4.33$; $P < 0.05$). There was no significant statistical effect of host plant or any other interaction effects on total parasitism.

The 2012 parasitism experiment

A total of 2032 and 1800 larval *E. postvittana* were recovered from the first and second sampling periods, respectively. Only two parasitoid species were recovered, *D. tasmanica* and *T. unimaculatus* (Fig. 3). *D. tasmanica* parasitised the most larvae in the vineyards at five out of the eight sites and was not found in the native vegetation. Parasitism by *D. tasmanica* was significantly higher in the

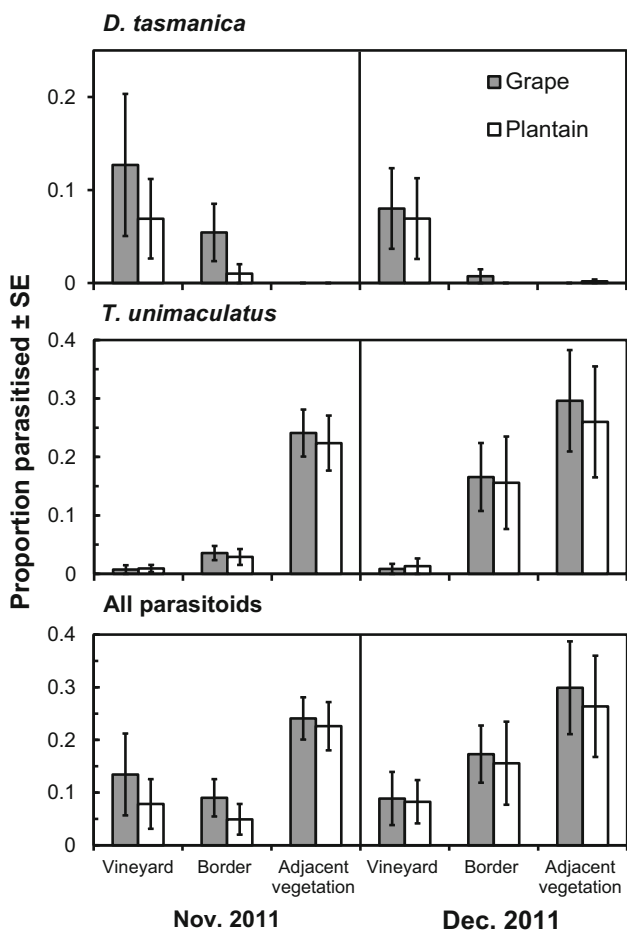


Fig. 2 Proportion of experimental *E. postvittana* parasitised by *D. tasmanica*, *T. unimaculatus* and all parasitoids (mean \pm SE). Data collected from two plants (grape and plantain), three locations (the vineyard interior, the border between the vineyard and the vegetation, and the adjacent woody habitats) and two different visits (November 2011 and December 2011). Standard errors are for descriptive purposes only; the analysis was done on transformed data

vineyards than in the adjacent vegetation ($F_{1, 7} = 7.30$; $P < 0.05$). There were no significant statistical interaction effects involving parasitism by *D. tasmanica*. Parasitism by *T. unimaculatus* was significantly higher in the adjacent vegetation than in vineyards ($F_{1, 7} = 13.70$; $P < 0.05$). There were no significant statistical effects of the replications, sampling points or any other interaction effects involving parasitism by *T. unimaculatus*. The total parasitism was significantly greater in the adjacent vegetation than in the vineyards ($F_{1, 7} = 11.40$; $P < 0.05$), in December 2012 compared to November 2012 ($F_{1, 56} = 6.08$; $P < 0.05$).

Parasitoid-host trophic links

In 2011, 110 leafrollers were collected from the vineyards, and 125 were collected from the adjacent vegetation. In

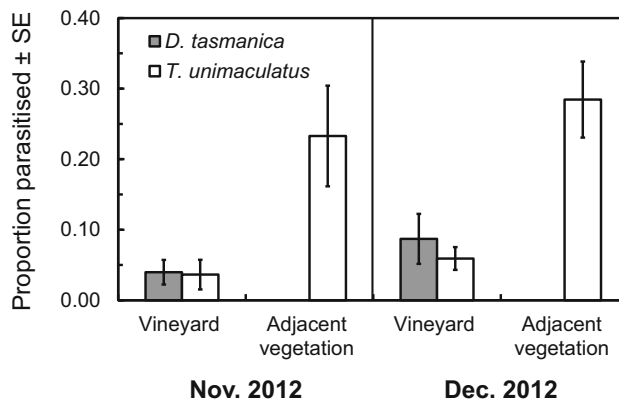


Fig. 3 Proportion of the experimental *E. postvittana* parasitised by *D. tasmanica* and *T. unimaculatus* given as the mean (\pm SE), using pooled data from eight sites at two locations (the vineyard interior and the adjacent woody habitats) and two different visits (November 2012 and December 2012). Standard errors are for descriptive purposes only; the analysis was done on transformed data

2012, 379 leafrollers were collected from vineyards, and 106 leafrollers were collected from the adjacent vegetation. *D. tasmanica* and *T. unimaculatus* were the most abundant parasitoids. Parasitism was greater in the adjacent vegetation than in the vineyards in both seasons (Fig. 4).

From February 2011 to January 2012, 834 leafrollers were collected from the Waite Conservation Reserve. The leafrollers collected were *E. postvittana*, *Merophyas divulsana* (Walker) (Tortricidae, Lepidoptera), *Acropolitis rudisana* (Walker) (Tortricidae, Lepidoptera) and other unidentified species. There were 365 parasitised leafrollers collected. These leafrollers were parasitised either by wasps (324) or other parasitoids (41). The hymenopteran parasitoids that were reared included *D. tasmanica*, *T. unimaculatus*, *P. celsissimus*, a species of Cheloninae

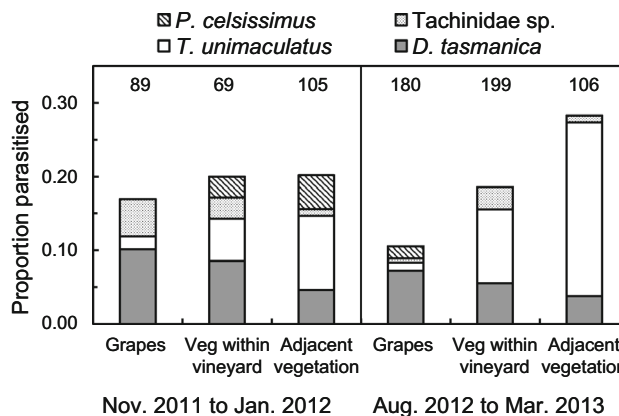


Fig. 4 Proportion of leafrollers parasitised by larval parasitoids of naturally occurring leafrollers using pooled data from six sites (November 2011 to January 2011) and eight sites (August 2012 to March 2013). The numbers above each bar indicate the number of leafrollers collected

(Braconidae), and a *Bracon* sp. (Braconidae). Among these parasitoids, *D. tasmanica* and *T. unimaculatus* were the two most common species (Fig. 5). In addition to parasitic wasps, parasitic Tachinidae (Diptera) and nematodes were collected.

MT-CO1 DNA was successfully sequenced from 61 samples of remnants left by parasitoids. The corresponding GenBank accession numbers for host remnants are KF146183-KF146214 and KM115588-KM115616. The results indicated that *D. tasmanica* and *T. unimaculatus* share a range of host species and are not specific to *E. postvittana* (Fig. 6). At least five host species MOTUs were revealed by the NJ tree, including *Epiphyas* spp., *Acropolitis* spp., *Merophyas* spp. and two other unidentified species groups.

Discussion

The two key larval parasitoids, *D. tasmanica* and *T. unimaculatus*, differ in their habitat use in vineyard ecosystems. *D. tasmanica* is mainly active in vineyards, while *T. unimaculatus* dominates in adjacent native vegetation. The parasitism pattern was consistent between the years and was supported by results from both field experiments (Figs. 2, 3) and vineyard sampling (Fig. 4). Even within the vineyards, *T. unimaculatus* mainly attacked hosts on cover crop plants under vines, rather than grape hosts (Fig. 4). There was a discrepancy in the observed levels of parasitism by *D. tasmanica* between sentinel plants and naturally occurring hosts. It was consistently found to parasitise leafroller hosts in non-crop habitats adjacent to vineyards (Fig. 4), while it rarely parasitised *E. postvittana* on the sentinel plants in those habitats (Figs. 2, 3). Foraging choice by parasitoids can be altered by their experience (Steinberg et al. 1992; Vet and Dicke 1992; Vet et al. 1995). The sentinel species plantain is not common in non-crop habitats adjacent to vineyards and grapes are absent. Therefore, naturally occurring *D. tasmanica* would have limited opportunities to gain experience on those plants and would be expected to prefer to forage for hosts on locally more common plants.

T. unimaculatus mainly attacked hosts on cover crop plants under vines, rather than grape hosts (Fig. 4). However, in the natural habitats, the two parasitoids co-existed throughout the year (Fig. 5). This indicates the vineyard ecosystem may strongly influence the composition of the parasitoid communities that attack leafroller species. For both parasitoid species, the parasitism level at the vineyard border was not higher than that in their preferred habitats. This indicates that there are no substantial edge effects for both parasitoid species, and reinforces the proposition that both species have habitat preferences. Studies have

indicated that some predator species or groups show strong habitat preferences either for natural habitats (Martin and Major 2001; Baldissera et al. 2004) or for cropping habitats (Duelli et al. 1990; Orr et al. 2000). In our study, two generalist parasitoids that attack the same hosts were assessed in both vineyard and adjacent ecosystems in which species interactions and differences between habitats could all affect their activities.

Habitat partitioning may affect ecosystem services such as pest control by parasitoids. In a study focussing on multispecies parasitoid-host systems, which involve three parasitoids that share the same whitefly species on cotton, different parasitoids attacked this host on different parts of host plants, and prey suppression was maximised when all three parasitoids were present (Bogran et al. 2002). In addition, a recent study indicates that different semi-natural habitats affect pest and predator abundance differently in local and landscape scales, while natural enemies seem to be more active in less disturbed habitats (Janković et al. 2016). Moreover, Derocles et al. (2014) demonstrated that aphidiine primary parasitoids of aphids rarely share hosts between crop and non-crop field margins. Furthermore, their result indicated that the non-crop field margins are not a substantial source of natural enemies that are active in crops. This finding is congruent with ours, even though the host insects are from different orders of insects.

The molecular barcode analysis confirmed that both parasitoids are not specific to *E. postvittana*, but attack a number of leafroller species (Fig. 6). Moreover, the findings of the field experiment and survey of naturally occurring leafrollers indicated that parasitism rates in the vineyards and adjacent vegetation are typically less than 30 % (Figs. 2, 3, 4), which suggests that there are plenty of un-parasitised hosts available for both parasitoid species. Therefore, there must be factors other than strong competitive interactions that affect the habitat partitioning of these parasitoids in vineyard ecosystems. In our study, vineyards and the adjacent vegetation are two distinguishable habitats that differ in both biotic and abiotic characteristics. In addition, vineyards typically occur in spatially heterogeneous agro-ecosystems. A number of factors generate spatial differences between vineyards and adjacent vegetation that may facilitate the compartmentalization of parasitoid species and their associated hosts in vineyards and adjacent semi-natural habitats. These factors include plant diversity, cyclical seasonal changes, landscape characteristics, alternative host insects, host density fluctuations and abiotic factors.

Plants play a role that affects the activity of natural enemies at both local and landscape scales. In this study, parasitism of *D. tasmanica* differed between grape and plantain (Fig. 2), which suggests that plant species in, or adjacent to, a vineyard should affect levels of parasitism. In

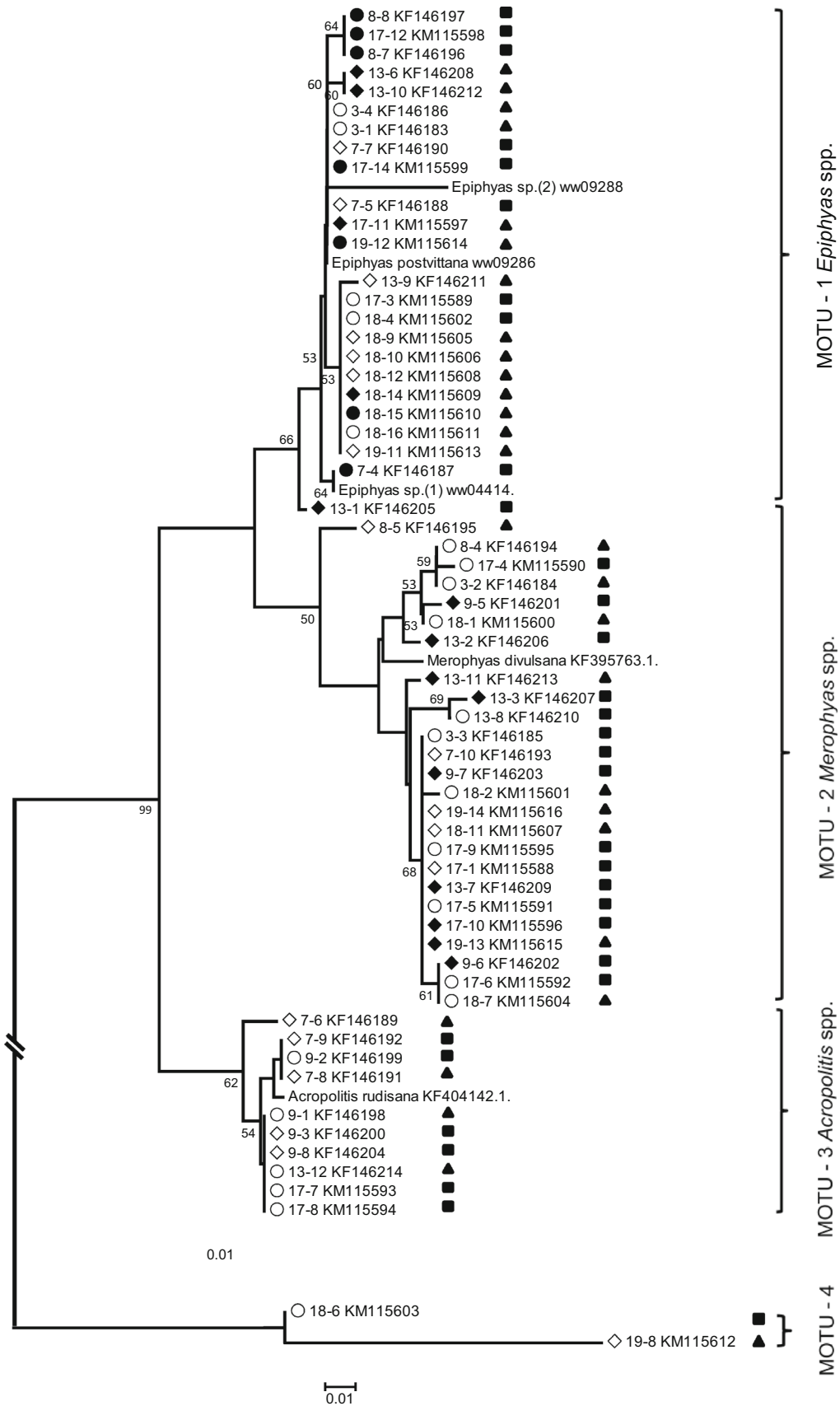


Fig. 5 Neighbour-joining tree constructed with partial MT-CO1 sequences from the leafroller remains left by parasitoids (based on K2P genetic distances), which indicate four MOTUs (within brackets). The branches are labelled with the sample number of the host leafrollers. The symbols on the right side of the sequence name indicate the reared parasitoids (triangles represent *T. unimaculatus*, and squares represent *D. tasmanica*). The symbols on the left side of the sequence correspond to the habitats from which the leafrollers were collected (black circle, wine grapes in the vineyard; white circle, natural habitats not adjacent to vineyard; black diamond, cover plants in the vineyard; and white diamond, adjacent woody habitats). For each sample, Accession numbers of sequences obtained from GenBank are presented. The numbers next to the branches represent the bootstrap values after 1000 replications. Values lower than 50 are not represented. The scale bar indicates a 1 % sequence divergence

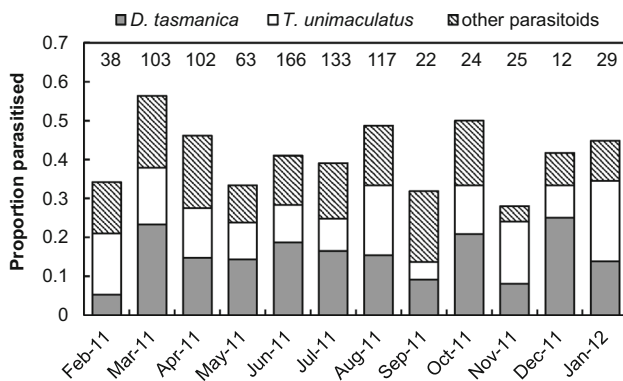


Fig. 6 Proportion of leafrollers parasitised by *D. tasmanica*, *T. unimaculatus* and other parasitoids collected monthly from February 2011 to January 2012 at the Waite Conservation Reserve, Urrbrae, South Australia. The numbers above each bar indicate the number of leafrollers collected

another study, parasitism of *E. postvittana* was consistently and significantly higher on the grape variety Cabernet Sauvignon compared to Chardonnay (Paull et al. 2013). Many other studies have demonstrated that plants affect the foraging success of predators and parasitoids through their architecture (Carter et al. 1984; Grevstad and Klepetka 1992; Cortesero et al. 2000) and by emitting herbivore-induced plant volatiles at sites of damage (Vet and Dicke 1992; Geervliet et al. 1994). Plants that emit highly attractive herbivore-induced plant volatiles are associated with higher parasitism rates under both field and laboratory conditions (Poelman et al. 2009). Parasitoids rely on innate mechanisms to locate their hosts during foraging and can also learn cues associated with host availability (Vet et al. 1995). Foraging experience on host plants can affect subsequent plant preferences (Papaj and Vet 1990). In a vineyard ecosystem, both exotic and native plants grow in, or adjacent to, vineyards. Indigenous parasitoids and their leafroller hosts have established novel interactions with introduced host plants. The two native parasitoids may have different abilities to perceive and learn host plant-

associated cues. For example, *D. tasmanica* may learn host-associated cues on grape and establish a preference for grape, while *T. unimaculatus* may not have the same capacity to perceive and learn cues associated with host plants, such as grapes. This hypothesis should be tested. Studies have demonstrated that planting species that support alternative hosts for natural enemies within or adjacent to crops may enhance parasitoid activity in crops (Thomas et al. 1991; Letourneau and Altieri 1999; Pfannenstiel et al. 2012). But simply providing host plants will not necessarily enhance the activity of parasitoids. The attractiveness of host plants to parasitoids and how this could affect the actual parasitism in crop and adjacent non-crop habitats needs to be thoroughly investigated. On the other hand, at the landscape scale, the quality and connectivity of remnant vegetation in agro-ecosystems is critical for parasitoid survival and diversity (Kruess and Tscharntke 1994; Holzschuh et al. 2010), especially near crop edges (Williams and Martinson 2000; Bianchi and van der Werf 2003; Miliczky and Horton 2005). In this study, each experimental site included adjacent native vegetation, which may facilitate the survival of some parasitoids, such as *T. unimaculatus*, that may not adapt well to cultivated crops (Paull 2007).

Cyclical seasonal changes in vineyard must influence the activity of parasitoids. In South Australian vineyards, wine grapes are deciduous plants, while the most native plants are evergreen. Vineyard are perennial agrosystems, which means the leafrollers leaving on grape can stay in vineyards all the year long, overwintering in the weeds or in the grape mummies. In addition, some parasitoid species such as *D. tasmanica* may persist with their hosts in vineyards during winter time. Therefore, the situation is quite different in agrosystems dominated by annual crops where the crop rotations force the organisms to move across the landscape. This is crucial for the compartmentalization of the trophic network between the different habitats. On the other hand, during winter dormancy, there are limited resources such as hosts and other foods in vineyards for the overall parasitoids and their host insects, while these resources are still available in adjacent natural habitats. Therefore, vineyards may still undergo cyclical colonisation by leafrollers and some parasitoids to some degree (Wissinger 1997). In this study, the field experiments were carried out during the early vine growing season. We hypothesise that the two parasitoids, *D. tasmanica* and *T. unimaculatus*, respond to the seasonal changes differently, possibly due to differences in their mobility. *D. tasmanica* is known to travel at least 30 m over 7 days (Scarratt et al. 2008), but nothing is known about the mobility of *T. unimaculatus*. Therefore, the mobility of these species needs to be investigated further to understand their ability to move between habitats.

Host density may also affect parasitoid activity. Natural enemies often respond to their hosts in a density-dependent manner. In a study involving both naturally occurring hosts and experimentally manipulated hosts, the response of *D. tasmanica* to different host densities was found to be inversely density dependent (Paull et al. 2013). But there is no published information about the response of *T. unimaculatus* to the density of *E. postvittana*. The numbers of both parasitoids are low in their preferred habitats. This may affect their functional and numerical responses to their hosts, including *E. postvittana*. In addition, host densities are often higher in crops than natural habitats (Segoli and Rosenheim 2013). Therefore, it is necessary to further determine if *D. tasmanica* and *T. unimaculatus* have responses to varying host densities, and whether these could affect their habitat preferences.

The activity of natural enemies could be affected by different abiotic conditions between crop and non-crop habitats, including temperature (Amat et al. 2006), light and moisture (Smith and Rutz 1991), or other environmental conditions (Fink and Volkl 1995). In this study, the woody native vegetation adjacent to the vineyards included more shaded areas, and the temperature may have been lower than in the vineyard during hot weather. Therefore, the two dominant parasitoid species may prefer different abiotic conditions, such as temperature and moisture. *T. unimaculatus* may prefer woody vegetation, while *D. tasmanica* may be more active in open canopy areas, such as vineyards. These effects can be critical for conservation biology and biological control and need to be tested.

A growing body of evidence has emphasised the importance of natural habitats in promoting and maintaining the natural enemy activity in agro-ecosystems (DeBach and Rosen 1991; Landis et al. 2000; Wilby and Thomas 2002). But our study demonstrates that parasitoids that attack the same host in agro-ecosystems can respond to crop and non-crop habitats differently. This indicates that the adjacent vegetation is not necessarily the likely source of some parasitoids of *E. postvittana* in vineyards. It implies more generally that non-crop vegetation may not be relied upon as a source of natural enemies in certain agricultural systems. Therefore, for the purpose of conservation biological control, attention should not only be paid to the management of natural habitats or cultivated cropping areas. It is necessary to thoroughly understand the ecology of key natural enemies and how they interact with their hosts in both crop and non-crop habitats. This could help functionally explain the tri-trophic interactions involving herbivores, parasitoids and plants.

Author contribution YF, MK, HS and SW conceived and designed research. YF and MK conducted experiment. YF, MK and OK analysed the data. MK contributed

reagents and analytical tools. YF and MK wrote the manuscript. The authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest All authors have no conflict of interest to declare.

Ethic statement No human participants and/or animals were involved in this study. We confirm that this work meets the international ethical guidelines and journal's policy on these matters, including adherence to the legal requirements of Australia where this work was carried out.

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