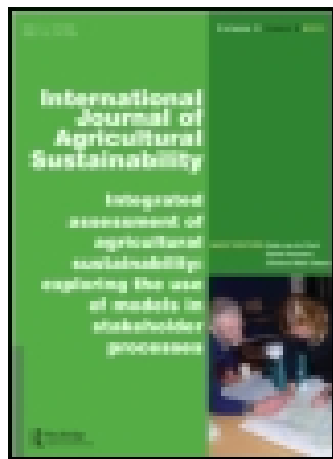


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Resource connectivity for beneficial insects in landscapes dominated by monoculture tree crop plantations

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Homogenization of agricultural landscapes affects ecological processes and biodiversity and can affect the community composition of ecosystem service providers. These effects can have particular impact in landscapes dominated by monocultures of pollinator-dependent tree crop plantations, which create both spatial and temporal homogeneity at the landscape scale. I looked for associations between the proportion of nearby unmanaged vegetation and potential wild pollinator groups collected within flowering almond orchards in two types of landscape. In the Complex landscape, characterized by a heterogeneous mosaic of multiple crops, semi-natural grassland and natural woodland, insect pollinator groups were not associated with unmanaged vegetation. In the Simple landscape, dominated by monoculture almond plantations, most pollinator groups showed positive relationships with the two unmanaged vegetation types (grassland and woodland). In particular, all wild bee and all but one hoverfly individual were found in remnant native vegetation patches within almond plantations, rather than within rows of almond trees. More research is necessary to identify how structural differences created in monoculture landscapes, between crops and the native vegetation they encroach on, influence ecological communities and the provision of ecosystem services.

Keywords: monoculture; broadacre; functional connectivity; almond plantation; orchard; wild pollinators

Introduction

Homogenization of agricultural landscapes can have widespread effects on insect community composition (e.g. Ekroos, Heliölä, & Kuussaari, 2010) and the provision of ecosystem services (e.g. Marino & Landis, 1996). These effects have often been studied in arable landscapes dominated by annual crops, but less attention has been given to homogeneous perennial crops, such as tree crop plantations. Plantation agriculture has traditionally been associated with tropical crops that have a global economic market and a limited cultivation range (e.g. sugar, coffee and oil palm) (Olivin, 1980; Tiffen & Mortimore, 1990). However, plantation agriculture can refer to any perennial crop grown on a large scale, usually in monoculture, and supported by large amounts of capital investment, labour and industrialized infrastructure (Tiffen & Mortimore, 1990). Hence, the term is increasingly applicable to tree crops and plantations outside of tropical regions (Gregor, 1965), such as temperate fruit and nut cultivars. In Australia, tree crop plantations, particularly almond (Almond Board of Australia, 2013; Wilkinson, 2012), are expanding across the southern temperate and Mediterranean climate zones that have traditionally been used for grazing and field crops, resulting in large-scale land-use change in places such as north-west Victoria (Luck, Spooner, Watson, Watson, & Saunders, 2014). Over 60% of Australian

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commercial almond plantings are established in the semi-arid mallee region of north-west Victoria (Almond Board of Australia, 2013), an area of high conservation value (Mallee Catchment Management Authority, 2008). In the northern hemisphere, similar changes are occurring as plantations of almond and olive expand across landscapes in Mediterranean regions such as California (USA) and Spain (Amate, González de Molina, Vanwalleghem, Fernández, & Gómez, 2013; Murua, Carman, & Alston, 1993). This type of land-use change can alter the structural and phenological dynamics of agricultural landscapes and impact local ecological communities; thus, the effects of such changes need to be integrated into management decisions and research goals (Watson, Luck, Spooner, & Watson, 2014).

Mediterranean and semi-arid landscapes are naturally dynamic and heterogeneous (Aguiar & Sala, 1999), especially in Australia (Morton, Stafford Smith, Friedel, Griffin, & Pickup, 1995), while most conventional plantations are managed as intensive monocultures with limited vegetation structure and diversity inside plantation boundaries. Unlike arable crop mosaics under short rotation that can provide temporal heterogeneity in the absence of spatial variation (Vasseur et al., 2013), tree crop plantations (e.g. orchard fruits) are generally embedded in the landscape for more than 15 years, creating a comparatively ecologically stable, semi-permanent ecosystem (Altieri, 1999; Tedders, 1983). If these plantations are managed as intensive monocultures, they create areas of permanent spatial and temporal homogeneity in the landscape that are inhospitable to pollinators for most of the year (Marini, Quaranta, Fontana, Biesmeijer, & Bommarco, 2012; Sheffield, Westby, Smith, & Kevan, 2008) and could potentially influence the structure of invertebrate communities in the long term (Olivin, 1980; Tschamtkke, Steffan-Dewenter, Kruess, & Thies, 2002). This could consequently affect long-term yields, as many fruit cultivars benefit from the presence of a diverse insect pollinator community during crop flowering to set fruit or produce optimal yields (Garibaldi et al., 2013; Kevan, 1999). Yet, there has been very little ecological research into how biodiversity, particularly ecosystem service providers, in semi-arid landscapes is influenced by habitat contrasts created between monoculture plantations and the heterogeneous ecosystems they encroach on (but see Luck et al., 2014; Saunders & Luck, 2014).

Flowers of orchard fruit cultivars, particularly Rosaceae species (e.g. sweet cherry, apricot, apple or almond), emit volatile compounds that are highly attractive to bee pollinators (Baraldi, Rapparini, Rossi, Latella, & Ciccioli, 1999), and it is likely that mass-flowering fruit plantations attract wild pollinators to the temporary surplus of flowers in crop fields (Lander, Bebbler, Choy, Harris, & Boshier, 2011). However, plant diversity is particularly important for supporting wild pollinator communities (Nicholls & Altieri, 2013) and long-term establishment of a diverse pollinator community depends on retaining unfarmed habitat throughout agroecosystems, providing permanent foraging and nesting sites (Kremen et al., 2007). Many studies have shown positive relationships between pollinator communities and non-crop habitats within agricultural landscapes, such as semi-natural grasslands (Öckinger & Smith, 2007), natural forest (Garibaldi et al., 2011 and references therein) or wildflower strips around crop fields (Haaland, Naisbit, & Bersier, 2010 and references therein). Yet a matrix that contains multiple habitat types providing complementary levels of spatial and/or temporal resource heterogeneity (i.e. functional connectivity) is more important for the long-term establishment of wildlife communities than a single permanent non-crop habitat (Vasseur et al., 2013; Williams & Kremen, 2007). Functional connectivity is a key element of sustainable agroecosystems (Scherr & McNeely, 2008) and can enhance crop yields indirectly by supporting source populations of beneficial insects such as pollinators and natural enemies (Mitchell, Bennett, & Gonzalez, 2013; Williams & Kremen, 2007).

Due to its relative permanence as a land-use type, tree crop agriculture has great conservation value (Altieri, Letourneau, & Davis, 1983; Smith, 1916), but the ecological role of fruit orchards

has been studied far less than tropical (Hartemink, 2005) or timber (Quine & Humphrey, 2010) plantation crops. This is an oversight, as temperate fruit and nut plantations are often managed very differently, particularly with regard to orchard floor vegetation, chemical applications and disturbance cycles. Because many fruit crops are pollinator dependent and prone to damaging pests, most studies have focused on pollinators (e.g. García & Miñarro, 2014; Sheffield et al., 2008) and biological control agents (e.g. Bugg & Waddington, 1994; Eilers & Klein, 2009) within the orchard. Fewer studies have considered the ecological context of fruit plantations or how they might influence ecosystems and communities in the surrounding landscape, particularly local pollinator communities present during an orchard crop's brief flowering period (e.g. Klein et al., 2012; Marini et al., 2012).

To investigate these questions further, I focused on plantations of almond (*Prunus dulcis* Mill.) trees in a semi-arid region of southern Australia. Almond production contributes to more than half of Australia's annual nut production and the country is the second largest almond producer in the world (Almond Board of Australia, 2013). Cultivated almond trees flower synchronously for three to four weeks at the end of winter (Hill, Stephenson, & Taylor, 1985) and are nearly 100% dependent on insect pollination to set fruit. Yet, there is little published information on potential wild pollinators of almond blossoms in Australia, or how communities of these insects are influenced by almond plantation management (but see Saunders & Luck, 2014; Saunders, Luck, & Mayfield, 2013). The data presented in this study were collected as part of the first investigation of wild pollinators that could potentially provide pollination services to almond crops in Australia's main almond-growing region, the Victorian Murray Mallee. Due to the lack of ecological information available on my study system, I sampled flowering orchards in two different types of agricultural landscape (heterogeneous and homogeneous) and documented patterns of association between potential wild pollinators collected in orchards and the presence of unmanaged vegetation immediately surrounding the sites. Specifically, I asked two questions: (i) is pollinator community composition different at sites surrounded only by crops, compared to sites surrounded by a combination of crops and unmanaged vegetation? (ii) Is there a relationship between abundance or richness of individual pollinator groups and proximity to either native mallee vegetation or semi-natural grassland?

Methods

Study area and landscape quantification

The study area was located in the Sunraysia agricultural region of north-west Victoria, Australia, in the localities of Wemen/Liparoo (approximately 34.8°S 142.6°E) and Nangiloc/Colignan (approximately 34.5°S 142.35°E). The region is dominated by irrigated horticulture and large remnant areas of native mallee vegetation. Sampling was conducted in August–September 2010 during the brief almond flowering period. Average rainfall in 2010 was wetter than average, with approximately 528 mm falling at Wemen/Liparoo (station 76,000, long-term average = 314.9 mm p.a.) and approximately 427 mm recorded at Colignan/Nangiloc (station 76,052, long-term average = 290.4 mm p.a.). Average temperatures across both districts ranged from minimums of 5–7°C to maximums of 15–20°C (Bureau of Meteorology, 2013). A total of 72 sites within commercial almond orchards were sampled across two distinct landscapes. One landscape was a heterogeneous agricultural mosaic (hereafter 'Complex') in which I sampled 27 sites within a landscape diameter of 5.3 km. This landscape was characterized by small patches of diversified organic and conventional farms (mostly tree fruits and vineyards) and semi-natural grassland, as well as large patches of natural vegetation (Figure 1(a)). The other landscape was a homogeneous landscape (hereafter 'Simple') dominated by broadacre

monoculture almond plantations, large patches of contiguous natural vegetation and occasional smaller patches of semi-natural grassland or other crops (Figure 1(b)). I sampled 45 sites in this landscape within a landscape diameter of 14.6 km. Sites in the Complex landscape were all located within stands of almond trees and sites in the Simple landscape were located in either stands of almond trees or in remnant patches of mallee vegetation within almond orchard interiors or along orchard boundaries (all remnant sites within 15 m of an almond tree). The two landscapes were approximately 36 km apart, and the minimum distance between any two sites within a landscape was 200 m. Complex landscape orchards were managed by the same family owned company and had a living ground cover of herbaceous vegetation (Figure 2(a)). Simple landscape orchards were managed by the same corporation and had predominantly bare soil throughout (Figure 2(b)). All orchards were managed without insecticide (see Saunders et al., 2013 for management details) and all consisted of mature trees within the industry's standard bearing age range (10–25 years). I did not consider orchard age as a factor in my analysis, as the focus of my study was spatial heterogeneity in floral resource availability within the study system, which is more likely to be influenced by local management practices and landscape composition than individual orchard age.

Vegetation types around each site were identified during sampling and the proportional area of each vegetation type within 100 m of each site was calculated in ArcMap 10 using spatial data of agricultural land uses in the study region (SunRISE 21 Inc., 2008). There was no physical overlap in 100 m radii around each site. I focused on a small spatial scale, as mounting evidence suggests that small-scale attributes related to farm-specific management practices can have more influence over local insect populations than landscape-scale heterogeneity or diversity (e.g. Kovács-Hosnyánszki, Batáry, & Báldi, 2011; Paredes, Cayuela, & Campos, 2013). Pollinators may also travel much shorter distances in agroecosystems when floral resources are plentiful (Lander et al., 2011; Zurbuchen et al., 2010), as they were in my study system. I did not calculate

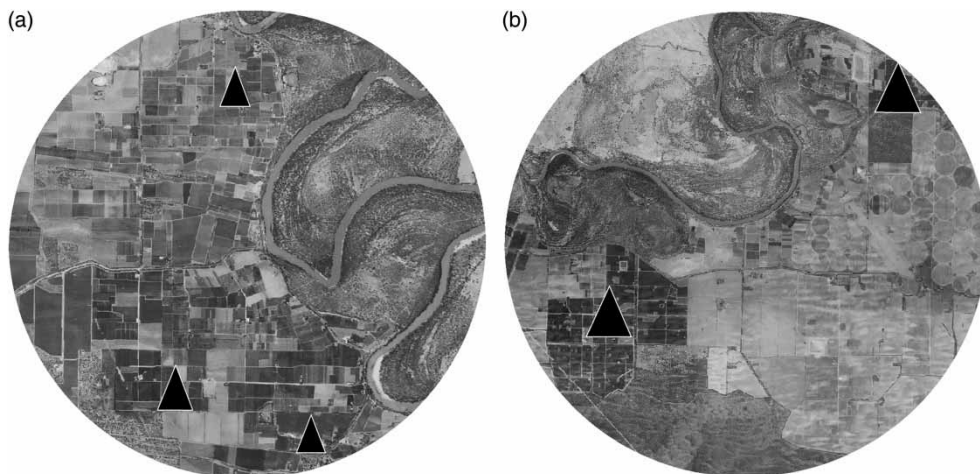


Figure 1. (a) The Complex landscape was dominated by diverse crops, including citrus, avocado, almond, walnut and table grape vineyards, with contiguous natural vegetation shown along the right of the figure (figure diameter = 5.3 km). (b) The Simple landscape was dominated by almond plantations, shown through the middle of the figure and in the top right corner, with contiguous natural vegetation visible at the top and bottom (figure diameter = 14.6 km). Triangles indicate the location of individual orchards within each landscape. Satellite images from Vicmap API (2015) WMS & WMTS licensed service, DELWP, Government of Victoria.

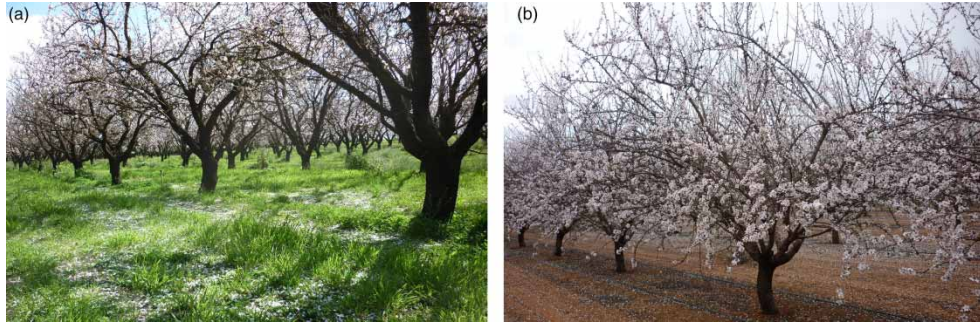


Figure 2. Representative images of (a) plant-diverse orchards in the Complex landscape and (b) monoculture plantations in the Simple landscape.

generalized heterogeneity indices, which often mask the influence of vegetation structure or resource availability (Tews et al., 2004); instead, I documented the proportional availability of specific resources and vegetation types that were ecologically meaningful to pollinator communities.

Insect sampling and identification

To identify potential wild pollinators of almond blossoms in my study system, I focused on individuals from the taxonomic orders Hymenoptera (non-*Apis* bees, wasps) and Diptera, as these taxa are common pollinators in natural and agricultural systems (Armstrong, 1979; Ssymank, Kearns, Pape, & Thompson, 2008). Information on wild pollinators in the study system is limited, but wasps and flies are known to pollinate native flowers in the area (e.g. Ford & Forde, 1976; Horskins & Turner, 1999) and individuals of these groups were seen visiting almond and native flowers during sampling. Managed and feral European honey bees (*Apis mellifera*) were present during sampling, but were not included in this targeted investigation of non-*Apis* pollinators. It is unlikely that potential inter-specific resource competition impacted my results significantly, as my sampling method was designed to assess taxonomic richness and abundance rather than foraging activity (Brittain, Williams, Kremen, & Klein, 2013; Steffan-Dewenter & Tscharntke, 2000).

I collected insects at each site using pan traps and placement of traps was standardized across all sites. Traps were made from white plastic picnic bowls (Woolworths Home Brand) that were either left white or painted with fluorescent yellow or blue paint (White Knight Paints). Although pan traps may underestimate the full composition of pollinator insect assemblages, I used this method to minimize collector bias (Westphal et al., 2008) and I selected trap colour and placement to increase the chance that the traps would provide ecologically meaningful results. Yellow and white were the most common flower colours in the system and blue traps are commonly thought to attract bees (see Saunders & Luck, 2013 for discussion on this). At each site, a set of traps (one bowl of each colour) was placed on open ground, in a triangular array, adjacent to a flowering tree and away from fully shaded areas. This was to ensure maximum visibility during the late winter sampling time, when many of the target insects would be emerging or building nests in ground-level substrate (Saunders, Luck, & Gurr, 2014). Each site was sampled once during almond flowering, with traps set out after sunrise (7:30–9:30 am) and collected before sunset (4.00–6.00 pm) in the sequence they were set out, so as to capture maximum insect activity during the warmest part of the day. All sampling days were fine and calm with maximum daytime temperatures

between 15°C and 20°C. This protocol was not intended to provide a comprehensive survey of all insect pollinators at each site; rather, it was designed to provide a comparative sample of potential wild pollinators using almond orchards during flowering across a very large region (Bennett, Radford, & Haslem, 2006).

Upon collection, insects were stored in 70% ethanol and counted and sorted in the laboratory. Trap data from each site were pooled across trap colours to obtain a single sample for each site. Native bees were identified to species or subgenus level by a taxonomic expert (K. Walker, Museum Victoria) and I identified wasp and fly individuals to family level using taxon-specific keys (Hamilton et al., 2006; Stevens et al., 2007). Wasp and fly individuals were further sorted into small (0–0.49 cm) and large (>0.5 cm) bodied groups for analysis, based on the average body length of the individuals in each family group. These size categories were chosen to represent the most likely candidates for almond pollination, based on the size of an almond blossom (3–5 cm) and position of its stamens; hence, individuals over 0.5 cm in length were considered more likely to transfer pollen while visiting blossoms than smaller bodied individuals. The fly family Syrphidae (hoverflies) was isolated as a separate taxonomic unit from other fly groups, as this dipteran family is a common pollinator in agroecosystems (Ssymank et al., 2008).

Data analysis

Response variables were abundance counts of each insect group (native bee, small wasp, large wasp, small fly, large fly and hoverfly) and overall species (native bee) and family (wasp, fly) richness per site (Table 1). All data were analysed untransformed (O'Hara & Kotze, 2010). Richness was represented by the bias-corrected Chao 1 abundance-based estimator. Because of the differences in orchard management practices and the lack of landscape-scale replication, I used a non-metric multidimensional scaling (NMDS) ordination on the entire data set to identify if there was a difference in pollinator community composition between the two landscapes. Data were highly aggregated by landscape type (Figure 3), so I focused on examining relationships within, rather

Table 1. Average abundance and richness of wild pollinator insects per site and average proportion of each vegetation type within 100 m of each site, \pm standard error, in Complex and Simple landscapes.

		Complex ($n = 27$)	Simple ($n = 45$)
Pollinator abundance	Native bee	2.26 \pm 0.81***	0.33 \pm 0.14
	Large wasp	0.89 \pm 0.23**	0.53 \pm 0.23
	Small wasp	1.93 \pm 0.30***	0.58 \pm 0.14
	Large fly	57.04 \pm 15.21***	7.71 \pm 1.07
	Small fly	29.96 \pm 4.10***	4.49 \pm 0.45
	Hoverfly	0.15 \pm 0.07	0.18 \pm .10
Pollinator richness	Native bee	1.2 \pm 0.28***	0.36 \pm 0.14
	Wasp	2.89 \pm 0.85***	0.86 \pm 0.17
	Fly	11.43 \pm 1.25***	7.36 \pm 0.64
Vegetation Type	Almond	0.66 \pm 0.05	0.55 \pm 0.04
	Mallee	0.09 \pm 0.03	0.23 \pm 0.04*
	Grass	0.08 \pm 0.03	0.04 \pm 0.01
	Grape ^a	0.10 \pm 0.03***	0.08 \pm 0.08
	Fruit	0.10 \pm 0.02	0

Note: Asterisks signify in which landscape each variable was significantly greater; no asterisk means there was no difference between landscapes.

^aMean proportion of 'grape' for the Simple landscape is based on one site.

* $p < .09$.

** $p = .05$.

*** $p < .001$.

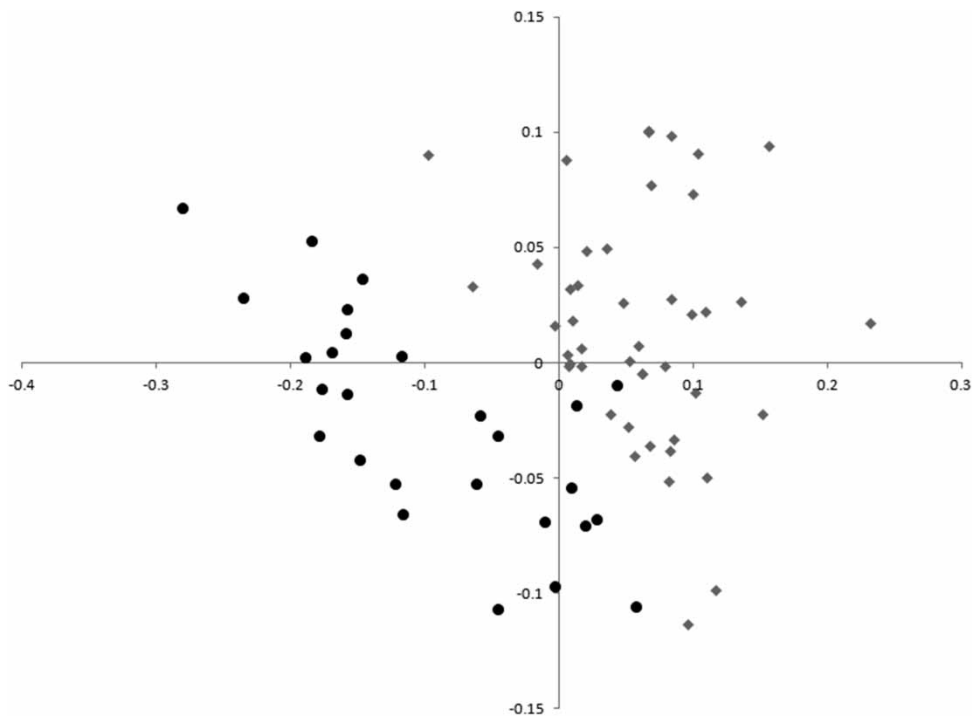


Figure 3. Within the study region, overall pollinator community composition differed between almond orchards in the Complex (black circles) and Simple (grey diamonds) landscapes. Stress value (goodness of fit) for the NMDS, based on Bray–Curtis similarities, was 0.12.

than across, landscapes. Hence, data were pooled by landscape type (Complex and Simple) for the remaining analyses.

First, I grouped sites based on their floral resource profile. This was determined by the combination of vegetation types within 100 m of each site: temporary – only perennial fruit crops with a single brief flowering period each year; or permanent – perennial crops plus native vegetation and/or semi-natural grassland. For each landscape, I used NMDS plots with Bray–Curtis distances to identify similarity among sites based on their resource profiles. I then used one-way non-parametric multivariate analysis of variance (NPMANOVA) with Bray–Curtis similarities (Anderson, 2001) to test for differences in overall community composition between groups of ‘permanent’ and ‘temporary’ resource sites in each landscape. This analysis was performed separately for groups of Hymenoptera and Diptera families. I then focused on relationships between individual insect groups and the proportion of native vegetation or semi-natural grassland around each site, as these represented the most permanent and least disturbed floral resources available throughout the year. I identified the nature of the relationship (positive, negative or neutral) between richness and abundance of each insect group and each of the two vegetation types using negative binomial generalized linear models (GLMs). Native bee data from the Simple landscape and hoverfly abundance from both landscapes were not included in these analyses, due to the very low number of individuals caught. I did not employ a model selection procedure to rank multiple different models, because my goal was to identify the nature of the relationship with each vegetation type, rather than to search for potential relationships among a suite of predictors. Because some Simple landscape sites were within natural mallee vegetation adjacent to

almond stands, I also examined whether pollinator diversity at these sites differed from diversity in almond stands by using a bootstrapping procedure to compare Shannon diversity indices of Hymenoptera and Diptera families between the two site groups. GLMs were conducted in IBM SPSS 20 (IBM Corporation, 2011) and all other analyses were conducted in PAST 2.17 (Hammer, Harper, & Ryan, 2001).

Results

Overall landscape and wild pollinator community patterns

The average proportion of almond trees and semi-natural grassland within 100 m of each site was similar in both Complex and Simple landscapes, but the average proportion of native mallee vegetation surrounding sites was higher in the Simple landscape (Table 1). Some Complex landscape sites were near other fruit trees and vineyards, but no other fruit trees were present in the Simple landscape and only one site had grape vines within 100 m (Table 1). Across the whole region, I caught a total of 3117 potential wild pollinator individuals, including 76 native bees, 126 wasps and 2915 flies (see online supplementary material for taxonomic list). Average abundance and richness per site of every pollinator group except hoverflies were highest in the Complex landscape (Table 1).

Relationships between wild pollinator communities and floral resource profiles

Ordination plots for each landscape showed that overall pollinator community composition at sites surrounded by ‘temporary’ floral resources (crops only) was similar to community composition at sites surrounded by ‘permanent’ resources (crops and natural vegetation) (Figure 4). In the Complex landscape, NPMANOVA tests showed that there were no differences in Hymenoptera or Diptera community composition between ‘temporary’ and ‘permanent’ sites: Diptera, Total Sum of Squares (SS) = 4.51, Within-group SS = 4.34, $F = 1.00$, $p = .36$; Hymenoptera, Total SS = 6.58, Within-group SS = 6.35, $F = 0.93$, $p = .46$ (Figure 5(a)). In the Simple landscape, there was no difference in the composition of Diptera communities (Total SS = 4.61, Within-group SS = 4.50, $F = 1.08$, $p = .36$), but Hymenoptera community composition was different between the two site types (Total SS = 15.43, Within-group SS = 14.55, $F = 2.61$, $p = .05$) (Figure 5(b)).

Relationships between wild pollinator groups and proximate unmanaged vegetation

Richness and abundance of individual pollinator groups showed contrasting relationships with the proportion of the two focal vegetation types, native vegetation or semi-natural grassland, around each site (Table 2). In the Complex landscape, most pollinator groups were negatively associated with both vegetation types and none of the relationships were statistically significant. The exceptions were large fly abundance, which was positively associated with both vegetation types, and small wasp abundance, which was positively associated with semi-natural grassland. In the Simple landscape, significant relationships were found between fly richness and native vegetation (positive); large wasp abundance and semi-natural grassland (positive) and small wasp abundance and native vegetation (negative).

In the Simple landscape, seven out of eight hoverfly individuals and all native bees were collected within native mallee vegetation adjacent to almond stands, rather than within stands of almond trees (Figure 6). Diptera family diversity was higher in the mallee patches inside almond orchards ($H = 2.25$) than in almond stands ($H = 1.99$; $p = .02$), but there was no

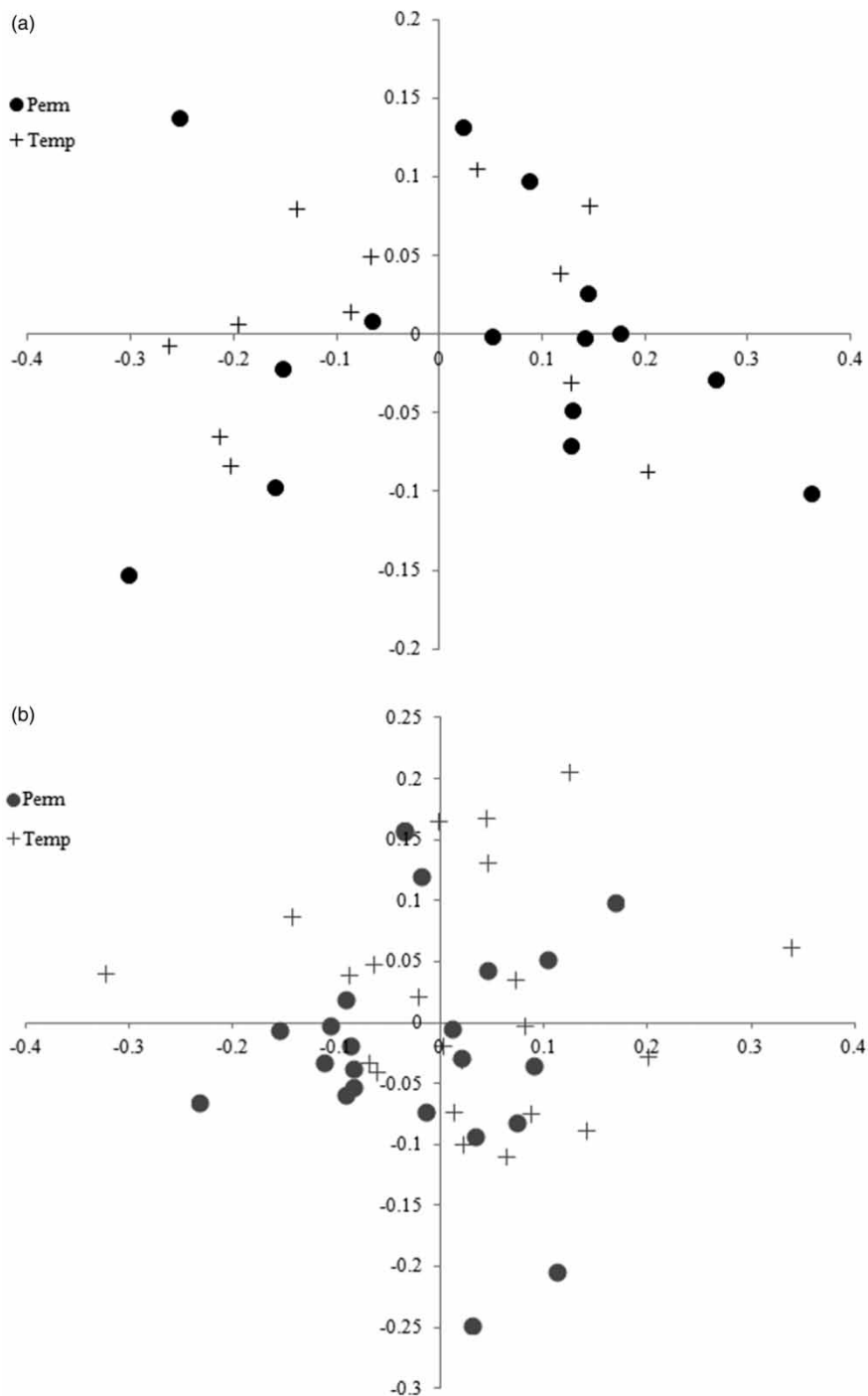


Figure 4. Within (a) Complex and (b) Simple landscapes, overall pollinator community composition in almond orchards was similar between sites that were within 100 m of temporary (Temp) floral resources (i.e. perennial fruit crops only) and sites that were within 100 m of permanent (Perm) resources (i.e. crops plus native vegetation and/or semi-natural grassland). Stress values for the ordination plots: Complex = 0.08; Simple = 0.14.

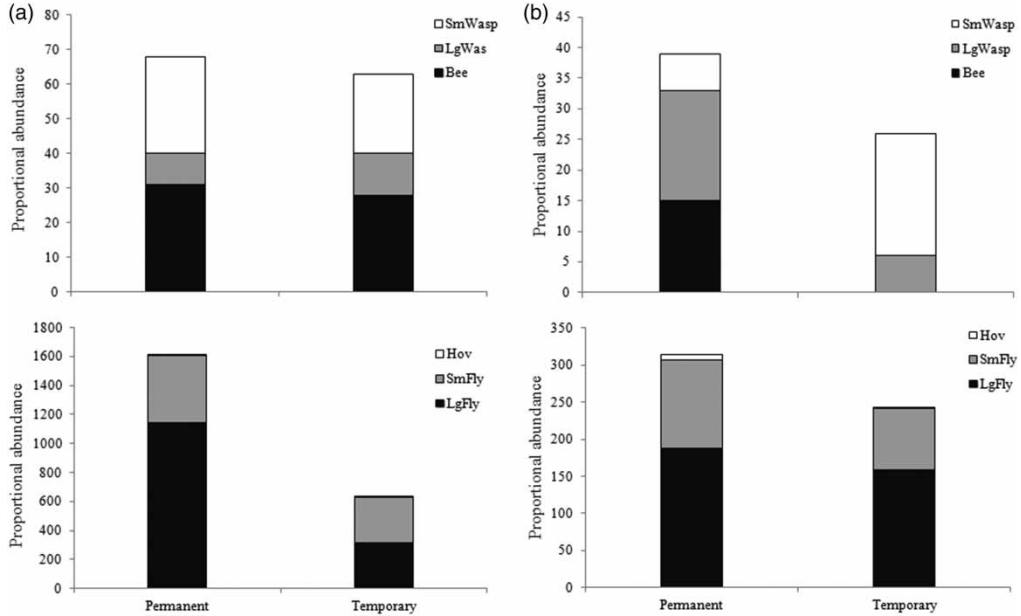


Figure 5. (a) In the Complex landscape, community composition of Hymenoptera (top) and Diptera (bottom) was similar between sites surrounded by temporary floral resources and sites surrounded by permanent resources. (b) In the Simple landscape, only Diptera (bottom) community composition was similar between sites surrounded by permanent and temporary resources.

Table 2. Relationships between richness and abundance of each insect group and the proportion of native vegetation (NV) or grassland (GS) within 100 m of each site (parameter estimates \pm standard error).

Landscape	Response		NV	χ^2	GS	χ^2
Complex	Pollinator abundance	Native bee	-0.34 ± 0.53	0.53	-0.15 ± 0.47	0.11
		Large wasp	-2.84 ± 2.23	2.71	-0.23 ± 1.10	0.04
		Small wasp	-1.38 ± 1.13	1.94	0.03 ± 0.89	0.001
		Large fly	0.01 ± 0.01	0.13	0.02 ± 0.01	1.65
		Small fly	-0.13 ± 0.10	2.38	-0.02 ± 0.07	0.07
Complex	Pollinator richness	Native bee	-0.72 ± 1.29	0.37	-1.22 ± 1.59	0.71
		Wasp	-0.53 ± 0.58	1.15	-1.57 ± 1.20	2.96*
		Fly	-0.15 ± 0.26	0.37	-0.46 ± 0.52	1.04
Simple	Pollinator abundance	Large wasp	1.10 ± 1.50	0.57	$7.50 \pm 3.97^*$	3.78**
		Small wasp	$-1.86 \pm 1.02^*$	3.63**	-5.97 ± 4.37	2.50
		Large fly	0.10 ± 0.44	0.05	1.53 ± 1.15	1.90
		Small fly	0.63 ± 0.40	2.42	0.99 ± 1.20	0.68
		Wasp	0.10 ± 0.71	0.02	0.21 ± 2.25	0.01
Simple	Pollinator richness	Fly	$0.82 \pm 0.42^{**}$	3.58*	-1.06 ± 1.94	0.29

Note: AIC_c = Akaike's information criterion corrected for small sample sizes; χ^2 = likelihood ratio chi-square goodness-of-fit test, indicates whether the model fits the data better than the constant-only model.

* $p < .09$.

** $p = .05$.

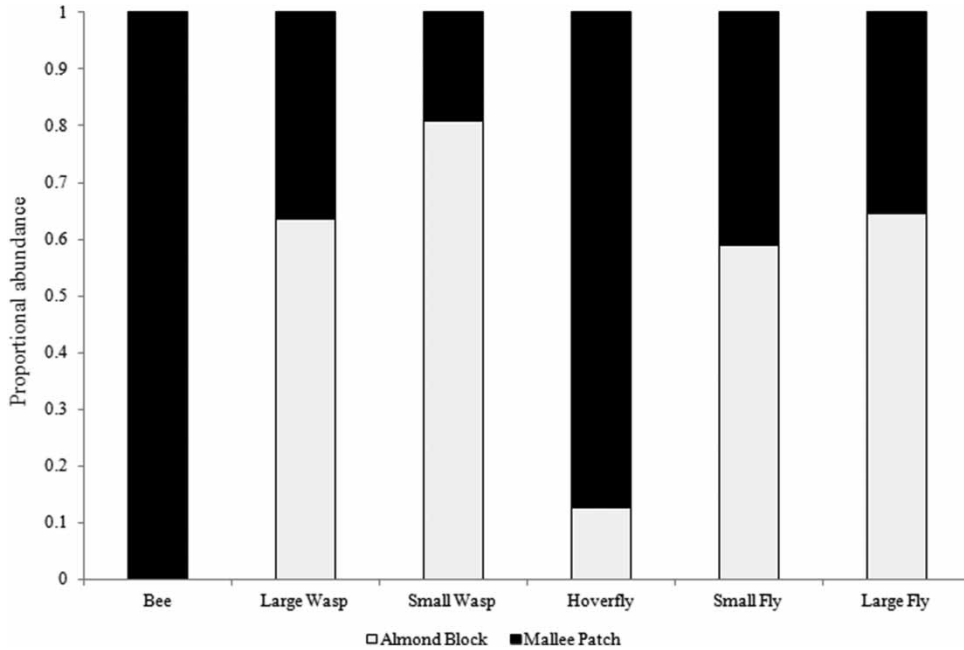


Figure 6. In the Simple landscape ($n = 45$), bee and hoverfly abundance was higher inside remnant patches of native mallee vegetation within plantation interiors (black), while wasp and fly abundance was higher within stands of almond trees (grey).

difference in Hymenoptera family diversity between the two site types (mallee $H = 1.47$, almond $H = 1.67$, $p = .37$).

Discussion

Average abundance and richness of all potential pollinator groups, except hoverflies, were higher in Complex landscape orchards than Simple landscape orchards. This result was likely influenced by the difference in weedy ground cover between orchards of each landscape type (Saunders et al., 2013) in conjunction with the overall structural differences between the two landscape types. Weedy ground cover in crop fields and orchards is often inherent to overall landscape complexity (Paredes et al., 2013; Roschewitz, Gabriel, Tschardtke, & Thies, 2005), but I was not able to separate the relative influence of these factors on the pattern seen here. However, similar differences in pollinator assemblages have been found in other studies comparing pollinators between simple and complex agricultural landscapes (e.g. Haenke, Scheid, Schaefer, Tschardtke, & Thies, 2009; Persson & Smith, 2013; Steffan-Dewenter, Münzenberg, & Tschardtke, 2001).

Complex landscape

Wild pollinators in Complex landscape orchards were not associated with unmanaged vegetation near almond sites. This could have been an artefact of the small sample size, or it could indicate that non-crop vegetation was less important for pollinator communities in the heterogeneous landscape, due to higher resource diversity in the landscape. Large flies were more abundant at sites near natural or semi-natural vegetation (Figure 5(a)), although this result was largely driven by the

extremely high abundance of the most common fly family, Tachinidae, at a few sites that were near established grassy/weedy meadows. This concurs with other studies that have found a strong association between increased tachinid abundance and perennial or weedy ground cover in farmland (e.g. Letourneau, Bothwell Allen, & Stireman, 2012). Abundance and richness of bees and wasps were generally higher at sites surrounded by perennial fruit crops than sites near native vegetation. Other studies have also found bee communities to have stronger relationships with heterogeneous flowering crop landscapes than with nearby natural or semi-natural vegetation (e.g. Westphal, Steffan-Dewenter, & Tschardtke, 2003; Winfree, Williams, Gaines, Ascher, & Kremen, 2008). Most fruit crops flower in late winter–early spring when wild pollinator species are emerging or reproducing; so agroecosystems containing these crop varieties may potentially enhance pollinator populations (Jauker, Peter, Wolters, & Diekötter, 2012; Westphal, Steffan-Dewenter, & Tschardtke, 2009). However, functional connectivity of complementary resources within the matrix around crop fields is also necessary to sustain beneficial insect communities in the long term (Williams & Kremen, 2007). Further sampling of orchards across time is needed to identify how wild pollinators use the surrounding landscape after almond trees cease flowering.

Simple landscape

In the Simple landscape, most pollinator groups showed positive relationships with native mallee vegetation or semi-natural grassland. Abundance of small wasps was the only group to be negatively associated with both vegetation types. The highest small wasp abundances were collected at interior almond sites more than 100 m from unmanaged vegetation, so the negative relationship was most likely a reflection that both vegetation types were negatively correlated with the proportion of almond trees around sites (almond/mallee, $r = -0.95$, $p < .001$; almond/grassland, $r = -0.55$, $p < .001$). This is surprising, as wasps are often strongly associated with plant diversity and structural complexity (Arnan, Bosch, Comas, Gracia, & Retana, 2011; Stephens, Schellhorn, Wood, & Austin, 2006), which were lacking in the Simple orchards. Placing pan traps at the ground level could have resulted in the collection of a higher number of species inhabiting leaf litter around tree bases, such as small parasitic wasps (Pucci, 2008); however, the most common parasitic family groups I collected (Diapriidae and Pteromalidae) were more abundant inside almond stands than near native vegetation, indicating that these species might prefer the resources available around almond trees. These species are unlikely to be useful for almond blossom pollination due to their small body size, but they could be important post-pollination control agents for almond pests (Eilers & Klein, 2009; Freeman Long et al., 1998), thereby indirectly contributing to fruit yields (e.g. Lundin, Smith, Rundlöf, & Bommarco, 2013). There is a need for further investigation into the synergies between these two ecosystem services in Australian agroecosystems.

Interestingly, all bee individuals and all but one hoverfly individual were collected within the remnant mallee patches located inside almond stands, rather than in rows of almond trees. This shows that these key wild pollinator taxa are present in the landscape, even within plantation boundaries, but environmental factors within the plantations could be limiting their dispersal into the homogeneous plantation interiors (Saunders et al., 2014). It is possible that pollinator abundance in orchards was low because the abundant floral resources diminished the effectiveness of the pan traps (Baum & Wallen, 2011); however, the sampling method used in the Simple landscape was identical to that used in the Complex landscapes, where numerous individuals were caught within almond stands, so the low pollinator abundance inside monoculture plantations was more likely to be a result of habitat attributes characteristic of these plantations.

Although some studies have found pollinator abundance to increase in mass-flowering monoculture crops, most of these study systems were ground-level or mid-height crops such as canola or arable crops/pasture (e.g. Holzschuh, Dormann, Tschardtke, & Steffan-Dewenter, 2013; Westphal et al., 2003). In contrast, studies of wild pollinators in intensively managed tree crops have found lower pollinator abundance or richness in homogeneous orchard interiors (e.g. Klein et al., 2012; Marini et al., 2012; Saunders & Luck, 2014). Many pollinator species prefer to forage in open areas dominated by early successional vegetation (Kremen et al., 2007) and this could explain why pollinators are generally found to respond positively to annual field crop monocultures and negatively to perennial tree monocultures. Resource richness is also relative to the local context; that is, natural vegetation patches in homogeneous landscapes function as resource-rich interstices that provide a more obvious contrast with adjacent broadacre monoculture crops than they would with the floral diversity present in heterogeneous agroecosystems (Haenke et al., 2009; Kohler, Verhulst, van Klink, & Kleijn, 2008). For example, Kohler et al. (2008) found that wild bees may not move more than 25–50 m from favourable habitat patches if the surrounding matrix does not provide necessary resources. Hence, the establishment of natural vegetation ‘reservoirs’ within farm boundaries to support pollinator communities (Brosi, Armsworth, & Daily, 2008) may not have much success in enhancing unmanaged pollination services if the farm interior remains an inhospitable environment for wild pollinators.

Conclusions and management implications

The expansion of monoculture crops beyond the field scale, resulting in broadacre monoculture landscapes in many parts of the world, has serious ecological implications for conservation of biodiversity and the sustainability of agroecosystems. Identifying how ecological communities and ecosystem services are influenced by changes to resource connectivity in intensive agroecosystems is critical to developing sustainable agroecosystems. The results presented here suggest that more intensive management of agroecosystems increases the need for more unmanaged habitat that can provide essential resources for potential wild pollinators and other beneficial insects. However, simply isolating unmanaged habitats in the landscape may not provide the necessary resource connectivity for beneficial insects if insect communities are unable to persist inside monoculture plantations beyond the flowering period. This could affect the long-term composition of insect assemblages that are available to provide essential pollination services to crops and native flowering plants. My findings agree with other studies that have found that patch-scale attributes, such as farm management intensity and functional connectivity, influence within-field pollinator communities more in homogeneous landscapes than in complex, heterogeneous landscapes (e.g. Kohler et al., 2008; Persson & Smith, 2013; Rundlöf, Nilsson, & Smith, 2008). Similar studies of tree crops in the USA and Europe have found that generalist wild pollinators are frequent visitors to orchard plantations, but their distribution is mostly limited to parts of the orchard with proximity to natural or semi-natural habitat that can sustain insect resource needs before and after trees are in flower (e.g. Klein et al., 2012; Marini et al., 2012).

If managed ecologically, tree crop plantations have the potential to support wild pollinator conservation and enhance multiple ecosystem functions, including biological pest control, soil formation and erosion control (Bugg & Waddington, 1994; Ramos, Benítez, García, & Robles, 2010). However, ecological management practices adopted at the landscape or regional scale may also be necessary to provide permanent spatial and temporary resource connectivity essential for wild pollinator communities to persist in the landscape (Holzschuh, Steffan-Dewenter, & Tschardtke, 2008; Williams & Kremen, 2007). This is particularly relevant to pollinator-dependent almond crops. Diverse insect pollinator assemblages have been directly linked to increased

yields in North American almond plantations (Brittain et al., 2013), but vegetation homogeneity can limit movement of wild pollinators into plantation interiors away from natural or unmanaged habitat (Klein et al., 2012; Saunders & Luck, 2014). Growers may be able to enhance yields by supporting mosaics of natural and semi-natural vegetation and increasing vegetation heterogeneity within plantations. These management practices are fundamental to sustainable agriculture, providing widespread benefits for farm productivity and ecological function (Bommarco, Kleijn, & Potts, 2013; Pretty, 2008). Smaller patches of trees and increased vegetation on plantation floors may cost growers by reducing mechanical efficiency during harvest (Bugg & Waddington, 1994), but the trade-offs between these costs and the long-term benefits of enhanced ecosystem services may increase the net return (Luck, 2013), which is more indicative of overall productivity. This study, the first to examine landscape influences on wild pollinator communities in Australian almond plantations, has highlighted the need to consider how the expansion of orchard crop plantations outside of tropical regions will affect ecosystem services and agricultural sustainability.

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