



Review

Ecosystem service of biological pest control in Australia: the role of non-crop habitats within landscapes

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Abstract

Semi-natural areas surrounding field crops are generally shown to enhance natural enemies of pests and biocontrol services within field crops worldwide. However, most of the evidence comes from work conducted in temperate regions of the northern hemisphere and it remains unclear to what extent these conclusions hold true in other parts of the world. Here, we provide an overview of the research in Australia investigating the link between populations of pests and their natural enemies and the type, quality, quantity and spatial arrangement of non-crop habitats surrounding field crops. There is strong evidence in Australia that exotic weeds support multiple pest species, but the link between weediness of semi-natural habitats and biological pest control within field crops remains to be investigated. Further, woody vegetation in good condition (not grazed, with mid- and under-story and good ground cover) appears to support multiple natural enemies that move into crops, especially when in close proximity to the crop. The role of grasslands is less conclusive, and in some cases, other crops, such as lucerne, may play a major role for biocontrol within neighbouring crops. At the landscape scale, proportion of non-crop vegetation had opposing results at different spatial scales and for different natural enemies. However, the research investigating landscape composition is scarce, particularly in relation to biological pest control. We conclude that non-crop vegetation in a good condition is critical for developing solutions for improving biological pest control and reducing risk of pest outbreaks, but more research is needed to understand the mechanisms and develop reliable recommendations.

Key words

biocontrol, landscape complexity, native vegetation, natural enemies, pest suppression.

INTRODUCTION

Biological pest control is estimated to provide 5–10 times higher control of pest insects compared to synthetic pesticides (Pimentel *et al.* 1992) and can save billions of dollars per year (Costanza *et al.* 1997; Losey & Vaughan 2006). However, loss of semi-natural habitats, such as grasslands and woodlands and homogenisation of landscapes due to agricultural intensification, has raised concerns about deterioration of biodiversity and biological pest control it provides (Foley *et al.* 2005, 2011). These concerns are likely to increase in the face of increasing need for agricultural products due to growing human population and wealth-driven changes to dietary preferences, together with increased side effects of insecticide applications (insecticide resistance, resurgence of secondary pests), market access issues, input costs and environmental degradation.

The majority of studies investigating effects of semi-natural habitats on pests and their natural enemies are conducted in the EU and the USA (Veres *et al.* 2013). These studies have demonstrated an important role of semi-natural habitats at field margins (Thomas & Marshall 1999; Landis *et al.* 2000; Marshall & Moonen 2002; Olson & Wäckers 2007) and in the landscapes surrounding crop fields (Thies & Tscharntke 1999; Gardiner *et al.* 2009; Gagic *et al.* 2011; Thies *et al.* 2011; Chaplin-Kramer

& Kremen 2012) for enhancing abundances and richness of various natural enemies of crop pests and increasing biological pest control. In a recent quantitative synthesis, landscape simplification due to reduction in semi-natural area was shown to reduce biological pest control in crops on average by 46% (Rusch *et al.* 2016). Semi-natural vegetation can affect biocontrol by providing alternative resources for natural enemies of pests (food, hibernation/over-wintering sites and shelter) and by disrupting the connectivity of agricultural areas that promote pests and delay pest arrival into crops (Landis *et al.* 2000; Tscharntke *et al.* 2005; Rusch *et al.* 2010; Chaplin-Kramer & Kremen 2012). However, it can also enhance pests (Gagic *et al.* 2011; Rusch *et al.* 2011a, 2011b; Plecas *et al.* 2014; Jankovic *et al.* 2017), although the evidence for the effects of non-crop area on crop pests is less compelling (Chaplin-Kramer *et al.* 2011; Veres *et al.* 2013).

Increasingly, similar information about the effects of non-crop habitats on pests and their natural enemies (hereafter referred to as ‘beneficials’) is being gathered in Australia in different production systems: vegetable (Stephens *et al.* 2006; Schellhorn *et al.* 2010; Costamagna *et al.* 2015), cotton/grain (Nash *et al.* 2008; Perovic 2009; Bianchi *et al.* 2013, 2015, 2017; Macfadyen *et al.* 2015a, 2015b; Parry *et al.* 2015; Heimoana *et al.* 2017) and viticulture (Thomson & Hoffmann 2009, 2010; Thomson *et al.* 2010). This review focuses on the field studies showing effects of type, quality, quantity and spatial

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arrangement of non-crop habitats (commonly referred to as 'native vegetation') within agricultural landscapes on pests and their natural enemies in Australia. We present findings from both, 'grey' literature and peer-reviewed publications, but give more weight to peer-reviewed studies when discussing results. We first give an overview of the history of agricultural landscape development in Australia and similarities and differences with the Northern Hemisphere. This is important if findings from international literature are to be considered within an Australian context and vice versa. Second, for semi-natural habitats to provide benefits to farmers, they need to support high abundances and/or diversity of natural enemies that then substantially colonise crop fields, reduce pest densities and thereby affect pesticide input costs, crop damage and yield (Bianchi *et al.* 2006). Thus, we ask (1) What habitat types and what characteristics of the non-crop habitats promote beneficials, but not pests in Australia? (2) What is the evidence for the movement of pests and their natural enemies between crop and non-crop habitats in Australia? (3) What is the evidence for the effect of non-crop habitats on abundance and diversity of Australian pests and beneficials within crop fields? and (4) What is the evidence for the effect of non-crop habitats on pest control within Australian crop fields, changes in insecticide use, crop damage and yield? Finally, we discuss similarities and differences between findings in Australian and international literature and suggest the ways forward. Although the landscape effects on pests and their natural enemies can depend on local, crop management practices (Tscharntke *et al.* 2005; Kleijn *et al.* 2011), the effects of crop management practices on Australian pests and beneficials is beyond the scope of this review.

History of agricultural landscape changes in Australia

Australia is a food and fibre exporting nation and uses 3% of the world's farmland area (Hamblin 2009); 32 out of 405 million hectares that Australia's agrifood industries currently utilise are used to grow crops (Barlow 2014). The landscapes started to be cleared for agriculture in 1800s (Lunt & Spooner 2005; Zalucki 2015), and since then, landscape fragmentation and homogenisation increased and farm management practices intensified (Australian State of the Environment Committee 2001; Maron & Fitzsimons 2007; Schellhorn *et al.* 2008, but see Lunt & Spooner 2005), as they did all over the world (Tscharntke *et al.* 2005). Semi-arid clay plains were converted to croplands, tropical rainforest to sugarcane monoculture, temperate forest to perennial pastures, heathlands on sand plains to wheat, canola and lupin fields (Williams 2001); 75% of Australia's native vegetation mainly in agricultural and urban areas has been cleared (13%) or disturbed and modified (62%), and only 25% remains intact (COAG Standing Council on Environment and Water 2012). Remaining native vegetation in agricultural landscapes is often not representative of natural habitats as it is fragmented and on the least productive land (Jellinek *et al.* 2013). In addition to vegetation clearance, changes to fire regimes, heavy grazing, exotic weed invasion, rabbit introductions, soil erosion and dryland salinity and the more recent increase in mining and mineral processing pose

additional pressure on Australian landscapes (Lunt & Spooner 2005; Tibbett *et al.* 2012, Sands 2018).

Arthropod community structure, composition and dynamics differ between Australia and Northern Hemisphere, although the same groups of natural enemies are important for biocontrol worldwide: *Hymenoptera* (ants and wasps), *Coleoptera* (carabid, coccinellid and staphylinid beetles), *Neuroptera* (lacewings), *Diptera* (syrphid and chamaemyiid flies), *Arachnida* (mites and spiders). For example, there are fewer species of carabids (Horne 2007), but phenomenal ant diversity in Australia (Andersen 2016). The pest complexes are also somewhat different and where in Northern Hemisphere some native pests are controlled, in Australia there is lack of natural enemies to control some of the exotic pests (Gu *et al.* 2007; De Barro & Coombs 2009). For example, when the silverleaf whitefly (*Bemisia tabaci* biotype B) was first detected in Australia in 1994 the existing, native parasitoid *Eretmocerus mundus* Mercet did not exert sufficient control with on average 3.4% parasitism (De Barro & Coombs 2009). In comparison, mean parasitism of a native silverleaf whitefly by this native parasitoid was more than three times higher. On the other hand, introduced species *Eretmocerus hayati* Zolnerowich & Rose exerted on average 24% parasitism on *B. tabaci* biotype B (De Barro & Coombs 2009). Further, climate and availability of resources affect arthropod temporal dynamics. While in temperate regions arthropods go through overwintering periods, in Australia they migrate, aestivate or enter diapause during long periods of hot and dry weather (Waterhouse & Sands 2001; Furlong *et al.* 2013). Availability of crops in the landscapes throughout the year in some parts of Australia allows pests and their natural enemies a continuous access to resources, and this may change the role of semi-natural area in comparison to temperate regions (Schellhorn *et al.* 2014, 2015b; Zalucki 2015). Finally, local habitat characteristics differ, particularly with respect to structural complexity and disturbance regimes. Woody vegetation in Australian agricultural landscapes is dominated by eucalypt trees in the over-story with more open canopy and less diverse mid- and under-story (dominated by acacia and grasses), often under stronger grazing pressure compared to the Northern Hemisphere (Thomson *et al.* 2010; COAG Standing Council on Environment and Water 2012). Farming in Australia is adjusted to ancient, flat, often shallow, poorly fertile, saline soils that occur in a mostly dry and variable climate (Williams & Saunders 2002). Given the differences in arthropod communities, climate, landscapes and farming practices between Australia and the rest of the world, patterns found in international literature cannot be easily translated to Australian conditions without testing.

The large area of Australia, covering different climate and biogeographic regions, resulted in somewhat different regionally specific patterns in agricultural development and management as well as in arthropod communities. For example, Schellhorn (2007) identified 19 vegetable pests unique to Queensland out of 39 found in that area, and 10 unique out of 30 found in South Australia. South-east Australia with the centre in Victoria is under particularly high environmental stress (NLWRA 2001). This region grows a substantial proportion of Australian grain, but it is also one of the most ecologically degraded with less than 5% of

remnant vegetation cover (NLWRA 2001). Crops replaced pastures that are now small, grazed, nutrient enriched and dominated by exotic annual species (Duncan & Dorrough 2009). Regeneration of ageing remnant eucalyptus remains feasible in the absence of livestock grazing, but the window of opportunity is decreasing quickly (Vesk & Mac Nally 2006; Dorrough & Moxham 2005). The Australian federal government has committed to reversing decline in native vegetation and to increasing the connectivity of fragmented landscapes (COAG Standing Council on Environment and Water 2012), but this is often challenging. In Western Australia, most farmers don't commit more than 10% of farm area to remnants and revegetation (Smith 2008) and even 10% is suggested to be an ambitious target for landowners whose primary source of income is on-farm (Jellinek *et al.* 2013). However, there is increasing recognition in Australia that native vegetation is not something to be cleared, but also has intrinsic value and can help ecosystem resilience in the context of multiple uncertainties, such as climate change (Reid *et al.* 2003; COAG Standing Council on Environment and Water 2012).

What habitat types and what characteristics of the non-crop habitats promote beneficials, but not pests in Australia?

Native plants within non-crop habitats in Australia have been repeatedly shown to have low occurrence of pests and high occurrence of their natural enemies, while exotic weeds and crops harbour more pests. For example, three exotic thrips species (Schellhorn *et al.* 2010) and the virus they transfer (TSWV, tomato spotted wilt virus, which is known to cause economic loss to *Solanaceae* vegetables, Latham & Jones 1997) were shown to be uncommon in native plants. On the other side, 16 out of 45 exotic weeds harboured this disease (Latham & Jones 1997). Brassicaceous weeds can harbour significantly higher abundances of the main vector of TSWV, Western Flower Thrips (*Frankliniella occidentalis* Pergande) compared to native plants (Schellhorn *et al.* 2010). These weeds can also support other pests, such as cabbage aphids (*Brevicoryne brassicae* L.), diamondback moth (*Plutella xylostella* L.) and Rutherglen bugs (*Nysius vinitor* Bergroth) (Gu *et al.* 2007; Furlong *et al.* 2008; Severtson *et al.* 2015). Exotic grasses along roadsides (particularly green panic, *Panicum maximum* Jacq.), harboured jassids (*Cicadulina bimaculata* Evans) that are pests in sweet corn, beans and other vegetable crops (Schellhorn 2006). Presence of thistles (*Onopordum acanthium* L.) in autumn is argued to affect an increase in slug populations (Nash *et al.* 2007). In a comprehensive study across Australia, Parry *et al.* (2015) showed that 75% of the surveyed exotic weed species hosted more pests than predators, while native plants supported lowest pest density and more predators than pests (see also Bianchi *et al.* 2013). Wood *et al.* (2010) demonstrated a benefit of native saltbushes as reservoirs of agromyzid leafminer parasitoids on horticultural farms, while this native plant is unlikely to support vegetable pests (Schellhorn *et al.* 2010).

Higher abundances of pests on Australian crops and weeds in comparison to native plants is at least partly due to their higher reproduction on these plants (Bianchi *et al.* 2013). Destruction

of weeds at field margins, such as capeweed (*Arctotheca calendula* L.) and thistle, is argued to reduce redlegged earth mite (*Halotydeus destructor* (Tucker)) abundances in canola because of the lack of pest breeding sites (Gu *et al.* 2007). The role of weeds, crops and native plants for the reproduction of beneficials is less clear (e.g. Bianchi *et al.* 2013), and the density of juvenile predators was found to be the highest in Australian pastures (Parry *et al.* 2015). Herbaceous plants in grassy areas, including exotic species, can be useful in providing nectar and pollen to beneficial insects, especially hoverflies and parasitic wasps (Gámez-Virués *et al.* 2009, Lu *et al.* 2014) and can be an important parasitoid (*Trichogrammatidae*, *Scelionidae* and *Eulophidae*) reservoir (Stephens *et al.* 2006). Thus, although weeds appear to promote pests, and relatively more so than native plants, they do not necessarily negatively affect beneficials (see for example Tsitsilas *et al.* 2006), but the effect of weediness at the habitat level on populations of pests and beneficials requires further investigation. For example, it remains unclear whether removing weeds from semi-natural habitats would result in lower pest abundances due to the reduced reproduction rates and higher predator-prey ratio, or in higher use of native plants by polyphagous pests.

Other characteristics of non-crop habitats, such as structural complexity, diversity and disturbance, can affect abundance and diversity of arthropods. Semi-natural areas in Australia vary from complex with under-story (mainly grasses), mid-story (small trees, shrubs) and over-story (trees), to simplified ecosystems without under- and/or mid-story. Beneficial Hymenoptera were found to increase with increased availability of floral resources, grass height, ground cover (Gámez-Virués *et al.* 2009; Smith *et al.* 2015b) and high habitat structural complexity in shelterbelts (tree canopy, shrub and ground herb cover), presumably owing to more potential microhabitat niches, shelters and hosts (Lassau & Hochuli 2005). Tsitsilas *et al.* (2006) observed that numbers of pest mites and lucerne fleas are lower, while predatory mites and spiders were higher in shelterbelts compared to pastures, especially so when shelterbelts carried a groundcover with high grass. This was confirmed in experimental study with ground cover manipulation where reduced height and cover of vegetation decreased predatory mites, beetles and spiders within windbreaks (Tsitsilas *et al.* 2011; see also Ridsdill-Smith *et al.* 2008). However, vegetation structure (number of trees and shrubs, canopy cover) had no effect on coccinellids in shelterbelts (Smith *et al.* 2015a). Species composition of the remnant grassland, vegetation height and percentage cover did not affect carabid predator abundance (Nash *et al.* 2008) and complex shelterbelts were associated with increased herbivory of *Eucalyptus blakelyi* Maiden saplings (Gurr 2009).

The most common disturbance factor affecting non-crop habitats in Australia is grazing (Sherren *et al.* 2012). Grazing favours exotic annual plants and prevents regeneration by native species through frequent disturbance and increased soil nutrients (Duncan & Dorrough 2009). Grazing intensity was shown to negatively affect spider (Churchill & Ludwig 2004) and ant assemblages (Woinarski *et al.* 2002) and can affect Mesostigmatid mites (an arthropod order of mites that are primarily predatory)

through its effect on litter accumulation, soil organic matter and microclimate (Beaulieu & Weeks 2007).

Although non-crop vegetation is commonly considered the major source of natural enemies of crop pests, crop fields can also be important sources of beneficials. Generalist predators were repeatedly shown to have higher abundances in lucerne fields in comparison to other crop or non-crop habitats, especially in spring (Gurr *et al.* 1998; Schellhorn & Silberbauer 2002; Pearce & Zalucki 2006) and to decline with increasing distance from lucerne (Mensah 1999; Pearce & Zalucki 2006; Costamagna *et al.* 2015). In summer, sorghum fields in Australia appear to be important for harbouring high abundances of generalist predators (Schellhorn & Silberbauer 2002).

What is the evidence for the movement of pests and their natural enemies between crop and non-crop habitats in Australia?

Landscape patterns of habitat selection do not necessarily represent fine-scale habitat use and movement dynamics (Turner *et al.* 2015). Although natural enemies of pests may be abundant in semi-natural vegetation surrounding crop fields, the stark contrast between crop and non-crop vegetation may limit movement of some species into a crop or the movement may not be sufficient to suppress pests within crop (Pearce & Zalucki 2005; Schellhorn *et al.* 2014; Macfadyen *et al.* 2015a). Ultimately, the goal of agroecology is to design agricultural landscapes that will not only reduce resources for pests and enhance natural enemy populations but also facilitate sufficient movement of beneficials into crops. In Australia, a number of generalist predators were shown to move between non-crop and crop area (Table 1). For example, predators were shown to move from shelterbelts to cotton fields (Perovic *et al.* 2011) and between non-crop area and brassica crops (Heimoana *et al.* 2017). Schellhorn *et al.* (2008) showed that there is immigration of insect predators from native vegetation (particularly riparian remnants) to crop, but also of some pests, such as jassids that use exotic grasses common in remnant edges (Schellhorn 2006). Macfadyen and Muller (2013) found frequent movement of aphids and their parasitoids from native vegetation into the canola crop, while parasitoids of caterpillars and predators moved more between cereals and canola. Predators move more often from native vegetation into cereal crops than vice versa irrespective of crop phenology, while pests and parasitoids exhibited similar movement patterns from native vegetation into crops only at early stages, i.e. after crop emergence (Macfadyen *et al.* 2015a). Bianchi *et al.* (2017) showed that ballooning spider immigration into crops is a continuous process influenced by meteorological variables and the population size in the surrounding landscape (supporting 'mass action hypothesis') with both crop and non-crop habitats being important for recruitment of ballooning spiders (see also Pearce *et al.* 2005). Crop management practices, such as mowing and harvesting of lucerne increase production of highly dispersive, alate aphids (Milne & Bishop 1987) and stimulate pest and predator movement between crop fields (Hossain *et al.* 2002; Farrell *et al.* 2008).

What is the evidence for the effect of non-crop habitats on abundance and diversity of Australian pests and beneficials within crop fields?

High species abundance and richness in non-crop vegetation, in combination with evidence that the same species move into crop fields, can provide circumstantial support that non-crop habitats increase natural enemies and thereby biocontrol within crop fields (Bianchi *et al.* 2015). More direct and robust evidence comes from studies that investigate the role of non-crop area as a source of pests and beneficials within crops and test the relationship between within-crop arthropod diversity and non-crop vegetation at field margins (Table 1) and within surrounding landscapes (Table 2).

Field margin effects

Semi-natural areas at field margins have been shown to enhance abundances and/or richness of beneficials within various crops and pastures in Australia: shelterbelts had benefits to pastures (Tsitsilas *et al.* 2006, 2011) and cotton fields (Rencken 2007; Perovic 2009), remnant native grassland to canola (Nash *et al.* 2008), woody vegetation (but not pastures) to vineyards (Thomson & Hoffmann 2009, 2010, 2013), windbreaks to citrus (Smith & Papacek 1991) and riparian/pasture/bush vegetation to brassica crops (Heimoana *et al.* 2017). More specifically, adjacent woody vegetation (shelterbelts and/or remnant woodland) is shown to increase abundance of generalist predators and parasitoids in cotton (Perovic 2009) and of smaller, but not larger, more dispersive parasitoids and ladybirds in vineyards (Thomson & Hoffmann 2009, 2010, 2013). *Eucalyptus torelliana* F. Muell. windbreaks enhanced Australian phytoseiid mites, *Amblyseius victoriensis* Womersley, in citrus orchards (Smith & Papacek 1991). Thus, woody vegetation at field margins appears to be the most commonly demonstrated source of beneficials within multiple crops in Australia. However, woody vegetation can harbour pests, such as *Australiodillo bifrons* (Budde-Lund) (the flood bug, Paoletti *et al.* 2008) and greyback canegrub *Dermolepida albohirtum* (Waterhouse) (Zellner *et al.* 2014). Trees and shrubs (Alexander, Livistona, Coconut palms, Wattles, Eucalyptus) bordering sugarcane fields (up to 154 m away) were argued to play a major role in canegrub infestation (Zellner *et al.* 2014). The benefit of adjacent grasslands is less clear. Adjacent remnant grassland was shown to increase predatory beetle *Notonomus gravis* (Chaudoir) in canola (Nash *et al.* 2008), but parasitoids in vineyards did not benefit from adjacent pastures (Thomson & Hoffmann 2009). Demonstrated benefit of grasslands mainly to annual crops and woodlands to both annual and perennial systems can be related to differences in habitat specialisation (grassland species do not utilise woody crops), or to system productivity; perennial crops support more natural enemies compared to grasslands (e.g. Jankovic *et al.* 2017); but this remains to be investigated.

Landscape composition and configuration effects

Landscape ecology explicitly addresses the importance of spatial patterns for ecological processes, and it is concerned with how

Table 1 List of manuscripts investigating arthropod pests, their natural enemies and biocontrol within crops and in relationship to the neighbouring non-crop habitat type, proximity of non-crop habitat to the target crop, distance from the crop edge with non-crop margin into crop field (edge effect; investigated distance ranges given in parentheses) and spill-over between crop and non-crop habitats

Sampled habitat	Response	Explanatory variable	Result	References
Experimental potato plots	Pest moth abundance Parasitism rates Crop damage	Proximity of flowering plants (coriander and faba bean, 1–16 m)	Proximity of flowering plants increased parasitism, pest abundances and crop damage	Baggen and Gurr (1998)
Sentinel cotton plants	Parasitism of whiteflies	Proximity to woody remnants (0–>400 m)	Proximity to woody remnant vegetation increased parasitism that was the highest in remnants	Bianchi <i>et al.</i> (2015)
Sentinel cotton plants	Spider abundance	Proximity to woody remnants (0–>400 m)	Proximity to remnant vegetation inconclusive. The highest spider density in remnant vegetation in one and in arable fields in another region.	Bianchi <i>et al.</i> (2017)
Vineyards	Spider abundance	Adjacent vegetation type: woody vegetation vs. pasture	Adjacent pastures increases abundances of some spiders (Lycosidae, Salticidae), while Linyphiidae were more abundant with adjacent woody vegetation.	D'Alberto <i>et al.</i> (2012)
Brassica fields and adjacent non-crop	<i>Hippodamia variegata</i> and <i>Micromus tasmaniae</i>	A mark-recapture trial from non-crop into brassica crop and recolonization after insecticide application (0–100 m into crop)	No effect of the type of non-crop vegetation (riparian/pasture/bush) on the numbers of marked or the total numbers of predators within crops. Predators decreased with distance from field margin. Predators increased over time after spraying and their abundances were higher when brassica field was adjacent to the non-crop vegetation, rather than to a brassica crop.	Heimoana <i>et al.</i> (2017)
Canola/NV, canola/cereal and canola/canola ecotone	Grain pests, predators and parasitoids abundances and community composition	Ecotone type	Source area for pests and parasitoids were cereals early in the season and NV late in the season. Parasitoids moved more commonly out of cereal and out of NV into canola than vice versa, and higher than the control. Predators moved less commonly from NV and more often between cereals and canola.	Macfadyen and Muller (2013)
NV/crop (cereal) and control crop/crop ecotone	Grain pests, predators and parasitoids abundances and community composition	Ecotone type	After crop emergence pest and parasitoids moved from NV to crop, but later in the season they moved more across control (crop/crop) interface. Predators consistently moved more often from NV into crops than vice versa.	Macfadyen <i>et al.</i> (2015a)
Cereal fields and adjacent remnant roadside grassland	Carabid beetle abundances and community composition	Edge effect (0–200 m) Field margin quality (burning, grazing, vegetation cover, height and species composition)	Greater abundance of the carabid <i>Notonomus gravis</i> at field edges and in remnant grasslands, with a reduction in populations as the distance increased into the field. Predator communities from field and roadside were associated. No association with field margin quality.	Nash <i>et al.</i> (2008)
Cotton field and shelterbelt	2 predator species abundances	A mark-recapture trial from shelterbelt into cotton field (0–320 m)	0.76% of <i>Oxyopes</i> spp. (Araneae:Oxyopidae) juveniles and 10.46% of <i>Dicranolaius bellulus</i> (Coleoptera: Melyridae) collected from cotton were marked with rubidium	Perovic <i>et al.</i> (2011)
Cotton field and shelterbelt	2 parasitoid species abundances	Spatial distribution of parasitoids within cotton and shelterbelt	Vegetation preference and spill-over between native vegetation and cotton fields highly variable	Perović and Gurr (2012)
Vineyard	Multiple predators and parasitoid abundances	Spatial distribution and associations with adjacent vegetation type: remnant native forests, shelterbelts, or pasture	Positive influence of adjacent wooded vegetation on Staphylinids, predatory thrips, and hymenopteran spiders, ladybird beetles and hymenopteran	Thomson and Hoffmann (2009)

(Continues)

Table 1 (Continued)

Sampled habitat	Response	Explanatory variable	Result	References
Vineyard	Pest moth egg predation and parasitism		parasitoids. Pasture edges had no effect or a negative effect on numbers of natural enemies. Parasitism, by <i>Trichogramma</i> but not predation was higher adjacent to remnant vegetation.	Thomson <i>et al.</i> (2010a)
	Multiple predators and parasitoid abundances Pest moth egg predation	Adjacent vegetation type: remnant native forests, planted woody margin, no vegetation	There was an increase in abundance of smaller natural enemies when woody vegetation was present, whereas larger potentially more mobile groups were not affected. Egg predation was higher when adjacent vegetation was present in comparison to no vegetation. Small parasitoids and 3 species of ladybird beetles exhibited aggregation close to the woody vegetation. Predation and parasitism were higher in vine rows closer to the woody vegetation and significantly associated with several parasitoid and ladybird beetles. The beetles moved across crop interfaces into the peanuts in one out of 2 sampling years but only up to 80 m.	
Vineyard	Multiple predators and parasitoid abundances	Spatial distribution and associations with adjacent woody vegetation		Thomson and Hoffman (2013)
Peanut/maize	Scarabeid beetle abundance	Movement across crop interfaces (20–440 m)		Ward and Rogers (2006)

Only peer-reviewed articles published before June 2017 are included (see the main text for additional findings from the grey literature). Due to perennial nature of pastures and that they can be sown or native, they were considered as non-crop area in this review. 'NV' means native vegetation.

much there is of a particular component (landscape composition) and how is it arranged (landscape configuration) (Turner *et al.* 2015). In Australia, the importance of landscape composition (commonly calculated as percentage of semi-natural or arable area and referred to as 'landscape complexity') for pests and their natural enemies within crop fields is inconclusive. Costamagna *et al.* (2015) did not find the expected positive effect of non-crop area in the landscapes on aphid natural enemies. D'Alberto *et al.* (2012) found only weak relationships between woodland area in the landscapes and spider abundances in vineyards. Woody vegetation at the landscape scale had lower effect on parasitoids in vineyards compared to the effect of field margins (Thomson & Hoffmann 2009; Thomson *et al.* 2010). On the other hand, woody vegetation in the landscape was shown to benefit some natural enemies, such as *Eulophidae* parasitoids in vineyards (Thomson *et al.* 2010) and important generalist predators (spiders, *Oxyopes* spp. and red and blue beetle, *Dicronolaius bellulus* Boiduval (Coleoptera: Melyridae)) in cotton (Perovic 2009). Some natural enemies of pests can also benefit from certain crops in the landscape, as shown for egg parasitoids (*Trichogramma* spp.) that benefited from increased cotton area (Perovic 2009). Herbivore taxa showed weak response to proportional area of different habitats and the vegetable leafhopper *Austroasca viridigrisea* Paoli, considered a minor cotton pest, increased with grassland area (Perovic *et al.* 2010).

The effects of landscape configuration on pests and beneficials have rarely been studied in Australia (but see Macfadyen *et al.* 2015b). Landscape structural connectivity is related to the habitat proportion in a landscape and its spatial arrangement (Turner *et al.* 2015), and it is recently emphasised as an additional, important predictor of grain pests and beneficials (Macfadyen *et al.* 2015b) and of red and blue beetle (*D. bellulus*) in cotton fields (Perovic 2009).

What is the evidence for the effect of non-crop habitats on pest control within Australian crop fields, changes in insecticide use, crop damage and yield?

Changes in colonisation time and frequency of crop fields by pests and beneficials is one way to measure benefits of the surrounding non-crop habitats. However, increased abundances and/or diversity of natural enemies of pests within crop field do not necessarily correlate with reduced pest numbers and yield (Jonsson *et al.* 2017). For example, Gagic *et al.* (2011) showed that parasitism rate of aphids increased with landscape complexity in Germany, although parasitoid species richness remained unchanged. To demonstrate benefits to farmers, measures such as increased pest suppression (reduction in pest numbers related to an experimental treatment), pest control (reduction in pest numbers below economic injury levels, see Chaplin-Kramer *et al.* 2013; Schellhorn *et al.* 2015a) and crop yield and reduced crop damage and insecticide spraying are needed.

In Australia, studies of the effects of field margins and surrounding landscapes on pest suppression within crop fields are limited, and the subsequent effect on crop management decisions, crop damage and yield is rarely tested (Table 1 and 2). Nevertheless, there is emerging evidence that proximity of

Table 2 List of manuscripts investigating arthropod pests, their natural enemies and biocontrol within crop and non-crop habitats and in relationship to landscape composition and configuration

Sampled habitat	Response	Landscape metrics	Result	References
Sentinel cotton plants	Parasitism of whiteflies	Proportion woody remnants Proportion grassland	% remnants at <1 km increased and at 1–1.5 km decreased parasitism. % grassland at 0.1–0.5 km decreased parasitism.	Bianchi <i>et al.</i> (2015)
Sentinel cotton plants	Spider abundance	Proportion NV Proportion crop Spider load within landscapes	At 2 km spider immigration increased with higher spider loads in crops and remnant vegetation. At scales >0.5 km spider load models had more support in comparison to the land-use models.	Bianchi <i>et al.</i> (2017)
Sentinel melon plants	Aphid abundances Multiple predator abundances Aphid survival	Proportion NV Percent riparian vegetation Proportion grassland Proportion alfalfa Proportion other crops Proportion cucurbits Habitat evenness Habitat diversity PCA of % woody vegetation across 11 spatial scales PCA of % pasture across 11 scales (95 m–3 km radius) 21 landscape metrics	Aphid survival decreased with % alfalfa and increased with % grassland and % NV at various spatial scales (1–2 km). Predator abundance increase with % other crops and % alfalfa at 0.5 km	Costamagna <i>et al.</i> (2015)
Vineyards	Spider abundance		Weak relationships: 3 out of 46 comparisons for PCA axes including % woody vegetation were significant. No comparisons significant for PCA axes including % pasture.	D'Albeto <i>et al.</i> (2012)
47 plant species in pasture, NV, crops	Multiple pest abundance Multiple natural enemy abundances	Proportion NV	Important landscape metrics differ across landscapes and years	Macfadyen <i>et al.</i> (2015b)
47 plant species in pasture, NV, crops	Multiple pest abundance Multiple natural enemy abundances Multiple herbivore abundances Multiple natural enemy abundances	Proportion NV Proportion grasses Proportion woody area Proportion cotton Connectivity (cost-distance)	No effect % woody area at 0.12 km increased abundances of <i>Oxyopes</i> spp; % cotton at 0.75 m increased abundances of <i>Trichogramma</i> spp; % grasses at 3 km increased the density of <i>A. viridigriseae</i> . Thripidae and <i>O. orientalis</i> were n.s. <i>Dicranolatus bellulus</i> was the only species for which the addition of cost–distance metrics improved models after the inclusion of the proportional-area data	Parry <i>et al.</i> (2015) Perovic <i>et al.</i> (2010)
Vineyard	Multiple natural enemy abundances	Area of woody vegetation PCA of woody vegetation at 11 scales (0.095–3 km)	Weak relationships: 56 of 330 comparisons for area of woody vegetation were significant (28 positive and 28 negative); 8 out of 75 comparisons for PCA axes were significant	Thomson <i>et al.</i> (2010b)

Only peer-reviewed articles published before June 2017 are included. 'NV' means native vegetation.

non-crop vegetation increases pest suppression, particularly parasitism of crop pests. Adjacent woody vegetation increased egg parasitism of the light brown apple moth *Epiphyas postvittana* Walker in vineyards, while egg predation was either not affected (Thomson & Hoffmann 2009) or increased (Thomson & Hoffmann 2010, 2013). Similarly, proximity of non-crop vegetation (flower strips) increased parasitism rates of potato moth, *Phthorimaea operculella* Zeller (Baggen & Gurr 1998) and proximity of remnant woody vegetation increased the number of parasitised silver-leaf whiteflies (per unit of time) within arable fields (Bianchi *et al.* 2015). Adjacent native vegetation was also shown to be positively related to increased cashew yield presumably due to the increase in beneficials, especially the green ant *Oecophylla smaragdina* (Peng *et al.* 1998). The mechanistic relationship between the green ant and cashew yield has not been directly examined, but the trees in which this ant species was present produced more good quality nuts and greater yield, compared to the trees without the ant (Peng *et al.* 1998). Although adjacent non-crop vegetation generally shows positive effects on pest suppression within crop fields, adjacent flower strips were shown to be positively related to pest populations and potato crop damage (Baggen & Gurr 1998).

At the landscape level (Table 2), two studies have recently investigated the effects of landscape composition on pest suppression within Australian crop fields. The proportion of semi-natural vegetation (grasslands and native woodlands) within surrounding landscapes did not show expected positive effect on suppression of aphids on melon (Costamagna *et al.* 2015) and had contrasting effects on the number of parasitised silver-leaf whiteflies when different spatial scales were investigated (Bianchi *et al.* 2015). Instead, the percentage of lucerne within 1.5 km of the focal fields was shown to be better predictor of reduction of aphid numbers on melon plants than semi-natural area (Costamagna *et al.* 2015).

DISCUSSION

Studies investigating plant–arthropod relationships in Australia repeatedly showed that weeds are associated with crop pest abundances and reproduction, as well as crop diseases transferred by pests, although they might benefit some natural enemies (Stephens *et al.* 2006; Schellhorn *et al.* 2010; Parry *et al.* 2015). Pests, weeds and crops (with exception of some native bushfood known as ‘bush tucker’ and macadamia) are generally exotic species in Australia, while much of Australia’s native flora is in plant families unrelated to agricultural crops (Schellhorn *et al.* 2009). Thus, it is of no surprise that most native plants in Australia are shown to support mostly native beneficials, while exotic pests are supported by exotic weeds. Enhancing native predators in Australia by maintenance and revegetation of native plants is crucial for conservation biological control because majority of predators that attack crop pests are native (Sands 2018).

Within semi-natural habitats, structurally complex woody vegetation in good condition (not grazed, with abundant floral resources, tall grasses and dense ground cover) appears to support the highest abundances of beneficials. Good quality ground

cover can also be important for tree crops, as found in Australian citrus plantations, where dense ground cover enhanced predatory mites and reduced thrips damage (Smith & Papacek 1991; Colloff *et al.* 2013). In comparison to woodlands, Australian grasslands appear to support less, but different species of natural enemies (D’Alberto *et al.* 2012; House *et al.* 2012) and they can be important for predator reproduction (Parry *et al.* 2015). Further, studies investigating pest suppression within crop fields showed that field margins and (mainly woody) non-crop habitats in close proximity to crops increased parasitism rates and abundances of several predators within crops. However, this was not always the case (Bianchi *et al.* 2017) and the direction of the arthropod movement between crop and non-crop area can change throughout the season (Macfadyen & Muller 2013). Temporal changes in resource availability due to crop phenology and crop-management disturbances may affect direction and timing of arthropod movement, and these changes are likely to be more pronounced in annual compared to perennial cropping systems.

Landscape complexity (increased proportion of semi-natural area) is generally accepted to enhance natural enemies of pests (Bianchi *et al.* 2006; Chaplin-Kramer *et al.* 2011; Veres *et al.* 2013; Rusch *et al.* 2016), but there is no strong support for this hypothesis in Australia and studies reported negative, positive and neutral results; but see Lindenmayer *et al.* (2003) for the landscape effects on Australian plantation forests. Recently, Tschamntke *et al.* (2016) identified several hypotheses when semi-natural habitats in the landscapes can fail to support biocontrol in crops, some of which might be relevant for the Australian context: (1) Semi-natural area may not be necessary (in Australia continuous cropping throughout a year in some areas may provide enough resources for some natural enemies; crops such as lucerne may be more important in some cases, Costamagna *et al.* 2015); (2) Semi-natural area may not be sufficient for successful biocontrol in terms of amount, proximity, composition or configuration. For example, there is less than 22% reported native vegetation in Bianchi *et al.* (2015, 2017), Macfadyen *et al.* (2015b) and Parry *et al.* (2015), and all these landscapes can be considered ‘simple’ sensu Tschamntke *et al.* (2005). Lower percentage of non-crop area is typically related to greater distances between crop and non-crop area (Turner *et al.* 2015). Further, Australian forests in agricultural areas are often open, intensively grazed, with poor complexity (Thomson *et al.* 2010), while crop fields are generally larger compared to Europe (Schellhorn *et al.* 2008; Thomson *et al.* 2010); (3) Semi-natural area can be a greater source of pests than natural enemies (some Australian pests were shown to increase in crop fields with increased proportion of grassland area, Perovic *et al.* 2010, but the effect of non-crop area on the majority of pests and beneficials requires further investigation); (4) Agricultural practices can disrupt biocontrol, e.g. possible herbicide and pesticide drift to native vegetation due to use of aerial applications of insecticide in Australia, a practice that is highly restricted or prohibited in many countries including EU (Directive 2009/128/EC, October 2009); and finally, (5) Pests might not have effective natural enemies in the region; many of the agricultural pests are exotic, while most

predators are native (see e.g. De Barro & Coombs 2009, Sands 2018). Although there are several studies that point to the direction of some of these hypotheses, explicit testing of these hypotheses remains a challenge in Australia and worldwide.

At present, it would have been premature to make general conclusions about the effects of landscape composition on Australian pests and beneficials due to a low number of peer reviewed studies (eight peer-reviewed studies using five or six independent set of sampling sites out of which only two measured biocontrol, Table 2), exploratory nature or low power in some studies (low replication at the landscape scale) and differences in spatial scales tested among studies (from a few hundred meters up to 14 km diameter). The issue of testing only large spatial scales (several kilometres) is of a particular importance if the dominant predators are poor dispersers. For example, ants are shown to be important predators in cashew fields (Peng *et al.* 1998), mango orchards (Peng & Christian 2005) and in african mahogany *Khaya senegalensis* (Desr.) plantings in Australia (Peng *et al.* 2011), but ants generally respond to local habitat characteristics and to small landscape scales of few hundred meters (De la Mora *et al.* 2013, 2015; Campbell & Crist 2017). Thus, for testing landscape effects on biocontrol of the target pest, the most effective natural enemies as well as their dispersal range need to be evaluated.

The most effective natural enemies and the link between predator community (species/trait identity and diversity effects) and pest suppression within most Australian crops requires further investigation (but see e.g. Mansfield *et al.* 2003; Hosseini *et al.* 2012), particularly so in tropical areas. A few studies investigated biodiversity-ecosystem functioning relationship in tropical ecosystems, and it is unclear whether this relationship follows the same shaped saturation curve as in temperate regions (Clarke *et al.* 2017). First, the saturating point (adding species has no effect on ecosystem functioning) can be higher in tropical compared to temperate systems due to higher specialisation and therefore tighter niche packing in the tropics (Clarke *et al.* 2017). Second, even if the shape of biodiversity-ecosystem functioning curve is the same in the tropics and temperate regions, high species richness in the tropics may be above the saturating point and a small species loss may not affect ecosystem functioning (Clarke *et al.* 2017). Evaluating these hypotheses is important to understand vulnerability of ecosystems, including crop fields to loss of beneficial species.

There is emerging evidence that spatio-temporal distribution of crops together with semi-natural area in the landscapes is important for biological pest control (Schellhorn *et al.* 2015b). For example, perennial crops such as lucerne are shown to support beneficials (e.g. Costamagna *et al.* 2015; Jankovic *et al.* 2017), although some other crops, such as sorghum, might be important at different times of a year (Schellhorn & Silberbauer 2002). Lucerne provides a relatively low risk (in terms of supporting crop pests) and easily managed habitat where movement of the beneficials to the target crop can be encouraged by applying attractant within crop or by cutting the lucerne (Gurr *et al.* 1998). However, the best planting/harvesting management cycle in relation to the target crop needs to be investigated. Additionally, harvesting lucerne for hay can partly offset the loss of land taken out of

primary crop production, but the profit from pasture legumes is well below that of annual crops which may remain an important barrier to their adoption (Williams & Gascoigne 2003).

Future directions

Semi-natural area surrounding crop fields appear to be crucial for sustaining populations of natural enemies in Australia and worldwide. Given the strength of the evidence that exotic weeds in Australia support pests and native plants support beneficials, investment in management of weeds and enhancement of native plants within semi-natural areas and particularly so within woody field margins appears essential for sustainable pest management. However, there is a clear need for more research and we propose several future research directions that can help decision making:

- 1 Moving beyond measuring species abundances to measuring impact of beneficials (Furlong & Zalucki 2010; Macfadyen *et al.* 2015c). This is because pest abundances can be influenced by factors other than natural enemies and high abundances of natural enemies do not necessarily translate to higher biocontrol. The impact can be evidenced through increased predation/parasitism, reduced pest abundances/survival (see Birkhofer *et al.* 2017 for an overview of field methods) and linked to pest control decision making (e.g. how long pest populations stay below Economic Thresholds, Schellhorn *et al.* 2015a, or timing and consistency of predation, Macfadyen *et al.* 2015c). Plant damage and yield are highly valuable metrics to farmers, but depend on inputs from both humans and ecosystems and partitioning of these two contributing factors can be challenging (but see Gagic *et al.* 2017).
- 2 Identifying what habitat, in what condition, where and how much should be planted/maintained for successful short-term pest control and long-term resilience to disturbances and climate events. Both spatial and temporal dimensions of distribution of species and their resources need to be better understood in Australia and worldwide to identify resource requirements, as well as resource bottlenecks and interruptions limiting key beneficials (Schellhorn *et al.* 2015b). This would allow more targeted management interventions by identifying for example the context within which investing in particular field margins produces the highest return or when is a larger landscape area covered by particular semi-natural habitats necessary for achieving desired goals (e.g. support of less common species, higher ecosystem services). Plant phenology and spatio-temporal availability of resources within surrounding habitats, as well as life cycle requirements of the target organisms need to be considered to better understand functional importance of various habitats.
- 3 Moving beyond measuring individual species and functions to fully integrated ecosystem service management. Semi-natural area can affect multiple pests, weeds and diseases within a crop field and enhance other beneficial organisms, such as birds, bats and pollinators (e.g. Gurr 2009) that can non-additively affect crop yield (Bartomeus *et al.* 2015; Gagic *et al.* 2016; Kleijn *et al.* 2017). To better understand the net

effect of semi-natural area, these multiple ecosystem services and disservices need to be investigated simultaneously.

Although reviewed ecological studies have largely improved our knowledge about how to enhance biological pest control in Australia through utilising non-crop habitats, much remains to be done. Until then, the only reliable option for future sustainable land use is minimising pest-related risks through maximising biodiversity within highly diverse agroecosystems (Tschamtké *et al.* 2005).

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