Woodland habitat structures are affected by both agricultural land management and abiotic conditions.

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Date of manuscript draft: 23 October 2018

Manuscript word count: 6449

Abstract

Context. The identification of habitat structures with biologically meaningful links to habitat quality has enabled an increased understanding of wildlife distributions in fragmented landscapes. However, knowledge is lacking of where these structures occur in the landscape.

5 Objectives. For a broad-scale agricultural landscape, we investigated how the occurrence and abundance of wildlife habitat structures is related to abiotic conditions and land management practices, and whether this differed between old growth and regrowth woodland.

Methods. We used generalised linear mixed models to investigate the distribution of eight habitat structures in the South-West Slopes bioregion of south-eastern Australia.

10 Results. Only one habitat structure, canopy depth, was related to abiotic conditions alone, whereas only leaf litter cover was related to land management practices only. Each of the other structures (abundance of logs, large trees, hollow-bearing trees, mid-sized trees and dead trees, and amount of native grass cover) was related to a combination and/or interaction of abiotic conditions and land management practices. Old growth woodland had higher log,
15 large tree and hollow-bearing tree abundance, whereas regrowth woodland had higher mid-sized tree and dead tree abundance.

Conclusions. Our findings inform key management prescriptions that can be used to improve conservation efforts so they have strong, quantifiable effects on wildlife habitat in temperate agricultural landscapes. Our case study shows that by understanding how management
20 actions in specific abiotic conditions lead to the increased occurrence or abundance of particular habitat structures, management can be spatially targeted to alternative conservation strategies relevant to the landscape of interest.

Keywords

25 Agricultural intensification; Conservation; Habitat fragmentation; Habitat loss; Habitat structure; Patch quality; Woodland vegetation; Ecosystem restoration; South-West Slopes; Australia

30 Introduction

A major focus of applied research in fragmented agricultural landscapes is the identification of habitat structures important for the persistence of native wildlife (Miller and Cale 2000). In the last five years alone, over seven hundred articles and reviews have been written on this subject, covering a large range of taxa and countries (Web of Science search, 25 August 35 2014, using the search terms ‘agricultur*’ and ‘habitat’ within the ‘biodiversity conservation’ research area). These studies have shown how different habitat structures, such as trees, coarse woody debris, and ground cover, influence habitat quality through creating gradients of food, shelter and space for animals. These structures also produce diverse species-specific niches that can be exploited by wildlife with different habitat needs. Our assessment of the 40 literature revealed that similar habitat structures are important across different agricultural systems around the world. For example, large trees have been found to be keystone habitat structures in the United States (deMars et al. 2010), Australia (Manning et al. 2006), France (Sirami et al. 2008) and South Africa (Seymour and Dean 2010). Ground layer structures, such as leaf litter cover, also have been identified as valuable foraging resources for a wide 45 range of species in India (Bhargav et al. 2009) and Brazil (Carvalho and Vasconcelos 1999). The identification of these habitat structures with biologically meaningful links (i.e. key resources and factors affecting individual fitness) to the habitat quality of remnant vegetation patches (Mortelliti et al. 2010) has enabled an increased understanding of wildlife distribution patterns in fragmented landscapes (Knight and Fox 2000; Mortelliti and Boitani 2008).

50 Despite considerable knowledge of **what** habitat structures are important, there is a lack of knowledge of **where** these structures occur in the landscape. In agricultural landscapes, a combination of abiotic conditions and land management practices, both past and present, can influence the growth and distribution of many habitat structures. For example, climatic, topographic and biophysical conditions can affect energetics, evaporative

aerodynamics, temperature, and available water and nutrients, all of which influence the anatomical, physiological and biochemical attributes of the plant community (Specht and Specht 1999). In comparison, patch and landscape scale land management practices, such as clearing of native vegetation and livestock grazing, can affect ecosystem stability, structure and function, soil compaction, erosion, chemistry and water infiltration rates (Davidson et al. 2007), tree and understorey recruitment (Spooner et al. 2002; Fischer et al. 2009), and weed invasion (Holland and Bennett 2007; Peltzer and MacLeod 2014). Moreover, the use of herbicides and fertilisers associated with agricultural intensification can permeate into adjacent patches of native vegetation, modifying plant species composition and limiting tree regeneration (Dorrough et al. 2006; Fischer et al. 2009). Few studies, however, have considered how the interaction of abiotic conditions with past and present land management practices correlate with the occurrence and abundance of wildlife habitat structures (Davidson et al. 2007; Klimek et al. 2007). Without this ecological information, there is limited ability to implement management actions cost-effectively and successfully (Huth and Possingham 2011; Mortelliti 2013).

We aimed to address this knowledge gap within a large-scale landscape in south-eastern Australia. The temperate grassy woodlands in this region are among the most degraded ecological vegetation communities worldwide (Lindenmayer et al. 2010). Less than 15% of original vegetation remains (Benson 2008), and undisturbed remnants with intact tree and understorey strata are rare. Legislative controls on further land clearing have limited agricultural expansion, but it is likely that intensification will continue within current agricultural land (Cunningham et al. 2012). In the last 15-20 years, however, there has been an increase in native vegetation cover due to an expansion of regrowth (secondary) woodland following changes in land use and management (Bowen et al. 2009; Geddes et al. 2011). Regrowth woodland patches have a different structural composition to old growth (primary)

woodland, and their habitat suitability varies between wildlife species (Fuller et al. 2007; Michael et al. 2011; Lindenmayer et al. 2012). Previous research in south-eastern Australia (Appendix 1), in both old growth and regrowth woodland, has identified several woodland habitat structures (McElhinny et al. 2006) that are important for birds (e.g. Montague-Drake et al. 2009; Ikin et al. 2014), arboreal marsupials (e.g. Lindenmayer et al. 1999; Cunningham et al. 2007; Crane et al. 2008) and reptiles (e.g. Cunningham et al. 2007; Michael et al. 2008; Michael et al. 2010). These earlier studies recommended that important habitat structures be protected and perpetuated, but did not examine processes affecting the distribution of these key habitat structures across landscapes.

Here, we investigate how the occurrence or abundance of habitat structures that are important for wildlife in south-eastern Australia was correlated with the interaction of abiotic conditions and land management practices, and whether this differed between old growth and regrowth woodland. We focused on eight habitat structures: canopy depth, large-sized trees, hollow-bearing trees, mid-sized trees, dead trees, logs, native grass and leaf litter. Findings from our study inform management prescriptions that can be targeted towards specific abiotic conditions which may have strong, quantifiable effects on wildlife habitat in remnant temperate eucalypt woodlands. Our case study also provides general insights into the interactions between abiotic conditions and land management that may be useful for the management of habitat structures in other agricultural landscapes worldwide.

Methods

Study area and experimental design

Our study area was located in the South-West Slopes bioregion of New South Wales (NSW), south-eastern Australia (Fig. 1). This region spans an area of more than 80,000 km² (equivalent to the area of Austria, or 10% of NSW). The topography of the region is

105 undulating foothills and ranges, and the climate is sub-humid with no dry season and hot
 summers. Temperate woodland is the predominant form of native vegetation (although forest
 communities are also present), dominated by white box (*Eucalyptus albens*), yellow box (*E.*
melliodora), grey box (*E. microcarpa*) and Blakely's red gum (*E. blakelyi*). Additional tree
 species present include red stringybark (*E. macrohyncha*), mugga ironbark (*E. sideroxylon*),
 110 river red gum (*E. camaldulensis*), apple box (*E. bridgesiana*) and red box (*E. polyanthemos*
ssp vestita) (Benson 2008).

Undisturbed temperate woodland supports an herbaceous ground layer, dominated by tall
 perennial tussock grasses, with forbs and smaller grasses growing in the spaces between the
 115 tussocks (McIvor and McIntyre 2002). Of the 13 botanical regions in NSW, however, the
 South-West Slopes bioregion is the most extensively and intensively disturbed (Lindenmayer
 et al. 2010). Agriculture is the main land use, and ~85% of native vegetation cover has been
 cleared for grazing and cropping over the past 220 years (Benson 2008). Since the 1950s,
 fertilisation of natural grasslands has become a regular practice, causing changes in the
 120 ground layer and reduced eucalypt regeneration (McIntyre 2008). The cessation of
 Indigenous use of fire also has had a significant influence on vegetation structure and floristic
 diversity (Gott 2005). It has been estimated that less than 3% of white box and yellow box
 temperate woodland remains in good condition (Lindenmayer et al. 2010), that woodland
 remnants are frequently less than 1 ha in size (Gibbons and Boak 2002), and that the
 125 locations of these remnants poorly represent the former extent of this vegetation type
 (Watson 2011).

For our study, we selected 138 patches of native vegetation located on 46 farms within the
 southern half of the region (Cunningham et al. 2007). Of these, 72 were stands of old growth

130 woodland and 66 were stands of natural or coppiced regrowth woodland. Patch size ranged from 0.5 – 53.8 ha (mean 9.3 ha), and the majority (75%) were subject to disturbance by domestic livestock grazing. In each patch, we established a field site consisting of a randomly located 200 m transect. Along this transect, we placed three 20 x 20 m vegetation survey plots, located at distance 0, 100 and 200 m. Together, these plots totalled 1200 m² (0.12 ha) 135 per site.

Data collection

We surveyed the vegetation in each of the 138 woodland patches in the 2008 spring (early September to early December). We focused on eight habitat structures (Table 1) that are 140 known to influence the occurrence and/or abundance of a range of bird, marsupial and reptile species of conservation concern. In each of the three 20 x 20 m plots in each site, we counted the number of large trees (>50 cm DBH), hollow-bearing trees, mid-size trees (15-30 cm DBH), dead trees, and logs (>10 cm diameter and >100 cm length). We also measured the canopy depth (measured from crown base to tip) of the largest tree using a clinometer. We 145 established twelve 1 x 1 m sub-plots (located at the corners of the plots) and, within each, visually estimated the percent cover of leaf litter and native grasses to the nearest 5%. We then calculated site-level means of each of these habitat structures.

#Table 1 approximately here#

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We selected three features to summarise the abiotic conditions of each site (Table 2). Within a 25 m radius of each plot centre, we derived the mean northern component of aspect from the cosine of degrees aspect calculated from a 20 m resolution Digital Elevation Model (DEM) (Montague-Drake et al. 2011). This created a continuum ranging from completely

155 south-facing to completely north-facing, which we then averaged over the three plots to give
 a site-level mean value. Within 100 ha of the site centre, we classified mean surface lithology
 fertility using a spatial layer of inherent rock fertility developed by De Vries (2009)
 (Williams et al. 2010), as an indicator of substrate nutrient rating, and mean topographic
 wetness index (TWI), derived from the 20 m DEM, as a proxy for landscape position, ranging
 160 from ridges and upper slopes to lower slopes and drainage lines (Montague-Drake et al.
 2011). We also calculated mean elevation, annual mean precipitation and annual mean
 temperature for each site, but excluded these variables because of strong (>0.7 or <-0.7)
 positive (temperature) or negative (elevation, precipitation) Spearman correlations with TWI.
 All calculations were undertaken using ArcInfo v. 10.0.

165 #Table 2 approximately here#

We selected three management features to describe the land management context of
 each site (Table 2). First, we characterised the patch as ‘fenced’ or ‘unfenced’. Fenced sites
 170 represent separate management units within farms and have different management conditions
 to adjacent fields. That is, fencing did not represent exclusion of domestic livestock (19/38
 fenced sites and 84/100 unfenced sites had evidence of grazing disturbance) but was instead a
 proxy of management for higher environmental values. Second, we calculated the percentage
 of cropland within 100 ha of the site centre, using the ‘Land use: New South Wales, version
 175 1, May 2011’ spatial dataset supplied by the NSW Office of Environment & Heritage.
 Cropland represents the degree of land use intensification in the surrounding landscape.
 Third, we calculated the percentage of native vegetation cover within 100 ha of the site centre
 to represent the degree of past land clearing and fragmentation in the surrounding landscape.
 To do this, we used the Foliage Projected Cover (FPC) spatial dataset supplied by the NSW

Office of Environment and Heritage (Danaher 2011); we defined native vegetation as cells with FPC >0, including cells occurring in crop and improved pasture land uses as these reflect revegetation plantings in our study area. Percent vegetation cover was strongly positively correlated (>0.8) with the mean size of patches and the density of patch edges in the landscape.

Data analysis

We used generalised linear mixed models (Bolker et al. 2009) to investigate the additive and interactive effects on each of our eight habitat structures of the abiotic features, land management and growth type (old growth vs. regrowth) (Table 1). For each habitat structure, we started with a full model that fitted:

- Interactions of the three abiotic variables.
- Interactions of each abiotic variable with each of the land management variables.
- Interactions of growth type with each abiotic and land management variable.

We used the glmmPQL function of the MASS package in R (Version 2.15.0), with a quasi-poisson distribution for the count data and a quasi-binomial distribution for proportional and binary data. These models account for overdispersion in the data, and were found to be a better fit to the data compared with alternative approaches, such as negative binomial and zero-inflated models (Ver Hoef and Boveng 2007). We standardised the abiotic and management variables prior to analysis, which means that model beta coefficients reflect the relative importance of the variables in the model. We followed a backwards stepwise model selection procedure to remove least significant terms from the model until all remaining terms were significant (≤ 0.05).

Results

We found that the occurrence and abundance of the eight investigated habitat structures were significantly related to abiotic conditions and land management practices, but the nature of these relationships varied between the habitat structures (Table 3, Fig. 2).

#Table 3 approximately here#

#Figure 2 approximately here#

Canopy depth: We found that mean canopy depth was greatest on south-facing sites and increased with increasing lithology fertility and TWI (Table 3, Fig. 2a). We found that with each unit increase in TWI, canopy depth increased by ~9% in both north and south-facing sites.

Large trees: We found there were 70% more large trees per ha in old growth sites than regrowth sites, but the number declined by 60% in both growth types with increasing native vegetation cover in the landscape (Table 3, Fig. 2b). In south-facing sites, we found that large tree abundance declined with an increase in TWI but increased with increasing cropland in the landscape. In north-facing sites, these relationships were reversed.

Hollow-bearing trees: We found that the abundance of hollow-bearing trees was significantly higher in old growth woodland and in fenced sites (Table 3; Fig. 2c). The number of hollow-bearing trees also increased as sites became more north-facing, so that completely north-facing regrowth sites had similar numbers to unfenced old growth sites. With increasing

cropland in the landscape, the number of hollow-bearing trees increased in south-facing sites but remained similar in north-facing sites.

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Mid-sized trees: We found that regrowth woodland had significantly more mid-sized trees than old growth and that the number of mid-sized trees was positively related to lithology fertility (Table 3). When south-facing, fenced sites had less than half the number of mid-sized trees per ha relative to unfenced sites. However, when north-facing, fencing was associated with a 40% increase in the number of mid-sized trees per ha (Fig. 2d). With increasing native vegetation cover in the landscape, we found that mid-sized tree density in old growth remained similar but increased by approximately four times in regrowth.

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Dead trees: We found that the number of dead trees in each site was significantly higher in regrowth than old growth, and was positively related to native vegetation cover and negatively related to cropland and lithology fertility (Table 3). We found, however, that there was an interaction between lithology fertility and growth type, so that the number of dead trees per ha in regrowth doubled with increasing lithology fertility. Further, although we did not find an effect of aspect, *per se*, we found that with increasing cropland in the landscape, the number of dead trees decreased significantly as sites became more north-facing (Fig. 2e).

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Logs: We found that the abundance of logs at each site was significantly related to fencing and growth type (Table 3, Fig.2f). Old growth sites supported 30% more logs per ha than regrowth sites and fenced sites also had 30% more logs per ha than unfenced sites. Fenced old growth sites had 69% more logs per ha than unfenced regrowth sites.

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Native grasses: We found that native grass cover increased significantly with native vegetation cover in the landscape surrounding each site (Table 3). We also found that native vegetation cover interacted with TWI (Fig. 2g). When TWI was low, such as on ridge tops, native grass cover was ~10%, regardless of the amount of native vegetation cover in the landscape. When TWI was high, such as in valley flats with deeper soil depths and higher moisture availability, sites surrounded by high native vegetation cover had five times higher native grass cover than sites surrounded by low native vegetation cover.

Leaf litter: We found that leaf litter cover at each site was significantly related to native vegetation cover in the surrounding landscape (Table 3, Fig. 2h): with every 10% increase in native vegetation cover, leaf litter cover increased by ~5%.

Discussion

In our case study, we investigated how eight temperate eucalypt woodland overstorey and ground-layer habitat structures were related to abiotic conditions, land management practices, and growth type. In the remainder of this paper, we discuss our key findings, and review their implications for the management of temperate eucalypt woodland and the conservation of reptiles, mammals and birds in southeastern Australia. We outline ‘management prescriptions’, which will have strong and quantifiable effects on habitat structures important for the persistence of wildlife in these agricultural landscapes (Fig. 3). We also discuss general patterns and implications for agricultural landscapes worldwide.

#Figure 3 approximately here#

Habitat structures

Canopy depth: Increasing canopy depth and cover can positively affect other woodland structures and associated wildlife (Montague-Drake et al. 2009; Michael et al. 2010).

Previous research has demonstrated that soil water availability has a strong effect on the growth of stems, roots and foliage (Specht and Specht 1999), and our findings of increasing canopy depth with increasing south aspect, lithology fertility and TWI are consistent with this. For instance, south-facing sites experience lower evaporation of soil moisture compared to north-facing sites, and soils with higher lithology fertility have greater water storage capacity (Specht and Specht 1999). Furthermore, sites with high TWI, such as valley flats, are more likely to support deeper soils that have more available water (Specht and Specht 1999). Therefore, south-facing sites with high TWI and lithology fertility have high soil water availability and the uptake of this water by trees promotes vertical growth in the canopy. Several studies have postulated that canopy depth may be a proxy for site productivity (Manning et al. 2007; Montague-Drake et al. 2009), and our finding of deeper canopies where water availability was higher provides quantitative evidence to support this suggestion.

Large trees: Many studies have found positive associations between large trees and animal abundance or occurrence (e.g. Holland and Bennett 2007; Crane et al. 2008; deMars et al. 2010), as well as a positive relationship between large old tree abundance and old growth woodland (e.g. Montague-Drake et al. 2009). The lower number of large trees in regrowth is probably attributable to the younger ages of trees in this growth type; previous studies, however, have found reduced number of large trees in secondary forest (Waltert et al. 2005), indicating that the potential of trees to grow to large sizes may be limited in regrowth.

Surprisingly, we found that the abundance of large old trees (a component of native

vegetation cover) was negatively related to total native vegetation cover in the landscape. We hypothesise that this counter-intuitive relationship between large old trees and native vegetation cover in the landscape is correlative rather than causative. That is, large tree density is a legacy of past land management. The pattern of native vegetation clearing in the region has left a relictual landscape with scattered large old trees (Fischer et al. 2010). These landscapes, however, lack the younger age classes for future large tree succession. Gibbons et al. (2008) modelled the future abundance of mature trees in agricultural landscapes and predicted that, under existing agricultural practices (particularly intensive agriculture) there would be no trees remaining within 90-180 years. This is concerning given the keystone role of these structures in providing crucial habitat structures (reviewed by Manning et al. 2006). Conversely, landscapes with high amounts of vegetation cover reflect recent increases in tree cover due to restoration plantings and regrowth expansion (Bowen et al. 2009; Geddes et al. 2011) – two growth types which typically lack large old trees. A second unexpected finding was the interaction between aspect and cropland, however we note that this relationship was relatively weak. This correlation may again be a legacy of past management, with trees being retained in south-facing sites but cleared in north-facing sites.

Hollow-bearing trees: Nearly 300 Australian vertebrate species use tree hollows (Gibbons et al. 2000); many with specific and differing requirements in hollow characteristics (e.g. Stojanovic et al. 2012). Previous studies have identified trunk diameter as the strongest predictor of hollow occurrence in Australian eucalypts (Gibbons et al. 2000; Rayner et al. 2013). In our study, we found that old growth woodland supported more large trees. It is therefore expected that hollow-bearing tree abundance also was higher in this woodland type. Hollow-formation in eucalypts is more likely to occur when trees are physiologically stressed and/or suffering from poor health (Lindenmayer et al. 1993). These trees are more susceptible

to stochastic disturbance (e.g. fire, wind and biological agents) that injure the tree, exposing heartwood that is vulnerable to decay (Gibbons et al. 2000; Rayner et al. 2013). Rayner et al. (2013) found that trees in a later stage of senescence were more likely to contain hollows than those in early stages, irrespective of trunk diameter, indicating that disturbance increased the probability of smaller, younger trees containing hollows. This may explain why we found greater hollow-bearing tree abundance in north-facing regrowth and with increasing cropland in south-facing sites. North-facing sites receive more solar radiation and are thus more exposed to water stress (Specht and Specht 1999), which accelerates hollow-formation in the younger trees present in regrowth. South-facing sites contain less water-stressed trees with greater canopy depths (see above), delaying hollow-formation (Bennett et al. 1994; Gibbons et al. 2000; Rayner et al. 2013). However, fertiliser drift from surrounding cropland may negatively affect tree health and thus leave them more prone to the development of hollows (Lindenmayer et al. 1993). Manning et al. (2013b) predicted a decline in the number of hollow-bearing trees over the next 200 years, leading to potential extinctions of hollow-dependent wildlife species.

Mid-sized trees: Mid-sized trees contribute to the structural diversity of vegetation patches and may support high numbers of invertebrate prey and provide protection from predators, making them important habitat structures for wildlife (Holland and Bennett 2007; Hanspach et al. 2012). We found that mid-sized tree abundance in regrowth increased with increasing native vegetation cover in the landscape, particularly when sites were north-facing and fenced. Higher connectivity in the surrounding landscape creates more opportunities for pollination, dispersal and tree recruitment (Tewksbury et al. 2002; Levey et al. 2005), and this may explain why there was greater mid-sized tree abundance in landscapes with greater vegetation cover. Further, tree recruitment is more likely to occur in canopy gaps (McIntyre

2002): north-facing sites have less extensive tree canopies (see above), offering more gaps in the canopy and opportunities for seedling establishment. North-facing sites prioritised for conservation (i.e. fenced), therefore, may combine ideal abiotic and management conditions for high tree density.

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Dead trees: Standing dead trees are an important habitat structure in many vegetation types (McElhinny et al. 2005), particularly as a provider of hollows (e.g. Joseph et al. 2011), but are rare in some Australian woodlands (Rayner et al. 2013). Tree death is most likely due to dieback, water-stress caused by long-term drought, and wildfire. Our results indicate that the number of dead trees within remnants was more closely related to management practices than abiotic features. For instance, dead trees are often harvested for firewood, particularly in productive parts of the landscape (Lindenmayer et al. 2001). Dead (and living) trees are also likely to be cleared from cropping landscapes to improve cropping efficiency. Dead trees, therefore, are more likely to remain standing in more intact landscapes, especially as greater vegetation cover may buffer these trees from disturbances (e.g. windthrow) that cause tree collapse (Rayner et al. 2013). Tree death opens up canopy gaps, creating conditions suitable for tree regeneration (McIntyre 2002), which may explain the association between dead trees and regrowth: dead trees are more likely to occur in regrowth because regrowth is more likely to occur around dead trees where density-dependent competition is low.

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Logs: Logs are an important component of the woodland ecosystem, as they provide ‘focal points’ for many environmental processes, as well as being an important source of foraging and nesting resources for birds (Antos et al. 2008; Manning et al. 2013a) and basking and shelter sites for reptiles. Logs can be a proxy for farm management, as logs are often removed for firewood or to increase farm ‘tidiness’ (Killey et al. 2010). This can decrease structural

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heterogeneity and can compound detrimental effects of livestock grazing (Davidson et al. 2007; Holland and Bennett 2007) or overgrazing by overabundant native herbivores (Barton et al. 2011) on vegetation and wildlife. Thus, it was unsurprising that log cover was higher in fenced remnants, where levels of removal of logs for management purposes can be expected to be lower (Manning et al. 2013a). Regrowth is also less likely to have high log numbers due to the slow natural accumulation of logs. Previous studies have also found lower woody debris occurrence and abundance in revegetation (Kanowski et al. 2003; Manning et al. 2013a).

Native grasses: Native grass tussocks provide sheltered recruitment sites for tree seedlings (Spooner et al. 2002), as well as micro-scale spatial patchiness that promotes foraging and shelter resources (Cunningham et al. 2007; Montague-Drake et al. 2009). Some native grass species, such as kangaroo grass (*Themeda triandra*) and common tussock grass (*Poa labillardieri*), are grazing-sensitive, and have been found to be absent or rare in unfenced sites (Spooner et al. 2002). We did not identify an effect of fencing on native grasses in our study (likely because fencing was not a proxy for grazing exclusion), but instead found that a combination of landscape position and landscape vegetation cover were important. Lunt (1997) and Morgan (1998) suggest that grazing-sensitive native grasses lack persistent seed banks and have reduced colonisation potential due to fragmentation. Thus, our finding that native grass cover was highest when the landscape vegetation cover was highest supports these conclusions. Other studies have found that native plants, including grasses, are vulnerable to increases in excess nutrients due to pasture improvement (McIntyre and Lavorel 2007; Dorrough and Scroggie 2008; McIntyre 2008). Our study also supports these findings,

as landscapes with high woody vegetation cover can be expected to have been subject to less
 400 agricultural intensification (e.g. cropping).

Leaf litter: Leaf litter supports litter-associated invertebrates and is therefore an important
 foraging resource for vertebrates (Antos et al. 2008). Previous studies have found an
 association between leaf litter cover and woodland remnants with healthy tree cover
 405 (Davidson et al. 2007). Our results suggest that leaf litter cover is also higher in less
 fragmented landscapes. The multiple-edge effects created in small and isolated woodland
 fragments increase wind penetration and the loss of litter to adjacent land (Watson 2011).
 Studies in Central Amazonia, Brazil, also have found that litter decomposition rates differ
 between continuous and fragmented forests, affecting nutrient cycling and forest productivity
 410 (Didham 1998).

Management prescriptions

Several previous studies have established relationships between habitat structures and
 wildlife occupancy, and have recommended that these structures be conserved. These studies
 415 stop short, however, of investigating what affects the distribution of habitat structures across
 agricultural landscapes. Our study, therefore, makes an important advance by *quantifying* the
 effects of both abiotic conditions and farm management on wildlife habitat structures in
 remnant woodlands. From these findings, we are able to recommend management
 prescriptions to improve conservation efforts in agricultural landscapes (Fig. 3).

420 The percentage of native vegetation cover in the surrounding landscape was
 correlated with five of the eight investigated habitat structures, indicating its management
 importance. Thus, our findings support measures to increase and maintain native vegetation
 cover in agricultural landscapes, such as revegetation programs and retention of old growth

and regrowth woodland. Further, in recommending that native vegetation cover be increased
 425 across the landscape to increase individual habitat structures (e.g. leaf litter and native grass
 cover), we are advocating the restoration of important ecological processes (e.g. nutrient
 cycling and seed dispersal) (Lunt 1997; Didham 1998; Morgan 1998), complementary to the
 preservation of critical wildlife habitat.

Our data clearly showed that fenced sites were associated with three habitat
 430 structures: hollow-bearing trees, mid-sized trees and logs. Fencing is usually a proxy of
 grazing disturbance by domestic livestock (e.g. Spooner and Briggs 2008), but this was not
 the case in our study where half of the fenced sites showed signs of grazing. The relationship
 between fencing and some habitat structures may therefore be due to farmers managing
 fenced sites differently to unfenced sites. For instance, by not “tidying up” within fenced
 435 woodland, farmers can retain 30% more logs on their land. Similarly, by not clearing hollow-
 bearing trees within fenced areas, farmers can conserve five times the number of this
 important habitat structure. Fencing thus provides a “cue to care”, where the fenced areas are
 prioritised for conservation over production.

Our management prescriptions go hand-in-hand with other well-established
 440 management principles. These include the importance of increasing the size of woodland
 patches and conserving large remnants (Major et al. 2001), and the necessity of considering
 temporal scale (i.e. the time lag between the undertaking and outcomes of some management
 actions (Vesk and Mac Nally 2006)) and spatial scale (i.e. the benefits of farm actions being
 evident across the larger region (Cunningham et al. 2014a; Cunningham et al. 2014b)).

General insights

Agri-environmental schemes (AES), where farmers are financially supported to undertake
 environmental improvement on their land, are widely implemented across Australia, North

America and Europe (Tscharntke et al. 2005; Kleijn et al. 2011; Michael et al.

450 2014){Lindenmayer, 2012 #2028}. There have been several calls to formally include the restoration or creation of habitat structures within the landscape as part of increasing the biodiversity benefit of these schemes (Donald and Evans 2006; Frey-Ehrenbold et al. 2013). Moving beyond our specific recommendations relevant to temperate agricultural landscapes, our case study provides several general insights that may be useful to the conservation and
455 management of habitat structures in different ecological systems, and thus informative for AES.

First, we did not find an ‘ideal landscape’ with abiotic conditions suited to the promotion of all habitat structures. For instance, previous research has suggested that productive parts of the landscape (such as low lying areas with high soil fertility) should have
460 high conservation priority (Watson 2011; Polyakov et al. 2013). We found several positive associations of habitat structures with TWI and lithology fertility (e.g. canopy depth and mid-sized tree abundance) but we also found negative associations (dead trees) and several habitat structures were unrelated to productivity (e.g. hollow-bearing trees, logs and leaf litter). This suggests that conservation value can also be found in a range of abiotic conditions. This
465 finding complements that of Collard et al. (2011), who found that native plant richness, cover and composition were similar between grasslands of different management histories (previously cultivated vs uncultivated), and concluded that these disturbed areas could represent viable targets for management and restoration effort.

Second, we did not find a ‘silver bullet’ management action. Instead, the benefit and
470 effectiveness of management actions differed between habitat structures and also between abiotic conditions. For example, we found that increasing vegetation cover had a large effect on native grass cover on lower slopes and drainage lines but little effect on ridges and upper slopes. This finding supports the argument that management actions should be tailored to ‘on-

the-ground' conditions, and not dictated by 'one-size-fits-all' agri-environmental policy.

475 Understanding the relationship between habitat structures, abiotic conditions and land management can facilitate better spatial targeting of environmental policies, improving the cost-effectiveness of AES (van der Horst 2007; Uthes et al. 2010).

The consequence of these two general insights is that similar management actions in different parts of the landscape (and vice versa) will inevitably lead to certain habitat
 480 structures being promoted or retained over others. However, we do not believe that this should be a cause of disheartenment. The range of habitat structures that we investigated contribute to a heterogeneous landscape, providing diverse habitat niches for a multitude of wildlife species (Cunningham et al. 2008). Creating the 'same thing everywhere' would therefore be a perverse conservation outcome. Instead, by understanding how management
 485 actions in specific abiotic conditions lead to the increased occurrence or abundance of particular habitat structures, management can be targeted to alternative conservation strategies relevant to the landscape of interest.

490 **Acknowledgements**

We thank the Australian Research Council, the Murray Catchment Management Authority and the Caring for Our Country Program for funding for this project. We thank C. MacGregor, L. McBurney, D. Blair and S. Lucas for their important contribution to the collection of the field data, A. Smith for her patient help with R code, J. Newport for her
 495 generous assistance with preparing Fig. 3, and I. Stirnemann for her valuable feedback on the manuscript.

Tables

500 Table 1. Description of habitat structures analysed and their untransformed means and ranges for old growth and regrowth sites. Habitat structures b – f were modelled as total site abundance, but are presented here as numbers per ha.

Habitat structure	Mean [range]	
	Old growth	Regrowth
a Depth of canopy (meters, measured from crown base to tip)	15.08 [6.00 – 28.67]	13.74 [5.64 – 31.00]
b Number of large trees >50 cm DBH per ha	18.10 [0.00 – 45.76]	10.64 [0.00 – 32.24]
c Number of trees with visible hollows per ha	22.22 [0.00 – 91.67]	11.11 [0.00 – 50.00]
d Number of trees 15 - 30 cm DBH per ha	12.75 [0.00 – 72.25]	33.58 [0.00 – 197.25]
e Number of dead trees per ha	15.16 [0.00 – 75.00]	39.77 [0.00 – 291.67]
f Number of logs per ha	197.34 [0.00 – 1100.00]	162.75 [0.00 -766.67]
g Percent cover of native grasses	10.97 [0.00 – 62.08]	11.44 [0.00 – 38.75]
h Percent cover of leaf litter	28.73 [0.42 – 77.33]	36.25 [2.08 – 77.50]

505 Table 2. Description of the biotic, abiotic and land management variables analysed and their untransformed means and ranges. Variables in italics were not included in analysis because of strong correlations with TWI.

	Variable	Mean [range]
Biotic	Woodland growth type	Regrowth / Old growth
Abiotic	Mean northern component of aspect (total south (-1) to total north (+1))	-0.06 [-0.99 - 0.98]
	Mean lithology fertility (nutrient rating) of substrate	4.83 [2.00 - 6.00]
	Mean Topographic Wetness Index (TWI, landscape position)	0.65 [-1.64 - 5.75]
	<i>Annual mean temperature (°C)</i>	<i>14.37 [13.09 - 15.23]</i>
	<i>Annual mean precipitation (mm)</i>	<i>656.41 [524.25 – 886.55]</i>
	<i>Mean elevation (meters above sea level)</i>	<i>291.28 [181.60 - 484.03]</i>
Land management	Percent cropland cover in landscape (within 100 ha)	18.30 [0.00 - 99.98]
	Percent native woody vegetation cover in landscape (within 100 ha)	10.47 [0.09 - 46.70]
	If remnant is fenced	Fenced / Unfenced

Table 3. Results of final generalised linear mixed model for each of the habitat structures.

Terms are ordered by largest to smallest coefficient absolute values.

Habitat Structure	Terms	β	Std. Error	d.f.	t-value	p- value
Canopy depth	(Intercept)	2.65	0.03	89	77.52	<0.001
	TWI	0.13	0.03		4.08	<0.001
	Lithology fertility	0.10	0.03		3.11	0.003
	Aspect	-0.07	0.03		-2.62	0.010
Large trees	(Intercept)	0.73	0.08	85	9.05	<0.001
	Regrowth	-0.52	0.13		-4.14	<0.001
	Aspect*TWI	0.24	0.08		2.83	0.006
	Native vegetation cover	-0.20	0.07		-2.79	0.007
	Aspect*Cropland	-0.18	0.08		-2.37	0.020
	TWI	0.14	0.09		1.58	0.118
	Cropland	-0.04	0.08		-0.46	0.646
	Aspect	0.00	0.06		0.05	0.960
Hollow-bearing trees	(Intercept)	0.88	0.12	86	7.52	<0.001
	Regrowth	-0.84	0.16		-5.31	<0.001
	Fencing	0.37	0.16		2.38	0.020
	Aspect*Regrowth	0.34	0.16		2.15	0.034
	Cropland	0.18	0.08		2.24	0.028
	Aspect*Cropland	-0.15	0.07		-2.01	0.048
	Aspect	0.00	0.09		0.02	0.987
Mid-sized trees	(Intercept)	0.37	0.16	84	2.35	0.021

	Regrowth	0.91	0.17		5.30	<0.001
	Aspect*Fencing	0.46	0.22		2.06	0.043
	Native vegetation cover*Regrowth	0.36	0.15		2.37	0.020
	Fencing	-0.30	0.20		-1.51	0.136
	Lithology fertility	0.26	0.10		2.53	0.013
	Aspect*Native vegetation cover	0.17	0.07		2.30	0.024
	Native vegetation cover	-0.11	0.13		-0.81	0.420
	Aspect	-0.02	0.09		-0.20	0.843
Dead trees	(Intercept)	0.54	0.17	85	3.12	0.003
	Regrowth	0.75	0.21		3.59	0.001
	Lithology fertility*Regrowth	0.63	0.21		3.04	0.003
	Aspect*Cropland	-0.37	0.12		-3.17	0.002
	Lithology fertility	-0.34	0.15		-2.22	0.029
	Cropland	-0.27	0.13		-2.05	0.043
	Native vegetation cover	0.23	0.08		2.78	0.007
	Aspect	-0.06	0.10		-0.58	0.564
Logs	(Intercept)	3.04	0.12	90	25.33	<0.001
	Fencing	0.29	0.14		2.11	0.037
	Regrowth	-0.27	0.12		-2.21	0.030
Native grasses	(Intercept)	-2.14	0.14	89	-15.31	<0.001
	Native vegetation cover	0.23	0.09		2.69	0.009
	TWI*Native vegetation cover	0.14	0.06		2.27	0.026
	TWI	0.02	0.12		0.21	0.832

Leaf litter	(Intercept)	-0.71	0.13	91	-5.37	<0.001
	Native vegetation cover	0.21	0.07		3.21	0.002

Figures

515 Figure 1. Map of the study area in the South-West Slopes Bioregion of New South Wales, Australia. Locations of the 138 woodland sites are shown, in addition to native vegetation cover within the study area.

Figure 2. Relationships between the habitat structures and selected abiotic conditions and
520 management practices predicted from the final generalised linear mixed models (Table 3). Predictions were obtained by fitting the other variables in the model that are not presented at their mean (growth type was fitted as ‘regrowth’). Habitat structures (b) – (f) were modelled as total site abundance, but are presented here as numbers per ha.

525 Figure 3. Management prescriptions targeted for specific abiotic conditions that will have strong, quantifiable effects (see Fig. 2) on wildlife habitat in remnant temperate eucalypt woodlands.

530

Figure 1.

Figure 2.

Habitat structure***Management prescription*****Canopy depth**

To increase average canopy depth, managers should conserve south-facing remnants with fertile soils in low-lying areas of the landscape.

Large trees

To manage for current and future large trees, managers should preserve large trees abundance by retaining existing trees and conserving old growth remnants, especially in highly fragmented landscapes.

Hollow-bearing trees

To preserve hollow-bearing tree abundance, managers should conserve north-facing old growth and regrowth woodland. They also should limit removal of trees in later stages of senescence.

Mid-sized trees

To increase mid-sized tree abundance, managers should conserve north-facing regrowth woodland, particularly in landscapes with high vegetation cover. They should also increase native vegetation cover in the landscape, via revegetation plantings and regrowth.

Dead trees

To preserve dead tree abundance, managers should conserve regrowth woodland with fertile soils in landscapes with low agricultural intensification. They should also cease clearing dead trees and limit cropland around regrowth woodland.

Logs

To increase log abundance, managers should conserve old growth remnants, and cease removing logs for firewood or "tidying-up" purposes.

Native grasses

To protect native grass cover, managers should conserve woodland remnants in low-lying areas of landscapes with high native vegetation cover. They should also limit cropping and pasture improvement near areas of native grassland.

Leaf litter

To increase leaf litter cover, managers should restore native vegetation in the landscape by conserving regrowth woodland and revegetating cleared farmland.

Figure 3.

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Appendix 1. Selected examples of relationships between habitat structures and wildlife in south-eastern Australia.

Habitat structure	Relationship with wildlife
Canopy depth	<ul style="list-style-type: none"> Abundance of the southern rainbow skink (<i>Carlia tetradactyla</i>) was positively related to canopy cover [1]. Superb parrot (<i>Polytelis swainsonii</i>) occurrence was positively related to canopy depth [2].
Large trees	<ul style="list-style-type: none"> Probability of the squirrel glider (<i>Petaurus norfolcensis</i>) denning in large trees increased by nearly four times with every 100 cm increase in tree diameter [3]. Odds of detecting the marbled gecko (<i>Christinus marmoratus</i>) increased by ~6% for every 10% increase in the density of large trees [4]. Occurrence of agile antechinus (<i>Antechinus agilis</i>) related to eucalypt basal area [5].
Hollow-bearing trees	<ul style="list-style-type: none"> Nearly 300 Australian vertebrate species use tree hollows [6]. Woodland bird communities characterised by the presence of the superb parrot associated with sites with hollow-bearing trees [7].
Mid-sized trees	<ul style="list-style-type: none"> Increasing density of mid-sized trees increased the site occupancy of eight woodland bird species of conservation concern [2]. Richness of native small mammals and the probability of occurrence of agile antechinus and bush rat (<i>Rattus fuscipes</i>) were higher in dense, structurally diverse forest [5]. Microbat species richness and activity was positively related to tree density, and that the probability of occurrence for several species increased with tree density [8].
Dead trees	<ul style="list-style-type: none"> Occupancy of several birds of conservation concern, such as the eastern yellow robin and diamond firetail, has been shown to increase with increasing numbers of dead trees [2]. Ragged snake-eyed skink, Boulenger's skink (<i>Morethia boulengeri</i>) and southern rainbow skink positively related to dead trees [1,9]. Squirrel gliders preferentially use dead trees for dens [3].
Logs	<ul style="list-style-type: none"> Odds of detecting the common ringtail possum (<i>Pseudocheirus peregrinus</i>) increased by ~7% for every 10% increase in the number of logs per ha [4]. 22% of brown treecreeper (<i>Climacteris picumnus</i>) foraging observations in fallen timber [10].

Habitat structure	Relationship with wildlife
	<ul style="list-style-type: none"> Higher foraging activity of Gould's wattled bat (<i>Chalinolobus gouldii</i>) and higher probability of detecting the eastern freetail bat (<i>Mormopterus sp.</i>) in sites with greater log cover [8]. Higher richness and abundance of beetles at logs compared with open ground sites [11].
Native grasses	<ul style="list-style-type: none"> Several species of woodland birds [2] and reptiles [1,12] have been found to be positively related to native grass cover. Odds of detecting the southern rainbow skink increased by ~3.2% for every 1% increase in tussock grass cover [4].
Leaf litter	<ul style="list-style-type: none"> Ragged snake-eyed skink (<i>Cryptoblepharus pannosus</i>; as syn. <i>Cryptoblepharus carnabyi</i>) abundance was positively related to leaf litter cover [1]. More than 50% of all ground-foraging woodland bird foraging observations were in leaf litter, with this substrate being used more frequently than expected given its availability [10].

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