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# Contrasting beetle assemblage responses to cultivated farmlands and native woodlands in a dynamic agricultural landscape

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**Abstract.** There is an urgent need to identify ways of managing agricultural landscapes for biodiversity conservation without reducing food production. Farming practices that consider spatio-temporal heterogeneity of farm fields may be a feasible alternative to large-scale revegetation of farmlands for maintaining arthropod biodiversity and their important ecological function. We examined seasonal differences in beetle assemblages in woodland remnants and four adjoining farmland uses in a highly modified agricultural landscape in southeastern Australia. The farmland uses were crops, fallows, and two restoration treatments (fine woody debris applied over harvested crop fields, and restoration plantings). Unexpectedly, overall species richness was significantly lower in remnants than in adjacent farmlands. Remnants and farmlands supported significantly different assemblages, with a third of species found in both habitats. Abundance responses were taxon-specific and influenced by interactions between land use and season. In particular, predator abundance was significantly higher in plantings and fallows during spring compared to summer. Detritivore abundance was significantly higher in the woody debris compared to the adjacent remnants. Herbivore abundance did not differ between remnants and farmlands over time. Complex responses provide strong support for a mosaic of land uses to effectively conserve different beetle groups. Species richness results suggest that further agricultural intensification, in farm fields and through the removal of remnant vegetation, risks reducing beetle diversity in this region. Maintaining farmland heterogeneity with a mix of low-intensity land uses, such as conservation tillage, crop–fallow rotation, restoration plantings, and the novel application of fine woody debris over cultivated fields, may provide seasonal refuge and resources for beetles.

**Key words:** Coleoptera; fragmentation; landscape mosaic; matrix; restoration; tillage.

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## INTRODUCTION

Agriculture is a major cause of decline in biodiversity and ecosystem services globally (Bradshaw 2012, Newbold et al. 2015, Soliveres et al. 2016), due to widespread conversion and degradation of natural habitats (Gibson et al. 2011, Tilman et al. 2011) and increased intensification of agricultural practices (Benton et al. 2003, Hendrickx et al. 2007, Attwood et al. 2008). Retaining and restoring native vegetation has been identified as critical for conserving biodiversity in agricultural landscapes.

This is because higher species richness and abundance of many taxonomic groups are typically found in semi-natural habitats than in intensive land uses due to higher habitat heterogeneity and resource and niche availability associated with undisturbed, natural vegetation (Benton et al. 2003, Fischer et al. 2006, Attwood et al. 2008). Revegetating areas with native trees and shrubs in highly simplified landscapes also can improve biodiversity by providing habitat and increasing connectivity for some taxonomic groups (Gibb and Cunningham 2010, Lindenmayer et al. 2010, 2016).

While biodiversity conservation has traditionally focused on species associated with patches of remnant native vegetation, there has been growing emphasis on the effect of spatial heterogeneity of the overall landscape on species distribution and assemblages (Fahrig and Nuttle 2005, Turner 2005, Vasseur et al. 2013). This has led to repeated calls for conservation ecologists to shift away from a binary patch/matrix perspective to a mosaic view of varying land uses (Ricketts et al. 2001, Bennett et al. 2006, Vasseur et al. 2013), especially in human-dominated landscapes where little or no natural habitat remains (Pimentel et al. 1992, Fournier and Loreau 2001, Bradshaw 2012). More recently, intensively managed farm fields—such as crop monocultures, which typically form the bulk of agricultural landscapes—have been suggested as important drivers of population dynamics and persistence due to their "hidden" habitat value in space and time (Vasseur et al. 2013). This hidden heterogeneity refers to the diversity in management practices and crop types, as well as more subtle changes in crop fields within and between growing seasons. For example, short-term disturbances such as agrochemical use, crop harvest, and grazing, as well as crop rotation over longer time periods (Baudry and Papyz 2001, Bennett et al. 2006), can influence resource availability and affect meta-population dynamics at different spatio-temporal scales (Burel and Baudry 2005, Holland et al. 2005, Bennett et al. 2006). The effects of fine-grained spatio-temporal changes of farm fields on the structure of biotic communities, however, have been rarely studied (Gagic et al. 2012, Vasseur et al. 2013, Puech et al. 2015).

Few studies have concurrently examined a wide range of farm and restoration management options for improving biodiversity (Scott and Anderson 2003, Bridle et al. 2009, Vasseur et al. 2013), while at the same time taking into account the hidden heterogeneity within farm fields (Vasseur et al. 2013). Management changes to alter the mosaic of resources within farm fields may present more cost-effective and practical options for increasing food production (Pywell et al. 2015) while maintaining biodiversity and ecosystem function (Benton et al. 2003, Tscharntke et al. 2005). This is important because not only does large-scale revegetation of productive farmlands reduce food production, but there are large knowledge gaps in the effectiveness of revegetation (especially for arthropod communities, Hunter 2002, Barton and Moir 2015) compared with other farm management strategies (Tscharntke et al. 2005, Holzschuh et al. 2009) potentially compatible with sustainable agricultural intensification (Pywell et al. 2015). For example, farming practices that increase landscape heterogeneity, such as applying fallow rotation and other measures to increase groundcover structural complexity, may be as effective as revegetation in improving farmland biodiversity for some taxonomic groups (Benton et al. 2003).

Arthropods comprise a major component of terrestrial biodiversity and provide important ecological functions in agricultural landscapes such as biological pest control (Lovei and Sunderland 1996, Kromp 1999), pollination, decomposition, and weed control (Grimbacher et al. 2006). However, limited knowledge of the distribution and ecology of many species—including habitat requirements in modified landscapes—impedes their conservation and the maintenance of the ecosystem services they provide (Holland et al. 2005, Cardoso et al. 2011, Marrec et al. 2015). Beetles (Coleoptera) are an ideal group for studying impacts of landscape modification because they are speciose and represent a wide range of trophic and functional groups (Lawrence et al. 2000). Beetles are also expected to respond to management actions because they are sensitive to small-scale changes in habitat and seasonal conditions (Bromham et al. 1999, Gibb and Cunningham 2010, Woodcock et al. 2010).

In agricultural landscapes, more structurally complex habitats (e.g., woodlands, plantings, and fallows) generally support higher species richness and abundance of all trophic groups of beetles and more specialized subfamilies of beetles compared to intensive land uses (e.g., crops; Lassau et al. 2005, Attwood et al. 2008, Newbold et al. 2015). Responses of different beetle groups might also fluctuate over time due to seasonal changes in food availability, habitat quality, or species life cycle (Janzen 1973, Thiele 1977, Grimbacher and Stork 2009). For example, species richness and abundance of most beetle groups might decline between spring and summer due to drier conditions in summer (Hill 1993). However, stronger declines are more likely in intensively cropped land uses due to removal of resources during summer harvest (Sackmann and Flores 2009).

Here, we compared ground-dwelling beetle assemblages between woodland remnants and four adjoining farmland uses comprising crop, fallow, and two restoration treatments (fine woody debris applied over harvested crop fields and restoration plantings). Our key research question was as follows: What are the differences in beetle assemblages between woodland remnants and adjacent farmlands, and over a crop-growing season (spring and summer)?

## MATERIALS AND METHODS

### *Study site and sampling design*

Our study area was a highly modified mixed-cropping landscape within the Lachlan River catchment, New South Wales, southeastern Australia (Fig. 1). Widespread clearing for agriculture has restricted native *Eucalyptus* woodland remnants to

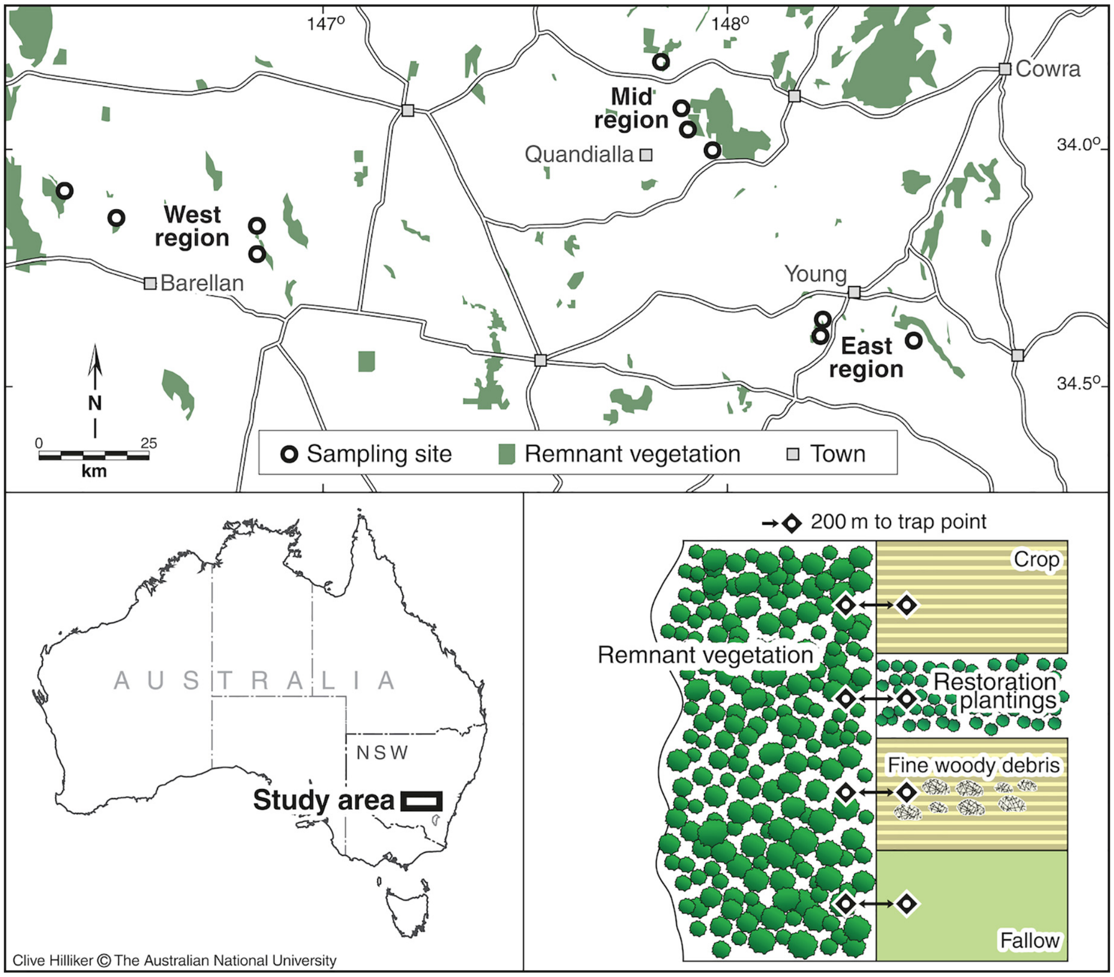

Fig. 1. Map showing study sites in New South Wales, southeastern Australia. Inset shows stylized image of experimental design and pitfall trap placement along four 400-m transects between a remnant patch habitat and adjoining farmland habitats.

infertile steeper areas (Hitchcock 1984, Bradshaw 2012), with many remnants modified by livestock grazing, weed invasion, and changed fire regimes (Norris and Thomas 1991). Our study sites were clustered in three regions along a decreasing elevation and rainfall gradient from the east, mid to west (Fig. 1).

For the purposes of our study, we defined a "patch" as remnant woodland vegetation surrounded by a mostly cleared farmland "matrix". We focused on eleven remnant patches [patch size 4010 ha ± 486.4 ha (mean ± standard error)] selected on the basis that they were *Eucalyptus* woodland communities with high ground-, mid-, and over-story native vegetation complexity (Appendix S1: Fig. S1), with the following adjoining farmland types: (1) winter wheat crop, (2) fallow (rested from crop rotation or sown-pasture rotation), (3) restoration plantings of native shrubs and trees (<7 yr old), and (4) application of eucalypt-based fine woody debris over wheat stubble after harvest prior to sampling (January 2015, Fig. 1; Appendix S1: Fig. S2). The fine woody debris addition is a novel treatment not used previously and piloted in our study to increase ground layer complexity in crop fields to provide resources for arthropod biodiversity. Farmers in our study area were receptive to this treatment because it does not impede cropping machinery unlike larger, coarse woody debris (logs) previously used to restore structural complexity in pastoral areas in Australia (Manning et al. 2013).

### *Beetle sampling*

We used a split-plot sampling design where each remnant patch was matched with the four different farmland matrix types (Fig. 1). We sampled beetles along a 400-m transect from 200 m in each patch out into 200 m in each of the four adjoining farmland matrix types. For consistency in terminology, we referred to each of the four matched patch–matrix combination as a "transect", and referred to either the matrix (which aggregated four matrix types) or patch side as "habitat." We then sampled beetles with a pair of pitfall traps located at each end of the transect: 200 m inside the remnant patch and 200 m in the adjoining farmland matrix (Fig. 1). We chose 200 m because it represented the interior position in smaller farm fields. Individual traps from each pair were placed on either side of a drift fence (60 cm long × 10 cm high) to help direct arthropods into the trap. Traps were plastic jars (6.5 cm diameter, 250 mL) dug into the ground with the rim level with the soil surface, filled with 100 mL of preservative (1:3 glycol–water mixture, and a drop of detergent to reduce surface tension).

We sampled from the same pitfall trap locations during two distinct periods of the cropping cycle (referred to as "time" in our study): spring when crops were at peak flowering, and summer after crop harvest (stubble retained). A total of 88 pairs of traps (11 replicate sites × 4 transects × 2 trap pairs) were opened for 14 d during spring (October–November 2014) and summer (January–February 2015).

Arthropods were preserved in 70% ethanol. All adult beetles were removed and sorted to family and to genus or species where possible. Beetle taxonomy followed Lawrence and Britton (1994) and Lawrence et al. (2000). Where specimens could not be identified to genus or lower, measures of abundance and richness corresponded to morphospecies (sensu Oliver and Beattie 1996), henceforth referred to as species. Each species was assigned to one of three generalized trophic groups: predators, herbivores, and detritivores (including fungivores), based on the predominant feeding behavior of adults at the family and subfamily level, where possible (Lawrence and Britton 1994). We assigned all carabids as predators because purely phytophagous species are considered uncommon in Australia (Gibb et al. 2017). We acknowledge that aggregating data by trophic and family groups may conceal species-level variation. However, this approach is an acceptable compromise for estimating species richness in highly diverse regions where taxa are still poorly described (Ricketts et al. 2001). Higher-level family- and trophic-level patterns may also help provide some capacity to generalize responses for functional groups and infer broad ecological processes (Tscharntke et al. 2005).

### *Statistical analyses*

Samples from each pitfall trap pair were pooled to provide one sample per trap point. Traps at ten sampling points were damaged by vertebrate fauna and discarded from analysis, leaving 166 trap points in total.

We first examined differences in beetle species composition between remnant patches and four farmland matrix types using permutational multivariate analysis of variance (PERMANOVA), based on Bray–Curtis dissimilarities. We ran 999 permutations, and stratified within site and transect to account for the nested sampling design of transects within sites. Singleton species were excluded, and we ran comparisons for spring and summer separately. *P* values were adjusted using sequential Bonferroni corrections to account for multiple comparisons. We used the "vegan" R package for PERMANOVAs (Oksanen et al. 2013).

To identify whether farmland use had an important effect on beetle assemblages in the remnant patch and/or farmland matrix and any interactive effects with time, we used generalized linear mixed-effect models (GLMM, Bolker et al. 2009). Response variables analyzed were the species richness and abundance of the overall assemblage, trophic groups, and the 15 most common families (see Appendix S1: Table S1). The main fixed effects tested were the two-way interactions of transect (four levels: planting, fallow, crop, and woody debris) and habitat (two levels: patch and matrix) or the three-way interactions of transect, habitat, and time (two levels: spring and summer). We controlled for possible effects of region (three levels: east, mid, and west) and remnant patch size (continuous variable) by including them as additive fixed effects, although these factors were not of primary interest in this study. We fitted site, transect location, and trap location as nested random effects (1|site/transect location/trap location) to account for the non-independent spatial structure of the study design and used a Poisson error distribution. If the data were too sparse to fit three-way interactions of transect, habitat, and time, we fitted two-way interactions of transect and habitat as main fixed effects, and (1|site/transect location) as random effects. Note that "transect location" is a four-level factor referring to the spatial placement of each transect nested within a site, while "trap location" is a five-level factor referring to trap placement at five possible locations along a transect. We ran Wald tests and pairwise post hoc Tukey–Kramer tests to identify the statistical significance of fixed effects, and between-treatment response differences, respectively. We also checked model fit by examining residual and fitted plots and checked for overdispersion by dividing the Pearson goodness-of-fit statistic by the residual degrees of freedom and ensuring values were below one (Mccullagh and Nelder 1989). Data were analyzed using R 3.2.0 (R Development Core Team 2015), with the "lme4" (Bates et al. 2015), "car" (Fox et al. 2013), and "multcomp" (Hothorn et al. 2008) R packages for the GLMM analyses.

It is important to note that the split-plot design of our study meant that we were primarily interested in testing for a significant interaction of "transect" and "habitat" (definitions given in the previous section) to provide meaningful information on the effect of the specific farmland uses. In addition, we also were interested in testing for a "habitat" effect because it provides useful information on broader land-use differences between human-modified farmlands and natural remnant patches (see Fig. 1).

## RESULTS

We collected a total of 4065 individual beetles, which comprised 280 species from 35 families (107 herbivore species, 100 predator species, and 73 detritivore species). The most abundant families were Anthicidae (10 species, $n = 1213$), Carabidae (48 species, $n = 757$), Staphylinidae (34 species, $n = 541$), Curculionidae (30 species, $n = 471$), and Tenebrionidae (25 species, $n = 383$; Appendix S1: Table S1).

There was adequate statistical power in the data for analyzing the responses of five families (Carabidae, Staphylinidae, Curculionidae, Anthicidae, and Tenebrionidae). Remnant patch size was discarded from the final models because the variation it explained was not significant (Appendix S1: Table S2).

### *Species composition*

Overall beetle species composition was always significantly different between remnant patches and all farmland matrix types ($P < 0.03$) during spring, and between remnants and woody debris during summer ($P = 0.03$, Table 1). These compositional differences are further demonstrated with 92 species exclusively caught in remnant patches (e.g., *Cubicorhynchus* sp. #262 and *Georissus* sp.), 96 species in the farmland matrix (e.g., *Csiro* sp.), and

Table 1. Pairwise comparisons of beetle species composition dissimilarity (Bray–Curtis) between different land uses, based on permutational multivariate analysis of variance.

| | Spring | | | Summer | | |
|---|---|---|---|---|---|---|
| Habitat pairs | *F* | $R^2$ | *P* adjusted | *F* | $R^2$ | *P* adjusted |
| Patch vs. crop | 3.07 | 0.06 | **0.015** | 2.31 | 0.05 | 0.090 |
| Patch vs. plantings | 1.98 | 0.04 | **0.030** | 1.01 | 0.02 | 1 |
| Patch vs. fallow | 2.02 | 0.04 | **0.030** | 1.92 | 0.04 | 0.120 |
| Patch vs. woody debris | 2.69 | 0.05 | **0.015** | 2.99 | 0.06 | **0.030** |
| Crop vs. plantings | 1.32 | 0.06 | 1 | 1.82 | 0.08 | 0.360 |
| Crop vs. fallow | 1.50 | 0.07 | 0.945 | 1.66 | 0.08 | 0.900 |
| Crop vs. woody debris | 0.34 | 0.02 | 1 | 1.14 | 0.06 | 1 |
| Plantings vs. fallow | 1.34 | 0.07 | 1 | 0.74 | 0.04 | 1 |
| Plantings vs. woody debris | 1.27 | 0.06 | 1 | 1.73 | 0.08 | 0.765 |
| Fallow vs. woody debris | 1.09 | 0.05 | 1 | 1.37 | 0.07 | 1 |

*Note:* Significant values ($P < 0.05$) are shown in bold.

92 species occurring in both habitats (e.g., *Omonadus hesperi* and *Gnathaphanus multipunctatus*, Fig. 2a). Within the farmland matrix, 14% of species occurred only in plantings, 14% only in fallows, 26% only in crops, and a large number of species (>26%) were shared between these different farmland uses (Fig. 2b). After woody debris was applied (only during summer), 36% of species were shared between the crop and woody debris (e.g., *O. hesperi*), while 27% occurred only in the woody debris (e.g., *Aridius* sp. #177 and *Longitarsus* sp. #272, Fig. 2c).

### Species richness

Regardless of specific farmland matrix type, overall beetle species richness was significantly higher in the combined farmland matrix than in remnant patches on a per-trap basis (i.e., significant "habitat" effect, Table 2, Fig. 3a), with nearly twice as many species found in farmlands than in remnant patches. Species richness of predators, detritivores, and herbivores were not influenced by land use (i.e., effects of "habitat" and "habitat" × "transect" were non-significant, Table 2). Patterns of significantly higher species in the farmland matrix than in remnant patches were also exhibited by Carabidae, Staphylinidae, Anthicidae, and Tenebrionidae families (Appendix S1: Fig. S3a, b, e, h).

Between spring and summer, overall beetle species richness significantly decreased in all habitats (Fig. 3b).

### Abundance

Responses for the abundance of a majority of beetle groups depended on interactive effects "transect" × "habitat" × "time", or "transect" × "habitat". Specifically, we found significant three-way interactive effects of "habitat," "transect," and "time" on the abundance of overall beetles, predators, herbivores, as well as predatory Carabidae and herbivorous Curculionidae families. We found significant two-way interactive effects of "habitat" and "transect" on the abundance of detritivores, and the detritivorous Tenebrionidae family (Table 2).

Between spring and summer, predator abundance increased significantly in the fallow and planting matrix (Fig. 4a), while Carabidae abundance significantly decreased in the crop matrix and increased significantly in the fallow matrix (Fig. 5a).

Between spring and summer, herbivore abundance showed no significant differences among all farmland matrix types. Herbivore abundance decreased significantly between spring and summer in remnant patches adjacent to the crop, fallow, and plantings, but not in remnant patches adjacent to the woody debris (Fig. 4b). Curculionidae abundance was highest in fallow fields during spring and decreased significantly in the fallow and woody debris between spring and summer (Fig. 5b).

Detritivore abundance was significantly higher in the woody debris than in the adjacent remnant patch, but not significantly different when comparing crops and plantings with adjacent remnant patches. Detritivore abundance was significantly lower in the fallow than in the adjacent remnant patch (Fig. 4c). Tenebrionidae abundance was significantly higher in the fallow, planting, and

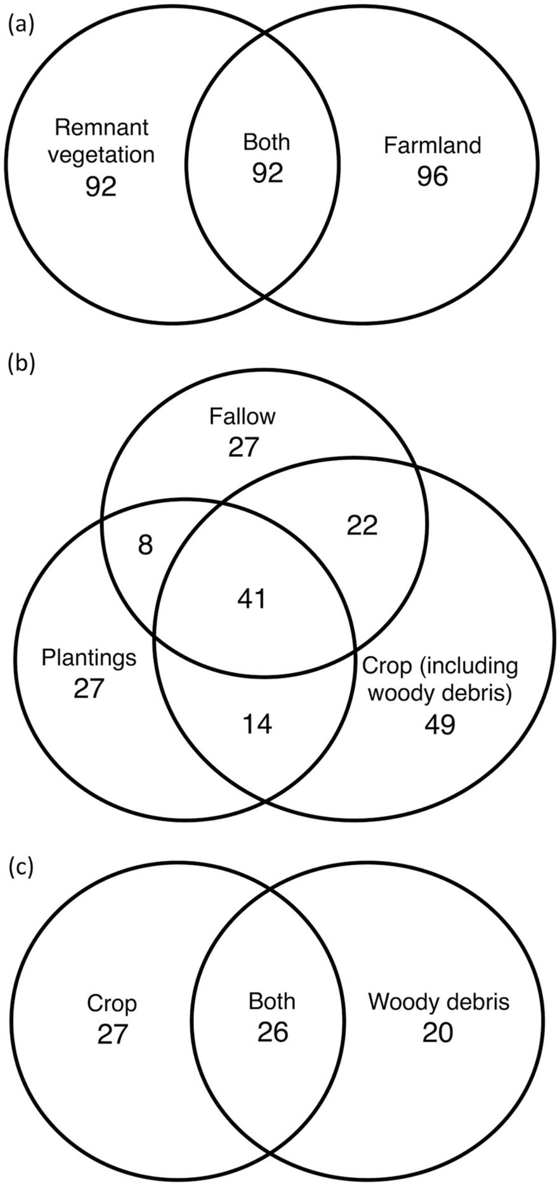

Fig. 2. Venn diagrams showing number of unique and shared species of beetles found (a) in remnant vegetation patch and farmland matrix habitats during both seasons; (b) in plantings, fallow, and crop fields (crop includes fields applied with fine woody debris) during both seasons; and (c) in crop and woody debris during summer only.

woody debris matrix than in the adjacent remnant patch, but differences between the crop matrix and adjacent remnant patch were non-significant (Fig. 5c).

## DISCUSSION

We examined seasonal differences in beetle assemblages between woodland remnants and four contrasting farmland uses in a highly modified agricultural landscape. There were three key findings in our study: (1) Beetle species richness (per trap) was significantly lower in remnants than in all farmland uses combined; (2) beetle composition was significantly different between remnants and farmlands, with a third of species found in both habitats; and (3) abundance responses were often trophic group- or family-specific and influenced by interactions between land use and season. Our findings highlight the importance of maintaining a mosaic of land uses with both spatial and temporal heterogeneity to support beetle biodiversity in agricultural landscapes.

### *Higher species richness in farmlands than in woodland remnants*

We found significantly higher beetle species richness in all farmland uses combined than in woodland remnants, on a per-trap basis. This pattern was underpinned by four abundant families of Carabidae, Staphylinidae, Anthicidae, and Tenebrionidae. This result was unexpected for this landscape because many arthropod taxa are associated with high levels of habitat complexity found in perennial native vegetation (i.e., habitat complexity hypothesis; Lassau et al. 2005, Attwood et al. 2008, Joern and Laws 2013) and are therefore adversely affected by habitat simplification and disturbance from intensive cropping and grazing land uses (Duelli et al. 1999, Hendrickx et al. 2007, Newbold et al. 2015). In addition, the majority of beetles sampled (>90%) were likely to be native species (K. Pullen, *personal communication*) and might be assumed to be associated with natural habitats. We also did not find abundance in farmlands represented by a few species, which is a pattern typically associated with higher productivity in agroecosystems (Ponce et al. 2011). Although our study did not directly examine specific mechanisms, we suggest three plausible interlinked reasons for why we found higher species richness in farmlands than in remnants.

The first possible reason for greater beetle richness in farmlands than in remnants is high nutrient inputs in farmlands, through fertilizer

Table 2. Summary of final generalized linear mixed models for species richness and abundance of (a) overall beetle assemblage, (b) trophic groups, and (c) common families, as predicted by transect type, habitat, time, or region.

| Species richness | | | | Abundance | | | |
|---|---|---|---|---|---|---|---|
| Model terms | $\chi^2$ | df | Pr ($>\chi^2$) | Model terms | $\chi^2$ | df | Pr ($>\chi^2$) |
| (a) All beetles | | | | | | | |
| Transect | 3.11 | 3 | 0.375 | Transect | 4.44 | 3 | 0.218 |
| Habitat | 87.25 | 1 | **<0.001** | Habitat | 69.05 | 1 | **<0.001** |
| Time | 20.17 | 1 | **<0.001** | Time | 21.47 | 1 | **<0.001** |
| Region | 32.55 | 2 | **<0.001** | Region | 16.19 | 2 | **<0.001** |
| Transect × habitat | 2.37 | 3 | 0.500 | Transect × habitat | 20.91 | 3 | **<0.001** |
| Transect × time | 3.99 | 3 | 0.263 | Transect × time | 105.94 | 3 | **<0.001** |
| Habitat × time | 2.65 | 1 | 0.104 | Habitat × time | 0.15 | 1 | 0.703 |
| Transect × habitat × time | 6.07 | 3 | 0.108 | Transect × habitat × time | 21.70 | 3 | **<0.001** |
| (b) Predators | | | | | | | |
| Transect | 0.81 | 3 | 0.847 | Transect | 2.18 | 3 | 0.537 |
| Habitat | 2.27 | 1 | 0.132 | Habitat | 7.59 | 1 | **0.006** |
| Time | 1.34 | 1 | 0.247 | Time | 0.41 | 1 | 0.523 |
| Region | 6.48 | 2 | **0.039** | Region | 6.90 | 2 | **0.032** |
| Transect × habitat | 0.08 | 3 | 0.994 | Transect × habitat | 8.17 | 3 | **0.043** |
| Transect × time | 1.69 | 3 | 0.640 | Transect × time | 13.91 | 3 | **0.003** |
| Habitat × time | 1.74 | 1 | 0.188 | Habitat × time | 33.15 | 1 | **<0.001** |
| Transect × habitat × time | 1.54 | 3 | 0.674 | Transect × habitat × time | 19.33 | 3 | **<0.001** |
| Detritivores | | | | | | | |
| Transect | 1.63 | 3 | 0.652 | Transect | 1.29 | 3 | 0.733 |
| Habitat | 0.00 | 1 | 0.978 | Habitat | 0.71 | 1 | 0.400 |
| Time | 0.19 | 1 | 0.662 | Time | 49.43 | 1 | **<0.001** |
| Region | 5.24 | 2 | 0.073 | Region | 11.43 | 2 | **0.003** |
| Transect × habitat | 1.61 | 3 | 0.656 | Transect × habitat | 34.90 | 3 | **<0.001** |
| Transect × time | 1.22 | 3 | 0.749 | Transect × time | 12.29 | 3 | **0.006** |
| Habitat × time | 0.05 | 1 | 0.818 | Habitat × time | 17.13 | 1 | **<0.001** |
| Transect × habitat × time | 0.10 | 3 | 0.992 | Transect × habitat × time | 6.53 | 3 | 0.088 |
| Herbivores | | | | | | | |
| Transect | 5.51 | 3 | 0.138 | Transect | 4.11 | 3 | 0.250 |
| Habitat | 0.07 | 1 | 0.798 | Habitat | 0.27 | 1 | 0.602 |
| Time | 3.22 | 1 | 0.073 | Time | 81.88 | 1 | **<0.001** |
| Region | 3.34 | 2 | 0.188 | Region | 7.94 | 2 | **0.019** |
| Transect × habitat | 2.69 | 3 | 0.442 | Transect × habitat | 8.52 | 3 | **0.036** |
| Transect × time | 1.99 | 3 | 0.574 | Transect × time | 31.85 | 3 | **<0.001** |
| Habitat × time | 0.03 | 1 | 0.863 | Habitat × time | 12.20 | 1 | **<0.001** |
| Transect × habitat × time | 3.04 | 3 | 0.386 | Transect × habitat × time | 13.09 | 3 | **0.004** |
| (c) Carabidae† | | | | | | | |
| Transect | 6.45 | 3 | 0.092 | Transect | 10.28 | 3 | **0.016** |
| Habitat | 32.89 | 1 | **<0.001** | Habitat | 229.89 | 1 | **<0.001** |
| Region | 11.71 | 2 | **0.003** | Time | 63.96 | 1 | **<0.001** |
| Transect × habitat | 4.52 | 3 | 0.211 | Region | 3.35 | 2 | 0.187 |
| | | | | Transect × habitat | 9.03 | 3 | **0.029** |
| | | | | Transect × time | 105.14 | 3 | **<0.001** |
| | | | | Habitat × time | 0.03 | 1 | 0.859 |
| | | | | Transect × habitat × time | 18.04 | 3 | **<0.001** |
| Staphylinidae† | | | | | | | |
| Transect | 2.65 | 3 | 0.449 | Transect | 3.49 | 3 | 0.322 |
| Habitat | 14.48 | 1 | **<0.001** | Habitat | 22.56 | 1 | **<0.001** |
| Region | 5.54 | 2 | 0.063 | Time | 93.75 | 1 | **<0.001** |
| Transect × habitat | 2.63 | 3 | 0.453 | Region | 7.41 | 2 | **0.025** |

(Table 2. *Continued*)

| Species richness | | | | Abundance | | | |
|---|---|---|---|---|---|---|---|
| Model terms | $\chi^2$ | df | Pr ($>\chi^2$) | Model terms | $\chi^2$ | df | Pr ($>\chi^2$) |
| | | | | Transect × habitat | 4.33 | 3 | 0.228 |
| | | | | Transect × time | 11.04 | 3 | **0.012** |
| | | | | Habitat × time | 0.62 | 1 | 0.432 |
| | | | | Transect × habitat × time | 3.97 | 3 | 0.264 |
| Curculionidae† | | | | | | | |
| Transect | 7.59 | 3 | 0.055 | Transect | 10.78 | 3 | **0.013** |
| Habitat | 0.53 | 1 | 0.466 | Habitat | 0.01 | 1 | 0.942 |
| Region | 2.85 | 2 | 0.240 | Time | 9.52 | 1 | **0.002** |
| Transect × habitat | 11.92 | 3 | **0.008** | Region | 4.09 | 2 | 0.129 |
| | | | | Transect × habitat | 17.95 | 3 | **<0.001** |
| | | | | Transect × time | 33.84 | 3 | **<0.001** |
| | | | | Habitat × time | 0.01 | 1 | 0.912 |
| | | | | Transect × habitat × time | 18.43 | 3 | **<0.001** |
| Anthicidae | | | | | | | |
| Transect | 7.57 | 3 | 0.056 | Transect | 10.80 | 3 | **0.013** |
| Habitat | 32.19 | 1 | **<0.001** | Habitat | 59.60 | 1 | **<0.001** |
| Time | 1.61 | 1 | 0.204 | Time | 148.35 | 1 | **<0.001** |
| Region | 13.97 | 2 | **0.001** | Region | 23.80 | 2 | **<0.001** |
| Transect × habitat | 0.71 | 3 | 0.871 | Transect × habitat | 4.34 | 3 | 0.227 |
| Transect × time | 1.51 | 3 | 0.679 | Transect × time | 43.40 | 3 | **<0.001** |
| Habitat × time | 0.23 | 1 | 0.635 | Habitat × time | 0.20 | 1 | 0.655 |
| Transect × habitat × time | 0.70 | 3 | 0.872 | Transect × habitat × time | 6.20 | 3 | 0.102 |
| Tenebrionidae† | | | | | | | |
| Transect | 0.35 | 3 | 0.950 | Transect | 3.33 | 3 | 0.343 |
| Habitat | 9.15 | 1 | **0.002** | Habitat | 94.63 | 1 | **<0.001** |
| Region | 1.89 | 2 | 0.389 | Region | 1.23 | 2 | 0.542 |
| Transect × habitat | 4.08 | 3 | 0.253 | Transect × habitat | 18.60 | 3 | **<0.001** |

*Note:* Significant values ($P < 0.05$) are shown in bold.
† Two-way interactions were fitted for species richness of families where data were too sparse to fit a three-way interaction.

use. This may have led to increased weed cover, which is a food resource for detritivores, as well as increased prey for insect predators (Abensperg-Traun et al. 1996). Other studies have, for example, found positive and unimodal relationships between productivity and species richness for arthropods and other taxonomic groups (Abensperg-Traun et al. 1996, Mittelbach et al. 2001).

Second, the dominance of extensive areas of farmlands (i.e., area effect) in the landscape may explain the high species richness in farmlands observed in our study (Fahrig 2003, Norton and Reid 2013). Increased resources and ecological niches in continuous farmland habitats may have led to more diverse assemblages, although species richness–area relationships in farmlands are strongly contingent on management practices in those areas (Norton and Reid 2013).

Lastly, the nature of predominant farming practices in the study region may have contributed to the persistence of many species in farmlands. Conservation tillage practices (i.e., reduced tillage and increased stubble retention, Llewellyn et al. 2012) have been adopted widely in Australian cropping systems over the past two decades, including in our study sites. The primary aim of these practices is to minimize soil loss (Holland 2004), but they may have had indirect conservation benefits for beetle assemblages. It is therefore possible that the biodiversity benefits from conservation tillage in Australia are comparable to "extensively managed" agroecosystems in Europe (Bennett et al. 2006, Kleijn et al. 2011) and Japan (Uchida and Ushimaru 2014). Several studies have found a large proportion of species adapted to early successional habitats associated with extensive farming practices (Duelli and Obrist

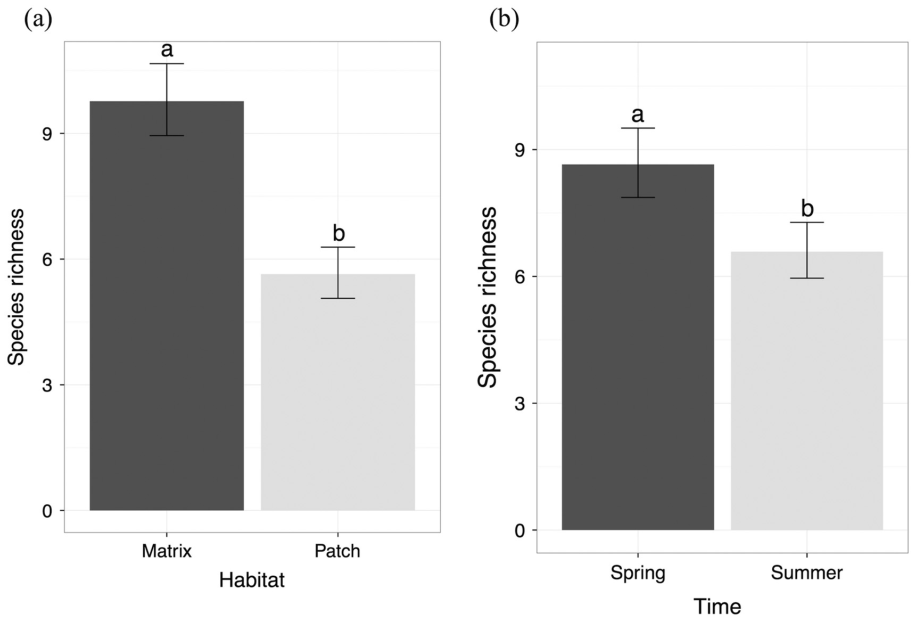

Fig. 3. Predicted mean species richness (per trap) of overall beetles by habitat (a) and time (b) (*P* values in Table 1). Patch refers to remnant vegetation, while matrix refers to four farmland uses combined (crop, fallow, planting, and woody debris). The 95% confidence intervals around predictions are shown. Different letters indicate significantly different results (Tukey–Kramer test).

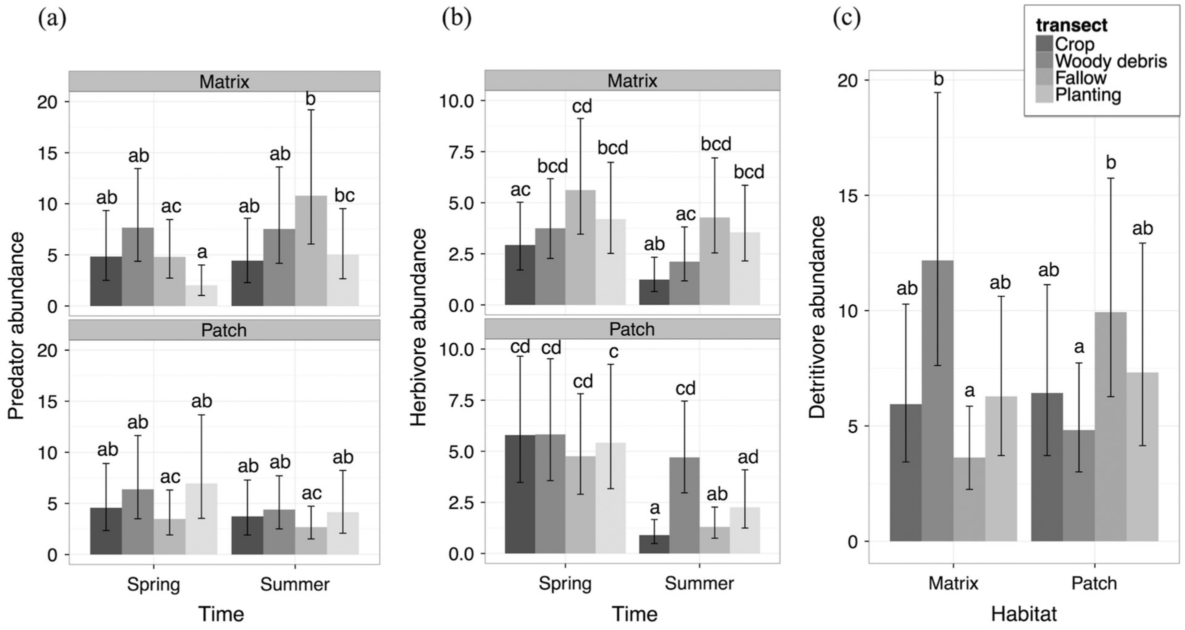

Fig. 4. Predicted mean abundance (per trap) of predators (a) and herbivores (b) to the interaction of "habitat," "transect," and "time," and of detritivores (c) to the interaction of "habitat" and "transect" (*P* values in Table 1). Patch refers to remnant vegetation, while matrix refers to four farmland uses adjoining the remnant (crop, woody debris, fallow, and planting). The 95% confidence intervals around predictions are shown. Different letters indicate significantly different results (Tukey–Kramer test).

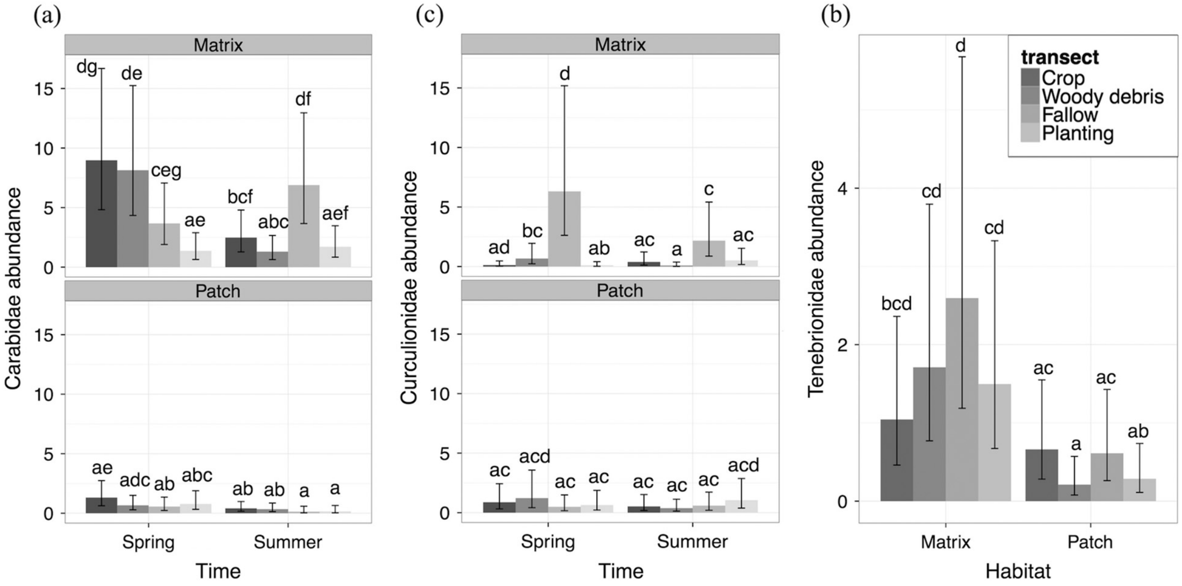

Fig. 5. Predicted mean abundance (per trap) of Carabidae (a) and Curculionidae (b) to the interaction of "habitat," "transect," and "time," and of Tenebrionidae (c) to the interaction of "habitat" and "transect" (*P* values in Table 1). Patch refers to remnant vegetation, while matrix refers to four farmland uses adjoining the remnant (crop, woody debris, fallow, and planting). The 95% confidence intervals around predictions are shown. Different letters indicate significantly different results (Tukey–Kramer test).

2003, Bennett et al. 2006, Sutcliffe et al. 2015), which are characterized by moderate levels of disturbance and high levels of within-field spatial heterogeneity (Bennett et al. 2006, Kleijn et al. 2011, Uchida and Ushimaru 2014).

More studies are needed to determine whether further intensification of agricultural practices, such as management changes from conservation tillage to conventional tillage techniques, would result in declines in arthropod diversity. Long-term studies indicate limited adaptability of arthropod to high-intensity and high-frequency disturbance of soil (Stinner and House 1990, Lovei and Sunderland 1996). In Europe, intensification of farming practices in the 20th century, through increased mechanization, altered disturbance regimes, and the removal of remnant vegetation, has led to drastic reductions in arthropod biodiversity that previously inhabited extensive farming systems (Duelli and Obrist 2003, Tscharntke et al. 2005, Sutcliffe et al. 2015).

### *Differences in species composition between land uses*

A high proportion of beetle species were captured in a variety of farmland uses outside of woodland remnants and appear to respond to spatial and temporal changes in resources or habitat quality associated with farmland heterogeneity. These results suggest that between-habitat heterogeneity (Benton et al. 2003, Vasseur et al. 2013)—particularly at the interface between farmland and remnants, and between different farmland uses—may be an important driver of assemblage patterns in mixed-farming landscapes.

We identified significant differences in species composition between farmlands and remnants (Table 2). Mechanisms underpinning beetle compositional differences could be explained by agricultural land-use changes, which have significantly modified native vegetation through introduction of exotic crops and pastures with agricultural intensification (Attwood et al. 2008, Newbold et al. 2015), and are consistent with the visualization in our principal components analysis showing contrasts in vegetation structure between remnants and farmlands (Appendix S1: Fig. S1). These compositional differences also likely reflect habitat specialization of some species, particularly open-habitat specialists in farmlands and woodland specialists in remnants (Thiele 1977). It should also be noted that the number of species unique to remnants was comparatively higher than those unique to any single farmland uses, which suggests a potentially high number of specialists associated with remnant woodlands.

### Spatio-temporal fluctuations of different beetle groups

Beetle species richness declined significantly in all land uses between spring and summer, a result that was consistent with predictions of stronger declines in species richness and abundance in more intensively managed land uses between spring and summer (Hill 1993, Sackmann and Flores 2009). Significantly lower species richness during late summer may be explained by life cycle dynamics (Sackmann and Flores 2009), with many species being less active or aestivating underground in adult or larvae form during hot summer conditions (Lovei and Sunderland 1996).

We observed interactive effects of land use and season on the abundance of all trophic groups and some families (i.e., Carabidae and Curculionidae), which supports previous work on the spatio-temporal dynamics of arthropods assemblages in agricultural landscapes (Benton et al. 2003, Vasseur et al. 2013). Different taxa have different habitat and resource requirements, which also change over time (Benton et al. 2003). We did not, however, observe stronger declines in abundance in more intensively managed land uses (Sackmann and Flores 2009). Our findings clearly show taxon-specific seasonal changes in habitat or food resources that were associated with specific farmland uses. Here, we discuss spatio-temporal abundance patterns exhibited by each beetle trophic group, and a representative family group, found in our study landscape.

*Predators.*—We found a significant increase in predator abundance in plantings and fallow fields between spring and summer, consistent with predictions of similar land uses having sufficient perennial elements as refuge during adverse summer conditions (Vasseur et al. 2013). For example, the abundance of Carabidae, which comprise the majority of predators in our study, likely followed peaks in resources between wheat crops during spring, and fallow fields during summer after crop harvest. This finding is consistent with studies in Europe and the United States, which identified wheat crops and weedy pastures as favorable habitat and a source of weed seed or prey for polyphagous spring-breeding Carabidae (Lovei and Sunderland 1996, Kromp 1999, Woodcock et al. 2010). An absence of an increase in Carabidae abundance in plantings during summer, however, was unexpected because fallow fields and recent plantings have broadly similar ground layer complexity (K. Ng, *personal observation*). We suggest that other factors associated with plantings (e.g., predation on flightless ground beetles) might explain the inconsistent responses in fallow and plantings for Carabidae compared to predators more generally.

*Detritivores.*—We found that detritivores had similar or higher abundance in farmlands compared to remnant vegetation. Detritivore abundance was generally stable in farmlands and remnant vegetation, and significantly improved in woody debris when comparing with adjacent remnants. However, there was a possible negative effect of fallowing on detritivores. This may be linked to common management practices of fallow fields in this region, particularly grazing by livestock (Barton et al. 2011) or herbicide use (Baudry and Papyz 2001), which are associated with reduced beetle diversity. We also found that abundance of detritivorous Tenebrionidae could be augmented in farmlands by planting native vegetation, fallowing or applying woody debris on crop fields. Our results suggest that non-crop farmland uses may provide population sources of Tenebrionidae, in contrast with woodland remnants which have low numbers of Tenebrionidae. Some members of the Tenebrionidae family, such as *Adelium brevicorne*, *Isopteron* spp., and *Pterohelaeus* spp., are native pests of crop seedlings at larval stages (Gu et al. 2007, Micic et al. 2008). We suggest that retaining woodland remnants near crop fields may help reduce overall deleterious impacts of potential Tenebrionidae pests, although more work is needed to confirm this.

*Herbivores.*—Herbivore abundance, in general, did not differ significantly between remnants and farmlands during both spring and summer, which suggest that these contrasting land uses provide suitable host plant resources for different herbivore assemblages. Interestingly, there was a decrease in herbivore abundance in remnants between spring and summer, except for remnants adjacent to the woody debris treatment. We suggest that woody debris may mitigate temporal decline of some herbivore species in remnants by increasing connectivity in crop fields, therefore facilitating colonization into remnants. Additional data would be needed to determine whether this pattern is related to observed declines in Curculionidae abundance in woody debris between spring and summer.

We also found higher abundance of herbivorous Curculionidae in fallow fields than other land uses during spring, which suggests that fallow fields provide optimal levels of spring-flowering weed or host plant resources for this family (Hangay and Zborowski 2010). This result is consistent previous studies which found high abundance of specialist Curculionidae species in grazed pastures (Batáry et al. 2007, Steiner et al. 2016), with the probability of occurrence for certain species increasing with grassland cover (Batáry et al. 2007). More research is needed to identify plant-species associations that may be driving high Curculionidae abundance when fallowing farmlands.

## Conclusion and Management Implications

Our findings contribute to growing evidence that effective conservation of arthropod diversity needs to consider entire landscape mosaics (Benton et al. 2003, Tscharntke et al. 2005, Bennett et al. 2006, Vasseur et al. 2013) as well as maintain farmland heterogeneity with a mix of low-intensity land uses (Bennett et al. 2006, Kleijn et al. 2011, Uchida and Ushimaru 2014), such as conservation tillage, crop–fallow rotation, and restoration plantings. Complex taxon-specific abundance responses to interactions of land use and/or season indicate that no one single land use had optimal beetle diversity; rather, a diverse mix of farmland uses, which also consider the spatio-temporal heterogeneity of farm fields, is needed to conserve different beetle groups.

How farm fields are managed over time can influence patch dynamics and reduce extinction risks by providing complementary habitats or temporary connectivity for fragmented populations (Bennett et al. 2006, Driscoll et al. 2013, Vasseur et al. 2013). We demonstrated that applying fine woody debris to crop fields is a novel way of providing seasonal refuge for detritivorous beetles (e.g., Tenebrionidae) and improving connectivity for herbivores (e.g., Curculionidae) without taking land out of food production. Fine woody debris may provide additional benefits, such as improving soil condition or providing resources for other litter-dependent fauna (Manning et al. 2013).

High overall species richness and abundance in farmlands suggest that farm fields can potentially be managed for both biodiversity conservation and agricultural production (Tscharntke et al. 2005, Attwood et al. 2008, Bailey et al. 2010, Pywell et al. 2015). However, further intensification of agricultural practices in farmlands, such as increased monocropping, tillage, or agrochemical inputs, may undermine the high level of beetle biodiversity in this region (Tscharntke et al. 2005, Cunningham et al. 2013, Sutcliffe et al. 2015).

Distinct assemblage composition in remnant vegetation patches indicates that farmland on its own is insufficient for conserving all beetle species. Retaining remnant vegetation is still critical for providing stable habitat and species persistence, especially for many species that depend on native vegetation (Bailey et al. 2010, Driscoll et al. 2013), are unable to survive agricultural disturbance, or use natural habitats at certain life stages (Thies et al. 2011, Driscoll et al. 2013).

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## LITERATURE CITED

Abensperg-Traun, M., G. T. Smith, G. W. Arnold, and D. E. Steven. 1996. The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of Gimlet *Eucalyptus salubris* woodland in the Western Australian wheatbelt. I. Arthropods. Journal of Applied Ecology 33:1281–1301.

Attwood, S. J., M. Maron, A. P. N. House, and C. Zammit. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecology and Biogeography 17:585–599.

Bailey, D., M. H. Schmidt-Entling, P. Eberhart, J. D. Herrmann, G. Hofer, U. Kormann, and F. Herzog. 2010. Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. Journal of Applied Ecology 47:1003–1013.

Barton, P. S., A. D. Manning, H. Gibb, J. T. Wood, D. B. Lindenmayer, and S. A. Cunningham. 2011. Experimental reduction of native vertebrate grazing and addition of logs benefit beetle diversity at multiple scales. Journal of Applied Ecology 48: 943–951.

Barton, P., and M. Moir. 2015. Invertebrate indicators and ecosystem restoration. Surrogates and indicators in ecology, conservation and environmental management. CSIRO Publishing, Melbourne, Victoria, Australia.

Batáry, P., A. Báldi, G. Szél, A. Podlussány, I. Rozner, and S. Erdős. 2007. Responses of grassland specialist and generalist beetles to management and landscape complexity. Diversity and Distributions 13:196–202.

Bates, D., M. Mächler, B. Bolker and S. Walker. 2015. lme4: fitting linear mixed-effects models using Eigen and S4. R package version 1.1-8. http://cran.r-project.org/web/packages/lme4/lme4.pdf

Baudry, I., and F. Papyz. 2001. The role of landscape heterogeneity in the sustainability of cropping. Pages 243–249 *in* J. Nösberger, H. H. Geiger, and P. C. Struik, editors. Crop science: progress and prospects. CABI Publishing, Oxfordshire, UK.

Bennett, A. F., J. Q. Radford, and A. Haslem. 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. Biological Conservation 133:250–264.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends in Ecology & Evolution 18:182–188.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Bradshaw, C. J. A. 2012. Little left to lose: deforestation and forest degradation in Australia since European colonization. Journal of Plant Ecology 5:109–120.

Bridle, K., M. Fitzgerald, D. Green, J. Smith, P. Mcquillan, and T. Lefroy. 2009. Relationships between site characteristics, farming system and biodiversity on Australian mixed farms. Animal Production Science 49:869–882.

Bromham, L., M. Cardillo, A. F. Bennett, and M. A. Elgar. 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Australian Journal of Ecology 24:199–207.

Burel, F., and J. Baudry. 2005. Habitat quality and connectivity in agricultural landscapes: the role of land use systems at various scales in time. Ecological Indicators 5:305–313.

Cardoso, P., T. L. Erwin, P. A. V. Borges, and T. R. New. 2011. The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation 144:2647–2655.

Cunningham, S. A., et al. 2013. To close the yield-gap while saving biodiversity will require multiple locally relevant strategies. Agriculture, Ecosystems & Environment 173:20–27.

Driscoll, D. A., S. C. Banks, P. S. Barton, D. B. Lindenmayer, and A. L. Smith. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in Ecology & Evolution 28:605–613.

Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic and Applied Ecology 4:129–138.

Duelli, P., M. K. Obrist, and D. R. Schmatz. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. Agriculture, Ecosystems & Environment 74:33–64.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fahrig, L., and W. K. Nuttle. 2005. Population ecology in spatially heterogeneous environments. Pages 95–118 *in* G. M. Lovett, M. G. Turner, C. G. Jones, and K. C. Weathers, editors. Ecosystem function in heterogeneous landscapes. Springer, New York, New York, USA.

Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4:80–86.

Fournier, E., and M. Loreau. 2001. Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. Landscape Ecology 16:17–32.

Fox, J., M. Friendly, and S. Weisberg. 2013. Hypothesis tests for multivariate linear models using the car package. R Journal 5:39–52.

Gagic, V., S. Hänke, C. Thies, C. Scherber, Ž. Tomanović, and T. Tscharntke. 2012. Agricultural intensification and cereal aphid–parasitoid–hyperparasitoid food webs: network complexity, temporal variability and parasitism rates. Oecologia 170:1099–1109.

Gibb, H., and S. A. Cunningham. 2010. Revegetation of farmland restores function and composition of epigaeic beetle assemblages. Biological Conservation 143:677–687.

Gibb, H., B. Retter, S. A. Cunningham, and P. S. Barton. 2017. Does wing morphology affect recolonization of restored farmland by ground-dwelling beetles? Restoration Ecology 25:234–242.

Gibson, L., et al. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:378–381.

Grimbacher, P. S., C. P. Catterall, and R. L. Kitching. 2006. Beetle species' responses suggest that microclimate mediates fragmentation effects in tropical Australian rainforest. Austral Ecology 31: 458–470.

Grimbacher, P. S., and N. E. Stork. 2009. Seasonality of a diverse beetle assemblage inhabiting lowland tropical rain forest in Australia. Biotropica 41:328–337.

Gu, H., G. P. Fitt, and G. H. Baker. 2007. Invertebrate pests of canola and their management in Australia: a review. Australian Journal of Entomology 46:231–243.

Hangay, G., and P. Zborowski. 2010. A guide to the beetles of Australia. CSIRO Publishing, Canberra, ACT, Australia.

Hendrickx, F., et al. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology 44:340–351.

Hill, C. 1993. The species composition and seasonality of an assemblage of tropical Australian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Australian Entomologist 20:121.

Hitchcock, P. 1984. The survey and allocation of land for nature conservation in New South Wales. Survey Methods for Nature Conservation 2:220–247.

Holland, J. M. 2004. The environmental consequences of adopting conservation tillage in Europe: reviewing the evidence. Agriculture, Ecosystems & Environment 103:1–25.

Holland, J. M., C. F. G. Thomas, T. Birkett, S. Southway, and H. Oaten. 2005. Farm-scale spatiotemporal dynamics of predatory beetles in arable crops. Journal of Applied Ecology 42:1140–1152.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2009. Grass strip corridors in agricultural landscapes enhance nest-site colonization by solitary wasps. Ecological Applications 19:123–132.

Hothorn, T., F. Bretz, P. Westfall, and R. M. Heiberger. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346–363.

Hunter, M. D. 2002. Landscape structure, habitat fragmentation, and the ecology of insects. Agricultural and Forest Entomology 4:159–166.

Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54: 687–708.

Joern, A., and A. N. Laws. 2013. Ecological mechanisms underlying arthropod species diversity in grasslands. Annual Review of Entomology 58: 19–36.

Kleijn, D., M. Rundlöf, J. Scheper, H. G. Smith, and T. Tscharntke. 2011. Does conservation on farmland contribute to halting the biodiversity decline? Trends in Ecology & Evolution 26:474–481.

Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agriculture, Ecosystems & Environment 74:187–228.

Lassau, S. A., D. F. Hochuli, G. Cassis, and C. A. M. Reid. 2005. Effects of habitat complexity on forest beetle diversity: Do functional groups respond consistently? Diversity and Distributions 11:73–82.

Lawrence, J. F., and E. B. Britton. 1994. Australian beetles. Melbourne University Press, Carlton, Australia.

Lawrence, J., A. Hastings, M. Dallwitz, T. Paine, and E. Zurcher. 2000. Beetles of the world a key and information system for families and subfamilies. Version 1.0. CSIRO Entomology, Canberra, ACT, Australia.

Lindenmayer, D. B., E. J. Knight, M. J. Crane, R. Montague-Drake, D. R. Michael, and C. I. Macgregor. 2010. What makes an effective restoration planting for woodland birds? Biological Conservation 143:289–301.

Lindenmayer, D. B., P. W. Lane, P. S. Barton, M. Crane, K. Ikin, D. Michael, and S. Okada. 2016. Long-term bird colonization and turnover in restored woodlands. Biodiversity and Conservation 25:1587–1603.

Llewellyn, R. S., F. H. D'emden, and G. Kuehne. 2012. Extensive use of no-tillage in grain growing regions of Australia. Field Crops Research 132: 204–212.

Lovei, G. L., and K. D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology 41:231–256.

Manning, A. D., R. B. Cunningham, and D. B. Lindenmayer. 2013. Bringing forward the benefits of coarse woody debris in ecosystem recovery under different levels of grazing and vegetation density. Biological Conservation 157:204–214.

Marrec, R., I. Badenhausser, V. Bretagnolle, L. Börger, M. Roncoroni, N. Guillon, and B. Gauffre. 2015. Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape. Agriculture, Ecosystems & Environment 199:282–289.

Mccullagh, P., and J. Nelder. 1989. Generalized linear models. Second edition. Chapman-Hall, London, UK.

Micic, S., A. A. Hoffmann, G. Strickland, A. R. Weeks, J. Bellati, K. Henry, M. A. Nash, and P. A. Umina. 2008. Pests of germinating grain crops in southern Australia: an overview of their biology and management options. Australian Journal of Experimental Agriculture 48:1560–1573.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology 82:2381–2396.

Newbold, T., et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Norris, E., and J. Thomas. 1991. Vegetation on rocky outcrops and ranges in central and south-western New South Wales. Cunninghamia 2:411–441.

Norton, D. A., and N. Reid. 2013. Nature and farming: sustaining native biodiversity in agricultural landscapes. CSIRO Publishing, Collingwood, Victoria, Australia.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. O’hara, G. L. Simpson, P. Solymos, M. H. H. Stevens and H. Wagner. 2013. Package ‘vegan’. Community ecology, R package version 2.3-0. http://CRAN.R-project.org/package=vegan

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology 10:99–109.

Pimentel, D., U. Stachow, D. A. Takacs, H. W. Brubaker, A. R. Dumas, J. J. Meaney, J. A. S. O’neil, D. E. Onsi, and D. B. Corzilius. 1992. Conserving biological diversity in agricultural/forestry systems. BioScience 42:354–362.

Ponce, C., C. Bravo, D. G. De León, M. Magaña, and J. C. Alonso. 2011. Effects of organic farming on plant and arthropod communities: a case study in Mediterranean dryland cereal. Agriculture, Ecosystems & Environment 141:193–201.

Puech, C., S. Poggi, J. Baudry, and S. Aviron. 2015. Do farming practices affect natural enemies at the landscape scale? Landscape Ecology 30:125–140.

Pywell, R. F., M. S. Heard, B. A. Woodcock, S. Hinsley, L. Ridding, M. Nowakowski, and J. M. Bullock. 2015. Wildlife-friendly farming increases crop yield: evidence for ecological intensification. Proceedings of the Royal Society B 282:20151740.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricketts, T. H., G. C. Daily, P. R. Ehrlich, and J. P. Fay. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conservation Biology 15: 378–388.

Sackmann, P., and G. E. Flores. 2009. Temporal and spatial patterns of tenebrionid beetle diversity in NW Patagonia, Argentina. Journal of Arid Environments 73:1095–1102.

Scott, W. A., and R. Anderson. 2003. Temporal and spatial variation in carabid assemblages from the United Kingdom Environmental Change Network. Biological Conservation 110:197–210.

Soliveres, S., et al. 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459.

Steiner, M., E. Ockinger, G. Karrer, M. Winsa, and M. Jonsell. 2016. Restoration of semi-natural grasslands, a success for phytophagous beetles (Curculionidae). Biodiversity and Conservation 25:3005–3022.

Stinner, B. R., and G. House. 1990. Arthropods and other invertebrates in conservation-tillage agriculture. Annual Review of Entomology 35:299–318.

Sutcliffe, L. M. E., et al. 2015. Harnessing the biodiversity value of Central and Eastern European farmland. Diversity and Distributions 21:722–730.

Thiele, H.-U. 1977. Carabid beetles in their environments. A study on habitat selection by adaptation in physiology and behaviour. Springer-Verlag, Berlin, Germany.

Thies, C., et al. 2011. The relationship between agricultural intensification and biological control: experimental tests across Europe. Ecological Applications 21:2187–2196.

Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. Proceedings of the National Academy of Sciences 108:20260–20264.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. Ecology Letters 8:857–874.

Turner, M. G. 2005. Landscape ecology: What is the state of the science? Annual Review of Ecology, Evolution, and Systematics 36:319–344.

Uchida, K., and A. Ushimaru. 2014. Biodiversity declines due to abandonment and intensification of agricultural lands: patterns and mechanisms. Ecological Monographs 84:637–658.

Vasseur, C., A. Joannon, S. Aviron, F. Burel, J.-M. Meynard, and J. Baudry. 2013. The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? Agriculture, Ecosystems & Environment 166:3–14.

Woodcock, B. A., J. Redhead, A. J. Vanbergen, L. Hulmes, S. Hulmes, J. Peyton, M. Nowakowski, R. F. Pywell, and M. S. Heard. 2010. Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. Agriculture, Ecosystems & Environment 139: 181–186.

## Data Availability

Data are available at CSIRO Data Portal: https://doi.org/10.4225/08/5a00f9ab9a8d1

## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2042/full