From plantings to the paddock: ground-dwelling beetles in a dynamic agricultural landscape

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Submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy
of The Australian National University
May 2018

THE AUSTRALIAN NATIONAL UNIVERSITY

Cover image: Green carab beetle, *Calosoma schayeri*, from a study site in Wombat NSW, Australia © Katherina Ng Tien Niu 2018

Candidate's Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author's knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

Katherina Ng Tien Niu Date:

Preface

This thesis is a compilation of four connected papers that have been published or have been submitted for publication in scientific journals. Each paper is a stand-alone body of work. However, there is unavoidable repetition of content and methodology between papers.

The formatting and content of my thesis complies with The Australian National University's College of Science guidelines. An Extended Context Statement has been provided at the beginning of the thesis, which provides a framework for understanding the relationship between the different components of my research. It also identifies themes of relevance to practitioners and future research through the inclusion of a synthesis section, which summarises key findings and emergent issues from my overall research. The Extended Context Statement is not intended to be a comprehensive literature review.

I completed the majority of the work, including: study design, data collection, laboratory work, data analysis and write-up. For all papers, I received substantial guidance from my supervisors: Professor David B. Lindenmayer (DBL), Professor Don A. Driscoll (DAD), Dr Philip Barton (PB), Dr Sarina Macfadyen (SaM) and Dr Sue McIntyre (SuM). For Papers I, II, III and IV, I received statistical advice from Dr Wade Blanchard (WB). For Paper III, I received statistical advice from Ding Li Yong. For Paper IV, I received statistical and intellectual support from Dr Maldwyn John Evans (MJE). All co-authors peer-reviewed written content and agreed to the submission of each paper. The author contribution statements below have been agreed to in writing by all authors listed. Detailed acknowledgments are provided at the end of each paper.

Paper I. Ng K, Driscoll DA, Macfadyen S, Barton PS, McIntyre S, Lindenmayer DB (2017), Contrasting beetle assemblage responses to cultivated farmlands and native woodlands in a dynamic agricultural landscape, *Ecosphere*, https://doi.org/10.1002/ecs2.2042

> Author contributions: KN and DAD conceptualised and designed the experiment; KN analysed data and led manuscript writing; KN conducted field and lab work, with early input from SaM on insect aspects and SuM on vegetation surveys; all authors edited the manuscript. Published in *Ecosphere*.

Paper II. Ng K, Barton PS, Macfadyen S, Lindenmayer DB, Driscoll DA (2017), Beetles' responses to edges in fragmented landscapes are driven by adjacent farmland use, season and cross-habitat movement, *Landscape Ecology*, https://doi.org/10.1007/s10980-017-0587-7

> Author contributions: KN and DAD conceptualised and designed the experiment; KN analysed data (including designing analysis approach) and led manuscript writing; KN conducted field and lab work, with early input from SaM on insect aspects; all authors edited the manuscript, with substantial contributions from PB and DAD during revisions. Published in *Landscape Ecology*.

Paper III. Ng K, McIntyre S, Macfadyen S, Barton PS, Driscoll DA, Lindenmayer DB, in review, Dynamic effects of ground-layer plant communities on beetles in a fragmented farming landscape, *Biodiversity and Conservation*

> Author contributions: KN and DAD conceptualised and designed the experiment; KN analysed data (including designing analysis approach) and led manuscript writing; KN conducted field and lab work, with early input from SaM on insect aspects and SuM on vegetation surveys; MJE contributed to lab work; all authors edited the manuscript, with substantial contributions from PB, SuM and SaM during revisions. Submitted/In review with *Biodiversity and Conservation*.

Paper IV. Ng K, Barton PS, Blanchard W, Evans MJ, Lindenmayer DB, Macfadyen S, McIntyre S, Driscoll DA, in review, Disentangling the effects of farmland use, habitat edges and vegetation structure on ground beetle morphological traits, *Oecologia*

> Author contributions: KN and DAD conceptualised and designed the overall experiment, KN, PB and SaM conceived and developed traits methodology; KN analysed data with statistical input from WB and MJE; KN and MJE conducted lab work; KN conducted fieldwork and led manuscript writing; all authors revised the manuscript. Submitted/In review with *Oecologia*.

Acknowledgements

I am very fortunate to have crossed paths with many people who have made my overall PhD a positive experience. My supervisors – Don Driscoll, David Lindenmayer, Philip Barton, Sarina Macfadyen and Sue McIntyre – have been instrumental mentors to my PhD project and personal development over the years. Their ongoing support and diverse perspectives have carried me through many challenging stages of my PhD, and taught me how to be an analytical, resilient and (ever so slightly) more confident researcher.

I am grateful to Central Tablelands Local Land Services (LLS) for instigating the project and its generous funding, particularly to Milton Lewis, Angus Arnott, Dom Nowlan in the LLS for making this study possible. I am also indebted to the Lake Cowal Conservation Centre (LCCC) for sponsoring and organising the logistics for the ambitious woody debris treatment, and to Mal Carnegie from the LCCC for his local expertise and moral support throughout the project. I am grateful for funding from the ANU under the Australian Government Research Training Program scholarship.

I also sincerely thank the landholders and land managers for access to their properties and support in my project: the Day, Foy, Conlan, Hall, Lucas, Nowlan, Aylott, Grimm, Robinson, Crawford, Daley families, and many other local people I have engaged with during site selection in the Lachlan catchment.

I am thankful for support from the team at the Australian National Insect Collection (ANIC) at CSIRO who have been so patient in helping a clueless insect ecology student gain important foundational knowledge in taxonomy from literally a zero base: Kim Pullen who taught me how to carefully “see” beetles, and many in ANIC who have given me lots of useful advice and reassurance over the years, including Cate Lemann, Debbie Jennings, Federica Turco, Lingzi Zhou, Tom Weir, Rolf Oberprieler, and Zhenhua Liu. I am also very lucky to have received help from other members of the “ento” community – their enthusiasm and genuine willingness to help newcomers have made me proud to be associated with this field: Michael Nash, Margaret Thayer, Vladimir Gusarov, Robert Mesibov, Roberto Pace, and others. I also appreciate plant ID help from the reliably helpful plant ecology community: Mikla Lewis (Young Landcare), Margaret Ning and Rainer Rehwinkel (Friends of Grasslands), Nicki Taws (Greening Australia), Ken Hodgkinson (CSIRO), David

Albrecht (Australian National Botanical Gardens), Mal Carnegie, Roger Good, and many others.

Thank you to volunteers and friends in the lab: John Evans, Daniel Martinez-Escobar, Shauna Priest, Imogen Moore, Krish Sanghvi, Jake Lennon… and in the field: Nicholas Shore, Alicia Ng, Margaret Ning, Dimitris Tsifakis, Hannah Selmes, Ding Li Yong, David Johnson, Hanh Huynh, Temma Carruthers-Taylor, Phil Pritchard, Greg Burgess, Michael Lai. Every additional pair of helping hands and eyes, and all the interesting conversations we've had, have made an impact on my project, in one way or another.

The technical and administrative support from various staff and peers from Fenner School ANU and CSIRO deserve special recognition: Fenner lab (Andrew Higgins); CSIRO lab (Mick Neave); Fenner field services (Mauro Davanzo, Piers Bairstow); Fenner admin (Amy Chen, Jack Pezzey, Kevin Mahoney, Cathy Gray, Julie Watson, Claire Shepherd, Tabitha Boyer); Fenner graphics and IT support (Clive Hilliker, Brendan Meyer); ANU Statistical Consulting Unit & Fenner statisticians (Wade Blanchard, Phil Tennant and Francis Hui).

I am fortunate to have the support of many fellow students, office-mates and friends who have shared useful advice, PhD horror stories, coffee, and smiles over the years: Nicole Hansen ("co-sufferer" working on the herpetofauna story of the joint project), David Johnson, Caroline Wenger, Yong Ding Li, Yuan Peng, Richard Beggs, Sandy Potter, Catherine Ross, Ross Dennis, Shana Nerenberg, Helen King, Depi Susilawati, Sara Nowrouzi, Keith Sclater, Michelle Stuckey, the CSIRO "Management of Biotic Threats" team, the "Lesser Studied Organisms" and "Fenner Union for Contemplative Knowledge" groups; senior/past students who have provided invaluable PhD tips at the early stages: John Evans, Nici Sweaney, Stephanie Pulsford, Dean Ansell, Nelida Villaseñor, Geoff Kay; and many others I might have unintentionally missed. Thanks also to Ann Milligan for editing and writing advice.

I also thank my peers at Australian Bureau of Agricultural and Resource Economics and Sciences for their moral support and in asking how I've been over the years. I'm grateful to my work supervisor Matt Miller for his agronomic advice and in allowing me to take "flexible working conditions" to the extreme. Last but not least, thanks to my husband Dimitris for his unwavering confidence in me finishing this PhD.

Abstract

The intensification of agriculture for increased food production is leading to new challenges for biodiversity conservation, particularly managing complex changing landscapes for mutually beneficial outcomes for agriculture and the environment. My thesis aimed to understand the diversity and distribution of beetles (Coleoptera), and the mechanisms shaping beetle assemblages across a dynamic and fragmented agricultural landscape. I used a landscape-scale study in south-eastern Australia to examine beetle assemblages in remnant woodland patches and four types of adjoining farmlands: crop, fallow, plantings, and fine woody debris applied over harvested crop.

My thesis comprised four chapters written as journal articles. In Paper I, I examined seasonal differences in beetle assemblages between the woodland interior and four adjoining farmland uses. I found that overall species richness was significantly lower in woodlands than farmlands, although both habitats supported significantly different assemblages. Abundance responses were taxon-specific, and influenced by interactions between land-use and season. These results suggest the importance of maintaining farmland heterogeneity with a mix of low-intensity land-uses, with further agricultural intensification a likely threat to beetle diversity in the region.

In Paper II, I examined temporal patterns of edge responses and movement of beetle assemblages between woodlands and the four farmland uses. The use of directional pitfall traps allowed inference of cross-habitat movement. Farmland use and season interactively affected beetle abundance across farmland–woodland edges. Applying woody debris was a novel way of reducing seasonal fluctuations in edge responses and increasing permeability for cross-habitat movement. Edges likely provided resources for beetles in adjoining habitats, but seasonal movement of predators into edges might negatively affect prey assemblages.

In Paper III, I quantified relationships between ground-layer structure, plant species richness and plant composition, and the diversity and composition of beetles from different habitats or seasons. Plant composition better predicted beetle composition than vegetation structure. Plant richness and vegetation structure both significantly affected beetle abundance and composition. The influence of these vegetation attributes often varied depending on habitat and season for all trophic groups. These dynamic plant–beetle relationships suggest a need for targeted ways of managing vegetation to improve beetle diversity in different parts of the landscape.

In Paper IV, I disentangled the effects of farmland use, edge effects and vegetation structure on the morphological traits of Carabidae species. Carabid body size increased across a distance from edges between woodlands and farmlands, and there were strong mediating effects of farmland use on this association. Vegetation structure was associated with traits relating to body size, flying ability and body shape, and helped explain some of the effects of farmland use and edge effects on body size. These results provide evidence of vegetation- and land-use-mediated filtering of traits as an important factor shaping carabid assemblages in human-modified landscapes.

My results indicate that farmlands can provide important habitat for many beetle species. However, spatio-temporal changes in farmland habitat strongly influence beetle assemblages across the landscape. Conservation strategies, therefore, need to take a whole-of-landscape approach, and exploit heterogeneity of mixed-farmlands over space and time to maximise outcomes for biodiversity.

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Extended Context Statement

Introduction

> "The truth is that we need invertebrates but they don't need us. If human beings were to disappear tomorrow, the world would go on with little change […]. But if invertebrates were to disappear, I doubt that the human species could last more than a few months" (Wilson 1987 p. 345)

It is increasingly recognised that the quality and management of human-modified areas (the "matrix") can strongly influence the distribution of species across the landscape, and be more important than the size and spatial arrangement of remaining natural habitat patches (Bender and Fahrig 2005; Kennedy et al. 2011; Prugh et al. 2008; Ricketts 2001; Williams et al. 2006). However, it is unclear how the intensification of food production in farmlands can be managed in a way that mutually benefits both agriculture and the environment (Benton et al. 2003; Millennium Ecosystem Assessment 2005; Smith et al. 2013; Tilman 1999; Tscharntke et al. 2005). This is because conservation has traditionally focused on biodiversity within non-cropped or natural habitats in agricultural landscapes (Benton et al. 2003; Krauss et al. 2004; Kromp and Steinberger 1992; New 2005; Tscharntke et al. 2007), with undisturbed habitats often linked to species survival and persistence at different life stages (Duelli and Obrist 2003; Petit et al. 2002; Sarthou et al. 2014). Conversely, intensive agricultural practices have typically been associated with species-poor communities attributed to habitat simplification, increased agrochemical use, and reduced habitat resources (Bianchi et al. 2006; Desender et al. 1994; Woodcock et al. 2016a).

Recently, more subtle changes in farmlands in space and time have been identified as a potentially important driver of population dynamics and communities in fragmented landscapes. These changes were also referred to as the spatial and temporal variation dimension in the conceptual matrix model of Driscoll et al. (2013). There is, however, limited empirical knowledge on how spatial and temporal changes in farmland quality might influence community assembly (Gagic et al. 2012; Puech et al. 2015; Vasseur et al. 2013), as well as influence core ecological mechanisms such as dispersal, resource availability and edge effects (Driscoll et al. 2013). This is, in part, because of most studies considering a limited number of land-uses, without explicitly accounting for the spatial and temporal heterogeneity that typically characterise human-modified landscapes (Gagic et al. 2012; Gagic et al. 2014; Sarthou et al. 2014). Improved understanding of the influence of this "hidden" farmland heterogeneity Vasseur et al. (2013) may help identify practical and cost-effective farm management strategies for improving biodiversity while still maintaining food production goals (Pywell et al. 2015; Tscharntke et al. 2005).

One of the key challenges in biodiversity conservation is determining whether changes in farming practices to increase structural complexity (e.g. by reducing grazing levels or changing crop type) are comparable with biodiversity-focussed plantings (Holzschuh et al. 2009; Tscharntke et al. 2005), in providing connectivity between habitat patches or providing supplementary resources for adjoining habitats (resource subsidisation; Rand et al. 2006). This is important because not only do large-scale revegetation of productive farmlands might fail to achieve food production, but there are large knowledge gaps in the effectiveness of revegetation (especially for arthropod communities; Barton and Moir 2015; Gibb et al. 2017; Hunter 2002) compared with other farm management strategies (Holzschuh et al. 2009; Tscharntke et al. 2005) potentially compatible with sustainable agricultural intensification (Pywell et al. 2015).

Widespread declines in global arthropod diversity have been the topic of much research (Hallmann et al. 2017; van Swaay et al. 2013; Woodcock et al. 2016b), and there is an urgent need to understand the ecological drivers behind these trends. This is because arthropods represent a major component of terrestrial faunal diversity, and provide a range of ecosystem services (Gibb et al. 2017; Joern and Laws 2013; Wilson 1987), such as pest control (Bianchi et al. 2006; Waterhouse and Sands 2001), nutrient cycling (Didham et al. 1996; Tyndale-Biscoe 1990), seed predation (O’Rourke et al. 2006), and pollination all of which are important in both natural and human-modified ecosystems (Didham et al. 1996; Woodcock et al. 2016a). Limited knowledge on the distribution and movement ecology of many arthropod species, including common and beneficial species, however, remains a key challenge in their conservation (Cardoso et al. 2011; Duelli and Obrist 2003; Holland et al. 2005; Saska et al. 2007). Beetles (Coleoptera) are an ideal arthropod Order for studying landscape modification and fragmentation effects because they are functionally diverse and are sensitive to small-scale environmental changes (Bromham et al. 1999; Gibb and Cunningham 2010; Woodcock et al. 2010). They are also major contributors to many ecological processes because of their abundance and diversity, such that their loss may result in negative cascading effects throughout communities and ecosystems (Coleman and Hendrix 2000; Hallmann et al. 2017; Keesing and Wratten 1998).

Overall research objectives

The overarching aims of my research were to (1) quantify the patterns of diversity of ground-dwelling beetles across a dynamic and fragmented mixed-farming landscape, as well as (2) identify mechanisms underpinning ground-dwelling beetle responses to land-use changes in farmlands. My study contributes to understanding patterns of biodiversity in a heavily cleared farming landscape in south-eastern Australia, where remnant native vegetation is at risk from additional clearing and further agricultural intensification. These kinds of landscapes occur in other parts of world such as South America, eastern Europe and Asia. However, the impact of land-use changes on biodiversity is less understood in these regions compared to North America, and northern and western Europe (Sutcliffe et al. 2015; Thiele 1977; Uchida et al. 2016).

Study area and methodology

My study was conducted in a mixed grazing–cropping landscape within the Lachlan River Catchment, New South Wales, south-eastern Australia (Figure 1). Widespread clearing for agriculture has restricted native *Eucalyptus* woodland remnants (patches) to less fertile steeper areas. Many remnants have been modified by livestock grazing, weed invasion, and altered fire regimes (Hitchcock 1984). However, my study region still contains patches of high quality remnant native vegetation, and there have been substantial efforts to plant native trees and shrubs (particularly *Eucalyptus* and *Acacia*) for biodiversity conservation. Planting is a common habitat restoration tool aimed at increasing biodiversity, ecosystem function, and connectivity between habitat patches (Gibb et al. 2017; Knop et al. 2011; Munro et al. 2009). In agricultural areas, plantings also have other benefits such as providing windbreaks for livestock, reducing soil erosion and soil salinity, improving aesthetics and attracting birds (Coombs 1994; Munro et al. 2009).

Farming in the Lachlan region is characterised as a mixed dryland (i.e. rainfed/non-irrigated) winter cropping–livestock system. Crops are usually planted on a rotational basis (e.g. canola–cereal–pasture) to reduce build-up of soil-borne pests, diseases and weeds, improve soil structure and nutrients (Bell and Moore 2012; Coombs 1994), as well as avoid soil acidity and salinity problems associated with continuous high input cropping (Coombs 1994). Crop rotation patterns may also be influenced by seasonal climate, soil moisture, and commodity prices (Coombs 1994). Crops are generally sown during autumn to early winter (depending on crop variety e.g. early vs.

late season), and harvested during summer, with pre- and post-emergent herbicides and insecticides normally applied. Fertiliser is applied during sowing and top dressed, if required, during spring. Pasture (i.e. fallow) rotations typically have a legume component (e.g. *Trifolium* and *Medicago*), or a legume-based crop (e.g. *Medicago sativa*, *Lupinus angustifolius* and *Lupinus albus*) may be sown as a break crop and to improve the soil nutrient profile. Minimum tillage practices aimed at conserving soil structure, such as direct drilling and stubble retention, are commonly practised. Pastures and crop stubble may be grazed by livestock (sheep or beef cattle) and/or harvested as hay or silage (Coombs 1994).

My study design was based on split-plot sampling with repeated measures. Beetles were pitfall-trapped across a 200 m distance from the edge between remnant woodland patches and four adjoining farmland uses comprising winter cereal crop, fallow and two restoration treatments (native plantings and fine woody debris applied over harvested crop) (Figure 1). Pitfall traps were placed at distinct distances “near” (0 m and 20 m) and “far” (200 m) from the edge, based on previous studies on the likely movement range of ground-active beetles [i.e. from under 10 m in forest ecosystems (Nash et al. 2008) up to 60 m in intensified agroecosystems (Roume et al. 2011)]. The addition of fine woody debris is a novel treatment piloted in our study to increase ground-layer complexity in crop fields after harvest. Farmers were receptive to this treatment because it does not impede cropping machinery. The beetle sampling and sorting methodology, as well as experimental treatments, are described in detail in each of my papers, including the variety of data collected and relevant statistical methods used. Full details on the beetle sampling and vegetation sampling can be found in Papers II and III, respectively.

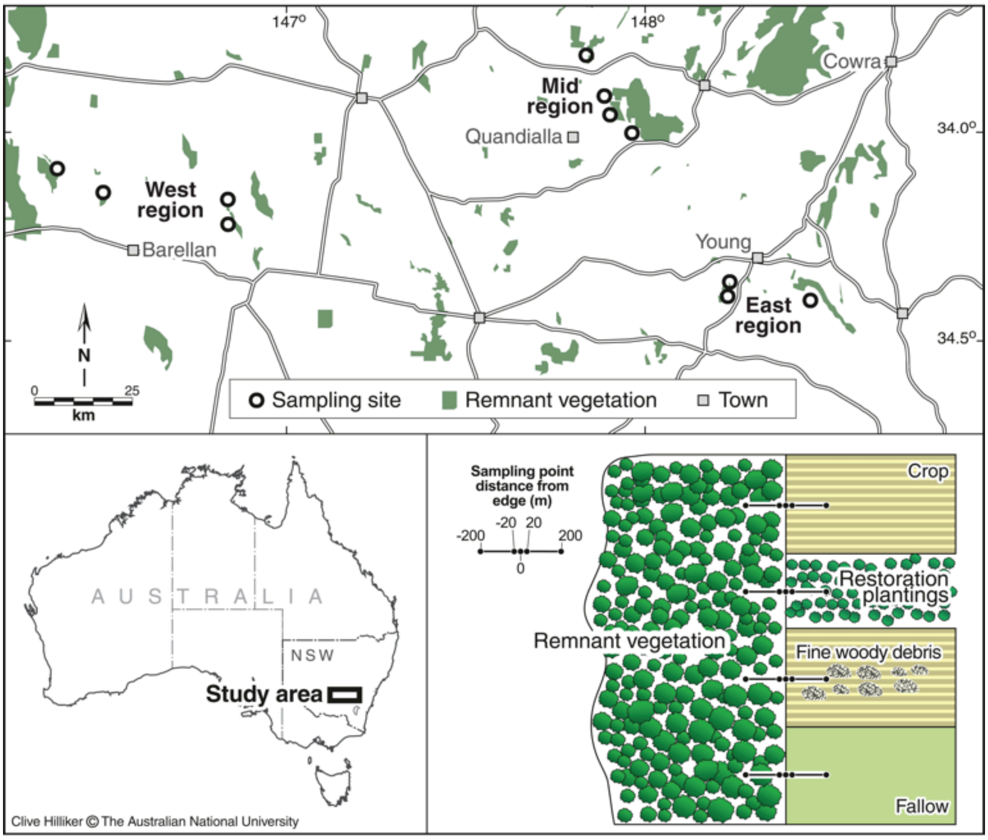

Figure 1. Map showing study sites in New South Wales, south-eastern Australia. Inset shows stylised image of experimental design and pitfall traps placement along four 400 m transects between remnant woodland patch and adjoining farmland habitats. Note that the spatial configurations of habitat types (i.e. ordering of farmland habitats) are varied across the study sites.

Overview of paper objectives and summary of outcomes

Paper I: Contrasting beetle assemblage responses to cultivated farmlands and native woodlands in a dynamic agricultural landscape

In Paper I, I examine differences in beetle assemblages between remnant woodlands and adjacent farmlands, and over a crop-growing season. This paper is an important starting point in understanding seasonal patterns change in of beetle assemblages across a spatially heterogeneous, mixed-farming landscape. I found that, unexpectedly, overall species richness was significantly lower in remnants than 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. These complex responses provide strong support for a mosaic of land-uses to effectively conserve different beetle groups.

Paper II: Beetles' responses to edges in fragmented landscapes are driven by adjacent farmland use, season and cross-habitat movement

Paper II explores the likely ecological mechanisms underpinning the diversity patterns found in Paper I by analysing data from all sampled points along a distance from the woodland–farmland edge. Here, I examine temporal changes in beetle responses to different farmland–woodland edges, and—using directional pitfall traps to infer movement—determine whether there was evidence of cross-habitat movement at certain edge types and time periods. I show that: (1) farmland use and season interactively affect beetle abundance across farmland–woodland edges, (2) applying woody debris is a novel way of reducing seasonal fluctuations in beetle edge responses and increasing permeability for cross-habitat movement, while plantings provide habitat during summer, and (3) that edges are likely to provide resources for beetles in adjoining habitats, but seasonal movement of predators into edges may negatively affect prey assemblages. This study highlights the importance of studying edge responses together with movement patterns to better understand the processes behind observed edge effects for each functional group.

Paper III: Dynamic effects of ground-layer plant communities on beetles in a fragmented farming landscape

In Paper III, I draw on habitat structure and plant species data to quantify relationships between ground-layer structure, plant species richness and plant species composition, and the diversity and composition of beetles from different habitats or seasons. In this paper, I discuss the extent to which different vegetation attributes might explain the dynamic beetle assemblage patterns observed in Papers I and II. I show that: (1) plant species composition better predicts beetle composition than vegetation structure; (2) plant species richness and vegetation structure both significantly affected beetle abundance and composition; (3) the influences of these vegetation attributes often vary in strength and direction between habitats and seasons for all trophic groups. The dynamic nature of plant–beetle relationships suggests a need for targeted ways of managing vegetation to maximise positive outcomes for beetle diversity in different parts of the landscape.

Paper IV: Disentangling the effects of farmland use, habitat edges and vegetation structure on ground beetle morphological traits

Little is known about how species traits of insects vary across different land-uses and their edges, with most studies focussing on single habitat types and not considering edge effects. A traits perspective may help uncover mechanisms shaping assemblage responses to landscape modification. In Paper IV, I examine variation in morphological traits of ground beetles (Coleoptera: Carabidae) on both sides of edges between woodland patches and four adjoining contrasting farmland uses. I show that smaller-sized species were associated with woodlands and larger-sized species with farmlands. Farmland use and edge effects further influenced the strength of these associations, and vegetation structure helped explain the effects of farmland use and distance from edges on body size. This paper highlights habitat complexity as a fundamental driver of ground beetle morphological traits at local and landscape scales, and the mediating role of vegetation structure, farmland use and edge effects in filtering these morphological traits.

Synthesis

This section synthesizes key findings and emergent themes from my overall research. It also provides a summary of recommendations and proposed research priorities for beetle conservation in agricultural landscapes in south-eastern Australia.

Unexpected contribution of farmlands to beetle biodiversity

Findings from my research reveal that farmlands could provide important habitat for a large proportion of native beetle species (results in Paper I revealed that a third of species occurred exclusively in farmlands, and another third of species used both farmlands and adjoining woodlands). My thesis shows that changes in land-use or management within farmlands (Papers I, II), including subtle changes in farmland vegetation structure and plant species composition (Papers III, IV), can significantly influence the assemblage of all beetle trophic groups in both farmland and the woodland habitats. This result was unexpected because farmlands in my study region comprise substantial areas of cultivated cropping, which is an intensive land-use broadly associated with global declines in terrestrial arthropod biodiversity (Benton et al. 2003; Hendrickx et al. 2007; Newbold et al. 2015). Nearly all broadacre cropping in Australia is based on exotic plants (Stoutjesdijk 2013). It is therefore remarkable that my study found high diversity of beetle assemblages, given that the beetles were largely dominated by native species, which could be assumed to be associated with native vegetation (Paper I). My findings highlight that extensive areas of cultivated farmlands cannot be assumed to be a hostile “matrix” for ground-dwelling beetles, and likely also for other arthropods (Driscoll et al. 2013; Fischer et al. 2006). Researchers, land managers and practitioners need to be cognisant of the opportunities to be had in sustainably managing farmlands for arthropod biodiversity at both local and landscape scales.

My results overwhelmingly support studies on the importance of the human-modified areas as potentially suitable new habitat and sources of preferred or supplementary resources for beetles and other fauna, even for species usually found in remnant patches (Driscoll et al. 2013; Fahrig et al. 2011; Lindenmayer et al. 2003; Tscharntke et al. 2005). Finding substantially high native beetle diversity in farmlands may be interpreted as many species having successfully adapted to the environment and disturbance regimes in these farming systems (Lövei and Sárospataki 1990; Tscharntke et al. 2005; Tscharntke et al. 2012). Species living in agricultural habitats are generally expected to be adapted to regular major disturbances from cultivation, including high tolerance limits and high dispersal abilities (Lövei and Sárospataki 1990). Findings from my research indeed suggest a degree of functional adaptation to habitat environments in different farmland uses compared to woodlands. In Paper IV, I found that large-bodied species may have persisted in disturbed habitats in the study landscape through behavioural adaptations such as increased dispersal ability and/or increased physiological tolerance to agricultural disturbances associated with tillage and agrochemical use (Ribera et al. 2001; Tscharntke et al. 2012). Soil conservation farming practices in the study region (i.e. reduced tillage and increased stubble retention; Llewellyn et al. 2012) might have also contributed to the persistence of many species in farmlands (Paper I).

Importance of overall landscape heterogeneity for beetle conservation

My study has highlighted the importance of different land-uses for landscape-level conservation of beetle biodiversity. Paper I, in particular, shows that remnant woodlands and mixed-farmlands supported significantly different assemblages, with differences in taxon-specific abundance in different land-uses over time (e.g. increased abundance of predatory beetles in native plantings and fallows between spring and summer). My findings broadly suggest that, to support diverse beetle assemblages, landscape heterogeneity should be maintained with an appropriate mix of permanent land-uses (particularly remnant woodlands and native plantings) and temporary low-intensity land-uses (such as fallowing and the novel application of fine woody debris over cultivated fields) to provide seasonal habitat resources and facilitate cross-habitat movement (Paper II) and support a range of different species sizes and traits (Paper IV). These results echo previous studies highlighting the important role of habitat heterogeneity in the landscape in driving the diversity and distribution of many different taxa, including beetle assemblages (Benton et al. 2003; Duflot et al. 2014; Fahrig et al. 2011; Kumar et al. 2006). For beetles, landscape heterogeneity is expected to benefit biodiversity because many species have different requirements at different stages of their lifecycles, which might be met in different habitats or at different time periods in a particular habitat (Benton et al. 2003; Fahrig et al. 2011).

Influence of spatio-temporal heterogeneity within farmlands

I found that beetle assemblages in both natural and modified parts of this landscape were strongly influenced by the spatial and temporal heterogeneity within farmlands, including linear farmland habitats such as field edges and plantings (Asteraki et al. 2004; Duflot et al. 2014; Vasseur et al. 2013). This was exemplified by the highly dynamic responses of beetles to changes in farmland uses (Paper I), edge effects (Paper II) and vegetation attributes (Paper III), which were linked to variability in farmlands over space and time. These patterns likely reflected different habitat requirements and population dynamics of distinct species compositions associated with different land-uses (Papers I and II), as well as the variable temporal scale of processes occurring at different spatial scales (Niemela et al. 1992). Species movement between habitats and changes in population patterns were likely dependent on species lifecycle patterns at certain seasons, for example, higher dispersal activity in spring compared to other seasons (Golden and Crist 2000; González et al. 2016; Lovei and Sunderland 1996).

To accurately represent subtle differences in landscape structure, spatio-temporal variability of human-modified areas needs to be considered at an adequate level of granularity for the organism being studied. This is especially important in understanding the drivers of arthropod assemblage patterns, which are often affected by fine-scale changes in environmental conditions (Barton et al. 2013b; Gibb and Cunningham 2010). In Australian cropping systems, seasonal sampling across multiple farmland uses, simultaneously, appears necessary to fully understand beetle distribution patterns, and uncover the likely mechanisms driving these patterns (e.g. Papers I, II and

III demonstrate that beetles use different habitats depending on season, which could be linked to farming practices, species lifecycle and vegetation phenology). This is because different habitat resources over space or time are often necessary to satisfy the varying habitat requirements of a range of different species (Benton et al. 2003). Frequent spatial and temporal changes in habitat quality may have also allowed populations of species to colonise suitable habitats (e.g. annual crops; Wissinger 1997) in a timely manner, enabling survival in mixed-farming landscapes (Perfecto and Vandermeer 2008).

It should be noted that the split-plot design used in my study controlled for the core effects of landscape heterogeneity (*sensu* Fahrig et al. 2011), and allowed detailed examination of the effects of spatio-temporal changes in the farmland "matrix" on beetle responses at both sides of the woodland–farmland interface. My research findings suggest that my study landscape could perhaps be classified as a moderately heterogenous farming landscape. It would be interesting for future studies to quantify whether there are interactive effects of landscape complexity on beetle responses to spatio-temporal dynamics of farmlands. There is still a need for more studies to quantify the effects of heterogeneity within human-modified landscapes by explicitly considering changes along a gradient between intact and highly simplified landscapes (such as those characterised by increasing proportions of natural and cultivated areas; see Fahrig et al. 2011). Such studies may also be able to determine whether many native species (e.g. woodland-specialists) have become locally extinct from land-clearing and historical changes in remnant management (Sweaney et al. 2015).

Remnant woodland patches are important

My research highlights the importance of remnant woodland patches for beetle assemblages, which, in some cases, were contingent on seasonality (Papers I, II, III and IV). The benefits of natural or semi-natural habitats in supporting high levels of biodiversity for various taxa (e.g. flowering plants, invertebrates, birds) are well recognised (Benton et al. 2003; Duelli and Obrist 2003; Sarthou et al. 2014). Besides providing direct resources for native habitat-dependent species, natural habitats also may act as corridors or stepping-stones for movement, and contribute to overall habitat heterogeneity at the landscape scale (Barton et al. 2013a; Benton et al. 2003; Duelli and Obrist 2003). Paper I shows that remnant woodlands supported significantly different beetle species composition compared to farmlands, indicating that farmland on its own is insufficient for conserving all beetle species. Paper III shows that woodland patches might provide vegetation-mediated structural refuge (e.g. ovipositioning or aestivation sites) for predatory beetles during the austral summer. More research on how different species use various parts of the landscape at different times of the year, including remnant habitats, can help determine the configuration of landscape elements that can provide critical habitat resources for species across different life stages. Paper IV shows that species in woodland patches were typically smaller and dispersal-limited, while species in adjoining open farmlands were larger and stronger dispersers. These results suggest that retaining native patches in highly modified landscapes is essential to support a wider range of different species sizes and traits across the landscape, thus promoting higher landscape-level diversity.

Mechanisms shaping beetle assemblages

My thesis identifies several mechanisms that potentially explain the responses of beetle assemblages to the spatio-temporal dynamics of agricultural landscapes: edge effects, cross-habitat movement, dynamic vegetation effects, and filtering of morphological traits.

The nature of edges between different adjoining habitats strongly influences the assemblage of beetles and other fauna, and is linked to changes in abiotic or biotic conditions relating to differences in edge contrasts (Murcia 1995; Ries et al. 2004). In Paper II, I demonstrate that the abundance of all beetle trophic groups at the interface of remnant woodlands and farmlands depended on interactions between distance from the edge, adjoining farmland use, and season. Further, edges likely acted as source habitats by supporting temporally more stable predator richness and higher herbivore richness than adjoining habitats.

In Paper II, I show that cross-habitat movement or spillover possibly explained temporal and spatial fluctuations in edge responses for some predators and detritivores. This supports the theory of cross-boundary agriculture subsidies (i.e. productive farmlands providing important resources for generalists in other habitats; Rand et al. 2006). The importance of inter- and intra-habitat dispersal, as well as the influence of structural attributes (e.g. land-use or vegetation) on dispersal, has been emphasised in other studies ('dispersal core effect' in Driscoll et al. 2013; 'cross-habitat spillover' in Tscharntke et al. 2012). Studies on predatory beetles have also found evidence of population exchanges between the edge and habitat interior, and have highlighted the role of field edges in providing refuges for overwintering species in cultivated farmlands (Sotherton 1984, 1985; Thomas 1990). It is possible that edge-related dispersal activities might have contributed to the survival of species with relatively strong dispersal abilities in agricultural landscapes.

My findings reported in Paper III demonstrate that plant species composition, as well as habitat and temporal context, had an integral role in mediating vegetation effects on beetle assemblages across different parts of the landscape. The paper underscores the highly dynamic influence of vegetation on beetle assemblages across a modified landscape, and that small-scale changes in vegetation attributes contribute to within-habitat heterogeneity in vegetation resources, and therefore having an impact on beetle assemblages. Paper III also identifies the need for more studies on the extent of plant host use at different stages of beetle lifecycles, and on the extent of indirect or direct effects of vegetation composition on predatory species (Joern and Laws 2013; Souza et al. 2016).

In Paper IV, I show the important role of structural complexity in affecting beetle species morphological traits at multiple spatial scales. There was evidence that vegetation and land-use act as a filter on morphological traits, and are important factors shaping ground beetle assemblages (Ribera et al. 2001; Wiescher et al. 2012; Winqvist et al. 2014). This could also be related to the landscape-moderated functional trait selection hypothesis as a factor underpinning community assembly in modified landscapes (Tscharntke et al. 2012).

Relevance of conceptual landscape models on the matrix

My findings are consistent with research on the role of spatial and temporal changes in the human-modified matrix in influencing core mechanisms (i.e. dispersal, resource availability, and edge effects), and ultimately driving patterns of species occurrence and dynamics across the landscape (Driscoll et al. 2013). This is because I found that many beetle species could respond to spatial and temporal availability in resources associated with dynamically changing, modified "matrix" habitats. My study further suggests that ecological mechanisms linked to the dispersal ability (Paper II), edge effects (Paper II), habitat-specific vegetation attributes (Paper III), and morphological traits of beetles (Paper IV) are particularly important in determining beetle responses to land-use changes. It should be noted that the edge effects identified in my study directly correspond to the "abiotic environment" core effect mentioned in Driscoll et al. (2013).

My results clearly indicate that theoretical models of landscapes that delineate patch–matrix habitats (e.g. patch paradigm, Forman 1995; metapopulation ecology, Hanski 1998; island biogeography theory, MacArthur and Wilson 1967) cannot be generalised across whole beetle assemblages in modified landscapes. This is because distinguishing an *a priori* preferred patch habitat is problematic for a large proportion of species. Rather, a more continuous population distribution between different natural and modified (e.g. farmlands) habitats suggests that beetles perceive the landscape as variegated, with a mix of habitats of different suitability (Gascon et al. 1999; McIntyre and Barrett 1992). For beetles, conceptual models that describe landscapes beyond the binary patch–matrix classification might be more applicable, such as mosaic-based (Wiens et al. 1993), or gradient-based models (e.g. continuum model, Fischer and Lindenmayer 2006). It is likely that a wider range of different conceptual models need to be considered to determine specific models that are relevant to individual species responses (Pulsford et al. 2017). Understanding how species or groups of species respond to landscape changes may be a more useful and precise way of classifying landscapes (McIntyre and Hobbs 1999).

Collaboration between conservation ecologists and agroecologists

Finding strong effects of spatio-temporal heterogeneity of farmlands on patch–matrix dynamics in my study highlights the importance of cross-disciplinary research between conservation ecologists and agroecologists. There is relatively little overlap in research focus and data collection between conservation ecologists and agroecologists (Cunningham 2017), which has likely contributed to long-standing rifts between activities aimed at advancing conservation and food production goals. Finding mutually beneficial collaboration opportunities is especially important, given that: (1) my study showed the need to increase sampling efforts to adequately quantify habitat heterogeneity across natural and modified parts of a landscape (both of which are used by many beetle species), (2) field-based landscape studies are constrained by logistical and resource requirements (McGarigal and Cushman 2002), (3) both agronomic and conservation biology knowledge is needed to determine conservation management options that farmers are willing to adopt in their production systems. For example, the fine woody debris treatment in my study is a novel way of increasing ground-layer complexity in the farm matrix to provide shelter resources for arthropod biodiversity with minimal impediment to cropping activities (Papers I, II, III, IV). This treatment was achievable only after consultation with farmers and agroecologists, which resulted in the size (fine mulch) and configuration (below stubble height) of the treatment implemented in a way that did not impede cropping machinery. This approach could be compared with larger, coarse woody debris (logs) that has been successfully used to restore structural complexity in pastoral areas in Australia (Manning et al. 2013), but would be unacceptable in cropped paddocks due to impediments to machinery.

Implications for beetle biodiversity management

I provide seven key management recommendations based on the findings from my research:

i. It is important to maintain a mix of land-uses with both spatial and temporal heterogeneity in habitat quality to support overall beetle biodiversity in agricultural landscapes. This includes farmlands, which if managed sustainably with a proportion of low-intensity land-uses (e.g. crop–pasture rotation and soil conservation practices), can support high beetle species richness (Paper I). Appropriate timing of vegetation management (e.g. promoting overall ground cover during spring and total herbaceous cover during summer) can also have positive outcomes for beetle diversity (Paper III).

ii. Retaining remnant woodland patches is critical for providing seasonal resources and habitat for beetles, particularly native vegetation specialists, and smaller-sized or weak-dispersing species (Papers I, III, IV).

iii. Native plantings may be used by woodland patch-dependent species for habitat resources during summer. Low contrast planting–woodland edges may facilitate higher cross-habitat movement of certain woodland species (Paper II). For example, small species characteristic of woodlands were associated with native plantings as well as woodland edges adjacent to plantings (Paper IV).

iv. Applying fine woody debris to crop fields may provide seasonal refuge and connectivity for detritivorous and herbivorous beetles. More research is needed to determine beetle responses to woody debris over the longer term. Increasing litter cover in cropping systems may provide other benefits such as improving soil condition or providing resources for other litter-dependent fauna (Paper II).

v. Compared to adjoining habitats, field edges between woodland patches and farmlands potentially provided a seasonal refuge for maintaining high species richness of predatory and herbivorous beetles (Paper II). Management that promotes plant species richness at edges, for example, can result in high local beetle diversity (Paper III), which may act as a useful reservoir of beneficial species (Asteraki et al. 1995). However, more work is needed to determine whether existing weed management strategies at field edges have off-target negative impacts on beetle biodiversity (particularly through the loss of plant diversity; Paper III). Research is also needed to determine whether there are detrimental source/sink effects between edges and adjacent habitats at certain times (e.g. spillover of predatory beetles from farmlands to woodlands during summer identified in Paper II).

vi. For relatively mobile taxa such as surface-active arthropods, it is important to design biodiversity monitoring to explicitly account for subtle differences in modified habitats over space (e.g. capturing adequate number of distinct land-uses) and time (e.g. intra-annual variability).

vii. Collaborations between conservation ecologists and agroecologists can help identify practical landscape-level farm management strategies that mutually benefit beetle biodiversity and agricultural production.

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Paper I: Contrasting beetle assemblage responses to cultivated farmlands and native woodlands in a dynamic agricultural landscape

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. In Paper I, I examined differences in beetle assemblages between the interior remnant woodland and the interior of four adjacent farmland uses (crop, fallow, restoration planting and fine woody debris applied over harvested crop), and between spring and summer. This paper is an important starting point in understanding seasonal patterns of beetle assemblages across a spatially heterogeneous, mixed-farming landscape.

Ng K, Driscoll DA, Macfadyen S, Barton PS, McIntyre S, Lindenmayer DB (2017), Contrasting beetle assemblage responses to cultivated farmlands and native woodlands in a dynamic agricultural landscape, *Ecosphere*, https://doi.org/10.1002/ecs2.2042

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 south-eastern Australia. The farmland uses were crops, fallows, and two restoration treatments (fine woody debris applied over harvested crop fields, restoration plantings). Unexpectedly, overall species richness was significantly lower in remnants than 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; matrix; tillage; landscape mosaic; restoration.

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 (Attwood et al. 2008; Benton et al. 2003; Hendrickx et al. 2007). 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 intensive land-uses due to higher habitat heterogeneity, resource and niche availability associated with undisturbed, natural vegetation (Attwood et al. 2008; Benton et al. 2003; Fischer et al. 2006). 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; Lindenmayer et al. 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 (Bennett et al. 2006; Ricketts et al. 2001; Vasseur et al. 2013), especially in human-dominated landscapes where little or no natural habitat remains (Bradshaw 2012; Fournier and Loreau 2001; Pimentel et al. 1992). 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 (Bennett et al. 2006; Burel and Baudry 2005; Holland et al. 2005). 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; Puech et al. 2015; Vasseur et al. 2013).

Few studies have concurrently examined a wide range of farm and restoration management options for improving biodiversity (Bridle et al. 2009; Scott and Anderson 2003; 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. 2005a). 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; Barton and Moir 2015; Hunter 2002) compared with other farm management strategies (Holzschuh et al. 2009; Tscharntke et al. 2005a) 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 (Kromp 1999; Lovei and Sunderland 1996), 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 (Cardoso et al. 2011; Holland et al. 2005; 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) (Attwood et al. 2008; Lassau et al. 2005; 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 (Grimbacher and Stork 2009; Janzen 1973; Thiele 1977). 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: 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, south-eastern Australia (Figure 1). Widespread clearing for agriculture has restricted native *Eucalyptus* woodland remnants to infertile steeper areas (Bradshaw 2012; Hitchcock 1984), 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 (Figure 1).

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

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 +/- SE)] selected on the basis that they were *Eucalyptus* woodland communities with high ground-, mid- and over-storey native vegetation complexity (Figure S1 in Paper I: Supplementary Material), 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 years old), and (4) application of eucalypt-based fine woody debris over wheat stubble after harvest prior to sampling (January 2015; Figure 1, Figure S2 in Paper I: Supplementary Material). 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 (Figure 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 (Figure 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 x 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 x 4 transects x 2 trap pairs) were opened for 14 days 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 behaviour 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 generalise responses for functional groups and infer broad ecological processes (Tscharntke et al. 2005a).

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 PERMANOVA analyses (Oksanen et al. 2013).

To identify if 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 analysed were the species richness and abundance of the overall assemblage, trophic groups and the 15 most common families (Table S1 in Paper I: Supplementary Material). The main fixed effects tested were the two-way interactions of transect (four levels: planting, fallow, crop, woody debris) and habitat (two levels: patch, matrix) or the three-way interactions of transect, habitat and time (two levels: spring, summer). We controlled for possible effects of region (three levels: east, mid, 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 analysed 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 Figure 1).

Results

We collected a total of 4,065 individual beetles, which comprised 280 species from 35 families (107 herbivore species, 100 predator species, 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) (Table S1 in Paper I: Supplementary Material).

There was adequate statistical power in the data for analysing 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 (Table S2 in Paper I: Supplementary Material).

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 92 species occurring in both habitats (e.g. *Omonadus hesperi* and *Gnathaphanus multipunctatus*) (Figure 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 (Figure 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) (Figure 2c).

Table 1. Pairwise comparisons of beetle species composition dissimilarity (Bray–Curtis) between different land-uses, based on permutational multivariate analysis of variance (PERMANOVA). Significant values (P < 0.05) shown in bold.

	Spring			Summer		
Habitat pairs	F	R2	P adjusted	F	R2	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

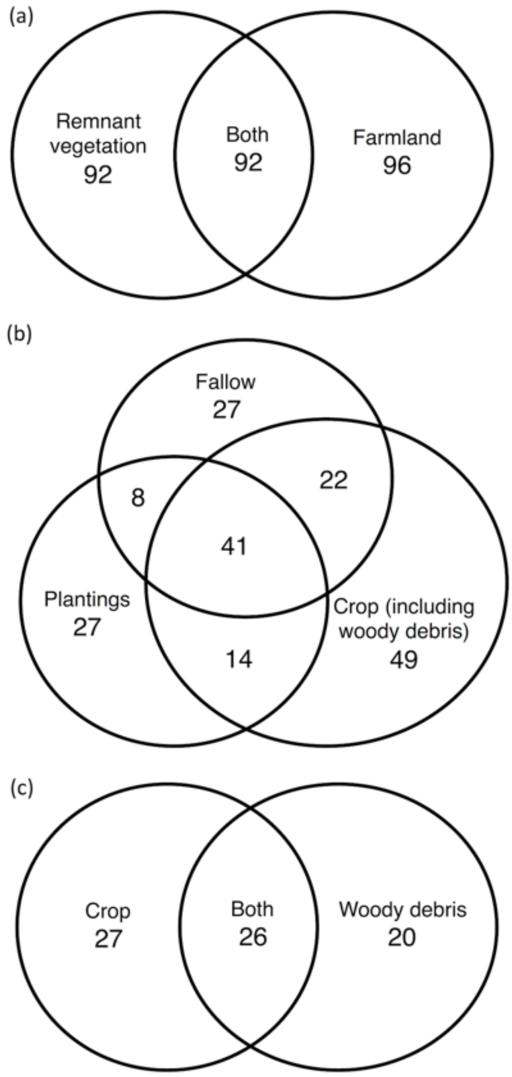

Figure 2. Venn diagrams showing number of unique and shared species of beetles found (a) in remnant vegetation patch and farmland matrix habitats during both seasons; (b) in plantings, fallow and crop fields (crop includes fields applied with fine woody debris) during both seasons; and (c) in crop and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

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, Figure 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 (Figures S3a,b,e,h in Paper I: Supplementary Material).

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

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. Significant values (P < 0.05) shown in bold.

	Species richness				Abundance			
Response	Model terms	Chisq	Df	Pr(>Chisq)	Model terms	Chisq	Df	Pr(>Chisq)
(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**
					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**

[†] Two-way interactions were fitted for species richness of families where data were too sparse to fit a three-way interaction.

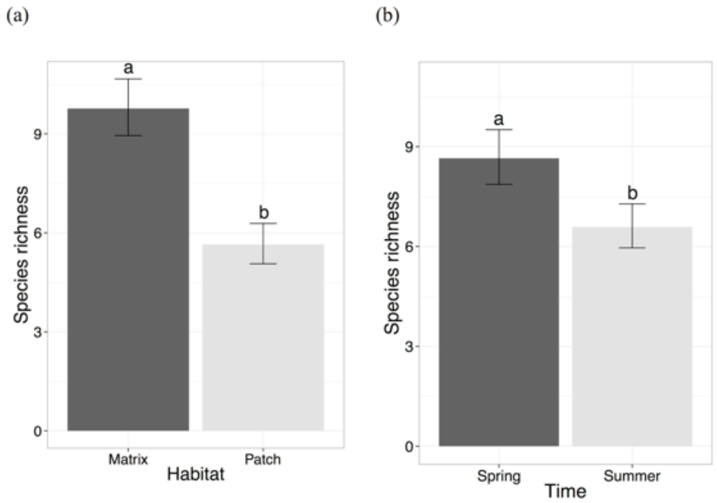

Figure 3. Predicted mean species richness (per trap) of overall beetles by habitat (a) and time (b) (P-values in Table 1). Patch refers to remnant vegetation, while matrix refers to four farmland uses combined (crop, fallow, planting, woody debris). 95% confidence intervals around predictions shown.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

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 (Figure 4a), while Carabidae abundance significantly decreased in the crop matrix and increased significantly in the fallow matrix (Figure 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 (Figure 4b). Curculionidae abundance was highest in fallow fields during spring, and decreased significantly in the fallow and woody debris between spring and summer (Figure 5b).

Detritivore abundance was significantly higher in the woody debris than 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 the adjacent remnant patch (Figure 4c). Tenebrionidae abundance was significantly higher in the fallow, planting and woody debris matrix than the adjacent remnant patch, but differences between the crop matrix and adjacent remnant patch were non-significant (Figure 5c).

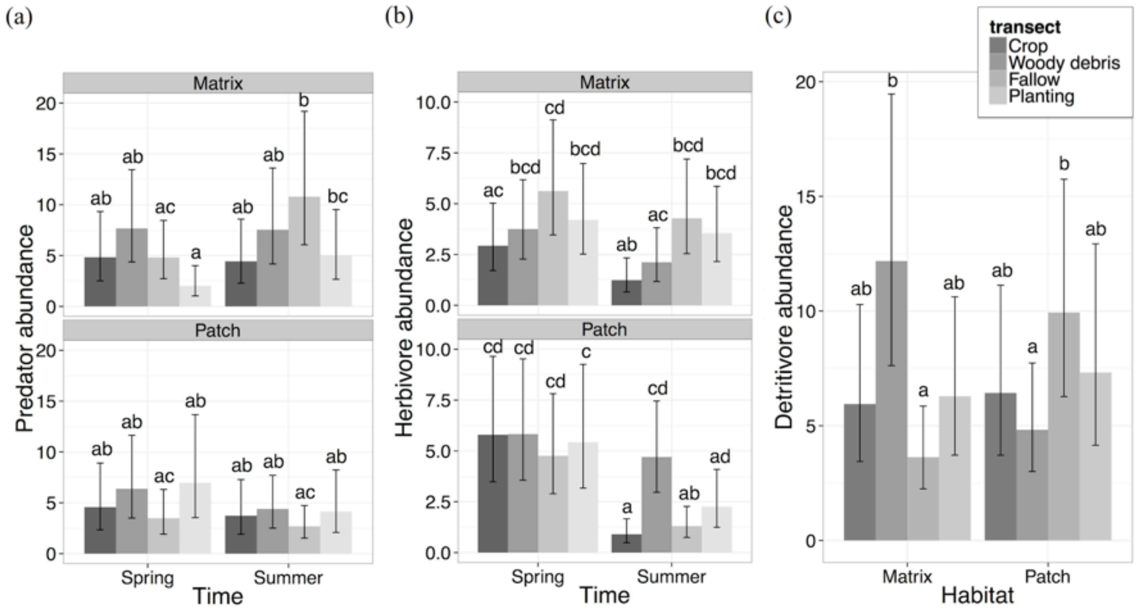

Figure 4. Predicted mean abundance (per trap) of predators (a) and herbivores (b) to the interaction of 'habitat', transect' and 'time', and of detritivores (c) to the interaction of 'habitat' and 'transect' (P-values in Table 1). Patch refers to remnant vegetation, while matrix refers to four farmland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

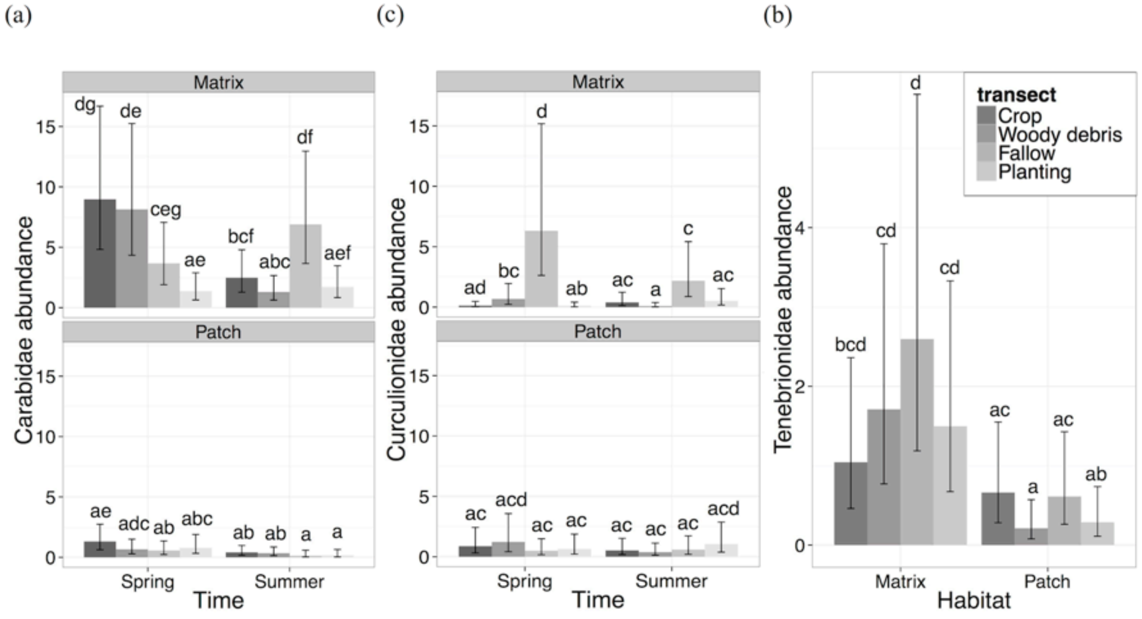

Figure 5. Predicted mean abundance (per trap) of Carabidae (a) and Curculionidae (b) to the interaction of 'habitat', transect' and 'time', and of Tenebrionidae (c) to the interaction of 'habitat' and transect' (P-values in Table 1). Patch refers to remnant vegetation, while matrix refers to four farmland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

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 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 woodland remnants

We found significantly higher beetle species richness in all farmland uses combined than 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; Attwood et al. 2008; Joern and Laws 2013; Lassau et al. 2005), 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 (Pullen, pers. comm.) 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 remnants.

The first possible reason for greater beetle richness in farmlands than remnants is high nutrient inputs in farmlands, through fertilizer 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 (Bennett et al. 2006; Duelli and Obrist 2003; 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 a 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 (Lovei and Sunderland 1996; Stinner and House 1990). In Europe, intensification of farming practices in the 20th century, through increased mechanization, altered disturbance regimes and the removal of remnant vegetation, have led to drastic reductions in arthropod biodiversity that previously inhabited extensive farming systems (Duelli and Obrist 2003; Sutcliffe et al. 2015; Tscharntke et al. 2005a).

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 is consistent with the visualization in our principal components analysis showing contrasts in vegetation structure between remnants and farmlands (Figure S1 in Paper I: Supplementary Material). 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 were 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 USA, which identified wheat crops and weedy pastures as favourable habitat and a source of weed seed or prey for polyphagous spring-breeding Carabidae (Kromp 1999; Lovei and Sunderland 1996; 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 (KN, pers. obs.). 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. 2011b) 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 *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 colonisation into remnants. Additional data would be needed to determine if 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 (Bennett et al. 2006; Benton et al. 2003; Tscharntke et al. 2005a; 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 suggests that farm fields can potentially be managed for both biodiversity conservation and agricultural production (Attwood et al. 2008; Bailey et al. 2010; Pywell et al. 2015; Tscharntke et al. 2005a). 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 (Cunningham et al. 2013; Sutcliffe et al. 2015; Tscharntke et al. 2005a).

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 (Driscoll et al. 2013; Thies et al. 2011).

Acknowledgements

This work was supported by Central Tablelands Local Land Services (through Australian Government funding), Lake Cowal Foundation and Mount Mulga Pastoral Company. Thanks to landholders (Day, Foy, Conlan, Hall, Lucas, Nowlan, Aylott, Grimm, Robinson, Crawford, Daley families) for property access. We are grateful to Alicia Ng, Nicholas Shore, Margaret Ning, Phil Pritchard, Dimitrios Tsifakis, Mal Carnegie, Hanh Huynh, Greg Burgess, Hannah Selmes, Yong Ding Li, Jake Lennon, Temma Carruthers-Taylor and Michael Lai for fieldwork assistance; Daniel Martinez-Escobar, Shauna Priest, Imogen Moore and Jake Lennon for lab assistance; Maldwyn John Evans, Kim Pullen, Michael Nash, Lingzi Zhou, Rolf Oberprieler, Vladimir Gusarov and Roberto Pace for beetle identification; Wade Blanchard for statistical advice; and Clive Hilliker for Figure 1 illustration. We thank Saul Cunningham, Loup Rimbaud and anonymous reviewers for helpful comments on the manuscript.

Data availability

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

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Paper II: Beetles' responses to edges in fragmented landscapes are driven by adjacent farmland use, season and cross-habitat movement

In Paper I, I showed that overall species richness was significantly lower in woodlands than adjacent farmlands, while abundance responses were influenced by interactions between land-use and season. Paper II studies the likely ecological mechanisms underpinning these patterns by analysing data from all sampled points along a distance from the woodland–farmland edge, and takes advantage of directional pitfall traps data to infer movement bias. This allows me to examine the temporal patterns of edge responses and movement of beetle assemblages between remnant woodlands and the four farmland uses.

Ng K, Barton PS, Macfadyen S, Lindenmayer DB, Driscoll DA (2017), Beetles' responses to edges in fragmented landscapes are driven by adjacent farmland use, season and cross-habitat movement, *Landscape Ecology,* https://doi.org/10.1007/s10980-017-0587-7

Abstract

Context. Farming practices influence the degree of contrast between adjoining habitats, with consequences for biodiversity and species movement. Little is known, however, on insect community responses to different kinds of edges over time, and the extent of cross-habitat movement in agricultural landscapes.

Objective. To determine temporal changes in beetle responses to different farmland–woodland edges, and document cross-habitat movement.

Methods. We examined species richness, abundance, and movement across edges between remnant woodlands and four farmland uses (plantings, fallow, annual crops, woody debris applied over crops post-harvest) in southeastern Australia. We used directional pitfall traps to infer movement, and sampled at edges, and 20 m and 200 m on both sides of edges, during spring and summer.

Results. Detritivore and predator abundance varied between seasons across the edge between woodlands and all farmlands, but seasonal differences were weaker for fallow–woodland and woody debris–woodland edges. Detritivores moved from farmlands towards woodlands, but not across fallow–woodlands and woody debris–woodlands edges during summer. During summer, predators showed short-range movement towards edges from all farmlands except plantings, and towards woody debris from woodlands. Edges showed temporally stable predator richness and higher herbivore richness than adjoining habitats.

Conclusions. Farmland use and season interactively affect beetle abundance across farmland–woodland edges. Woody debris can reduce seasonal fluctuations in beetle edge responses and increase permeability for cross-habitat movement, while plantings provide habitat during summer. Edges provide important resources for beetles in adjoining habitats, however, seasonal movement of predators specifically into edges may affect prey assemblages—a link requiring further study.

Keywords: agroecosystem; Coleoptera; dispersal; spatial subsidies; spillover

Introduction

Boundaries between distinct habitat types are increasingly forming a large proportion of human-modified landscapes (González et al. 2016; Haddad et al. 2015; Ries et al. 2004) due to clearing and fragmentation of native vegetation and the establishment of crops and pastures (Didham 2010; Ewers and Didham 2006b; Haddad et al. 2015). Ecological changes associated with these habitat edge interfaces – termed edge effects – can strongly influence populations of species and community structure by altering abiotic and biotic conditions (Cadenasso et al. 2003; Murcia 1995; Ries et al. 2004). These changes may result in differences in resource availability (Ries and Sisk 2004), microclimate conditions, or species interactions between the edge and interior of a habitat (Ewers et al. 2013; Fagan et al. 1999).

It is difficult to generalize how different taxa will respond to edges (Didham 2010; Laurance et al. 2007; Ries and Sisk 2004). Studies of edge effects have reported highly variable patterns, including scale- and context-dependent responses (Murcia 1995; Ries et al. 2004; Ruffell and Didham 2016). For many ecological communities, there are limited empirical data to assess the relevance of well known conceptual models of edge effects developed by Duelli et al. (1990) and Ries and Sisk (2004), which incorporate information on species habitat association and/or the distribution of resources across habitat edges.

There are three key knowledge gaps on edge effects in farming landscapes: (i) the interaction between spatial and temporal variations within farmland habitats, (ii) the role of species movement as a mechanism influencing edge responses, and (iii) quantifying responses at both sides of edges. First, most fragmentation studies consider a limited number of land-uses, or implicitly assume that species edge responses are spatially and temporally homogenous (Didham 2010; Murcia 1995). However, seasonal farm management activities, such as planting or harvesting, introduce a temporal dynamic that modifies the degree of contrast between habitats on each side of an edge (Ries et al. 2004; Vasseur et al. 2013). There is still limited understanding of how such spatial and temporal changes in habitats affect edge responses.

A second key gap is the potential role of species movement as a mechanism affecting variability in edge responses (González et al. 2016). Species movement across different edges and habitat types often shapes most edge responses (González et al. 2016). Despite available methods for tracking movement direction, most studies have inferred cross-habitat movement (also termed ‘spillover effects’) using density data, which ignores directionality (Madeira et al. 2016; Rand et al. 2006). Directional traps (Duelli et al. 1990; González et al. 2016; Macfadyen and Muller 2013), mark–recapture (Corbett and Rosenheim 1996) and direct tracking (Daniel Kissling et al. 2014) are examples of methods for collecting more robust movement information that may shed light on the influence of movement on edge responses.

Third, most edge studies restrict their observations to one side of an edge (Campbell et al. 2011; Ries et al. 2004). Studies on movement from farmlands to native habitats, specifically, are uncommon despite edge-mediated influences on microclimate, dispersal, and ecosystem processes affecting both sides of edges (Baker et al. 2016; Rand et al. 2006). Altered trophic interactions from spillover of functionally important taxa from farmlands may affect species persistence and ecosystem functioning in native habitats (Blitzer et al. 2012; Madeira et al. 2016; Rand et al. 2006). For example, higher predator abundance in farmlands may lead to predator spillover, and thus increased pest suppression, in adjacent remnants. Accurate knowledge of edge responses and mechanisms can be obtained only by examining both sides of edges (Ewers and Didham 2006b; Villaseñor et al. 2015).

We used directional traps on both sides of edges between woodland patches and adjoining farmlands to gather information on assemblage structure and movement between seasons. Our study aimed to understand how different types of farm land-use in a fragmented mixed cropping–grazing landscape affect temporal patterns in edge responses and movement of ground-dwelling beetle assemblages. We focussed on beetles because they are functionally diverse (different trophic groups using varying resources in each habitat; Lassau et al. 2005), sensitive to small-scale habitat changes (Gibb and Cunningham 2010) and have short reproduction cycles, making them ideal for studying edge effects over time (Murphy et al. 2016).

For species richness and abundance of all beetles, and their trophic groups, we asked the following questions:

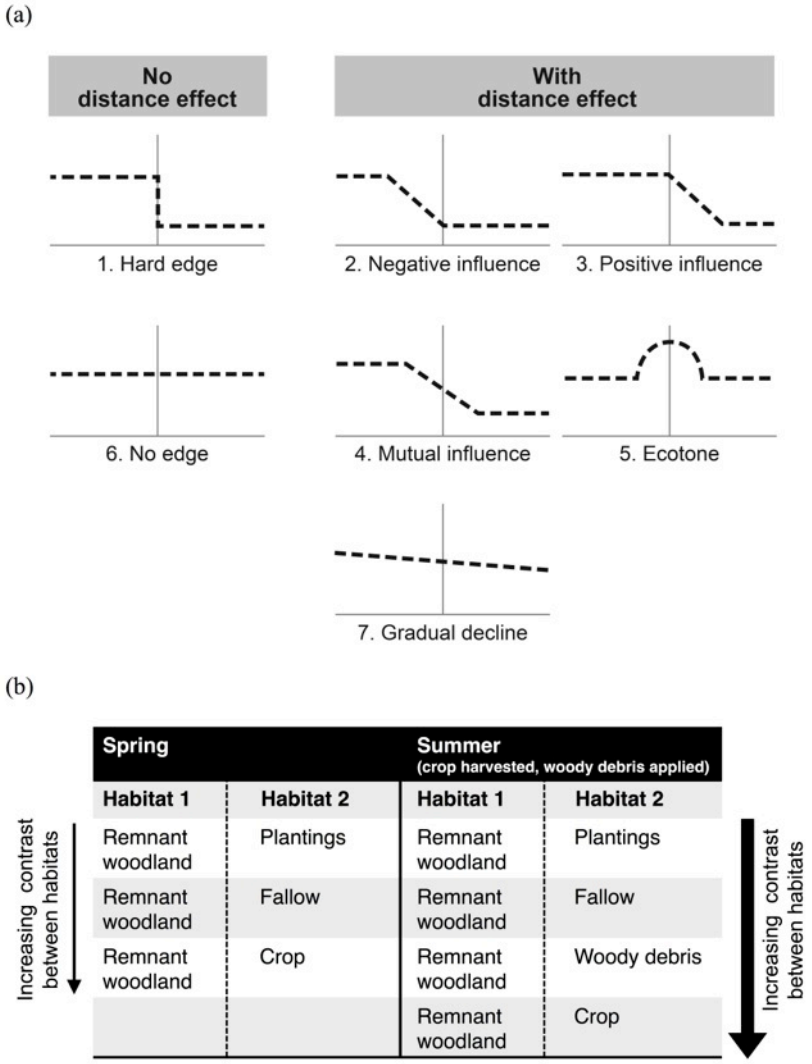
1. How do different farmland uses (crop, fallow, planting and woody debris) influence beetle responses with increasing distances from both sides of farmland–woodland edges?
2. How do beetle responses to the four types of farmland–woodland edge contrasts change over time?
3. Is there evidence of cross-habitat movement across the farmland–woodland edge, and are temporal changes in movement patterns related to temporal changes in beetle responses to the edge?

To guide interpretation of the occurrence and relative strength of edge effects on either side of the edge, we refer to seven theoretical edge response patterns that may be observed in our study (Figure 1a; adapted from Duelli et al. 1990). We followed the numbers and terminology used by Duelli et al. (1990) for the six original categories but added a new category 7 (“gradual decline”), which for the purposes of our study, could be interpreted as a transition between categories 4 (“mutual influence”) and 6 (“no edge”).

For *Question 1*, we expected the abundance of many species to vary with distance from the edge (Ries et al. 2004) (Figure 1a). We also expected that edges with higher habitat contrast would exhibit larger differences in beetle assemblages between adjoining habitats (i.e. stronger edge effects between crop–woodland edges) than lower contrast edges (i.e. weaker edge effects between planting–woodland edges) (Ewers and Didham 2006b) (Figure 1b). We also expected species richness to be highest at edges due to overlapping communities from adjacent habitats (Downie et al. 1996; Ewers and Didham 2006b).

For Question 2, we expected edge effect patterns to differ over time following seasonal patterns in resource availability and habitat use (Baker et al. 2016; Ries et al. 2004). We expected stronger temporal changes in edge effects where structural contrasts are larger between adjoining habitats (i.e. larger temporal changes for crop–woodland edges than planting–woodland edges; Figure 1b).

For Question 3, we expected beetles to exhibit cross-edge movement (Duelli et al. 1990; Tscharntke et al. 2012) following changes in resource availability and species lifecycle requirements (González et al. 2016; Ries and Debinski 2001). Specifically, we expected movement towards farmlands during spring, and towards remnant patches during summer following seasonal vegetation resources (Frost et al. 2015; Schneider et al. 2016; Tscharntke et al. 2005b).



Spring		Summer (crop harvested, woody debris applied)	
Habitat 1	Habitat 2	Habitat 1	Habitat 2
Remnant woodland	Plantings	Remnant woodland	Plantings
Remnant woodland	Fallow	Remnant woodland	Fallow
Remnant woodland	Crop	Remnant woodland	Woody debris
		Remnant woodland	Crop

Figure 1. (a) Seven categories of edge response patterns used to interpret our beetle data (adapted from Duelli et al. (1990)). (b) *A priori* degree of contrast between land-uses in this study. Direction and thickness of arrow indicates increasing degree of contrasts between adjacent habitats.

Methods

Study area

Our study area was a cropping-grazing landscape within the Lachlan River Catchment, New South Wales, south-eastern Australia (Figure 2; Figure S1 in Paper II: Supplementary Material). Widespread clearing for agriculture has restricted native *Eucalyptus* woodland remnants to infertile steeper areas. Many remnants also have been modified by livestock grazing, weed invasion, and changed fire regimes (Hitchcock 1984).

Experimental design

We selected eleven remnant woodland patches as our study sites on the basis that they were *Eucalyptus* woodland communities with high ground-, mid- and over-storey native vegetation complexity, and adjoined four farmland uses: (1) winter wheat crop (*Triticum aestivum*), (2) fallow (rested from crop rotation or sown-pasture rotation, dominated by exotic annual vegetation), (3) restoration plantings (native trees and shrubs <7 years old), and (4) winter wheat crop over which eucalypt-based fine woody debris was applied (January 2015; Figure 2; Figure S1 in Paper II: Supplementary Material). The fine woody debris is a novel treatment piloted in our study to increase ground-layer complexity in crop fields after harvest. Farmers were receptive to this treatment because it does not impede cropping machinery.

Our experimental design consisted of four 400 m transects running from inside each woodland patch and out into four adjoining farmland uses. We placed sampling points along the transect at five distances: -200 m, -20 m, 0 m, 20 m, 200 m from inside remnant patches out into farmlands (Figure 2). We chose 200 m because it represented the interior of smaller farm fields. Remnant patch size [mean 4010 ha +/- s.e. 486.4 ha] was previously found not to have a significant effect on beetle species richness and abundance and thus was not considered in this study (Paper I).

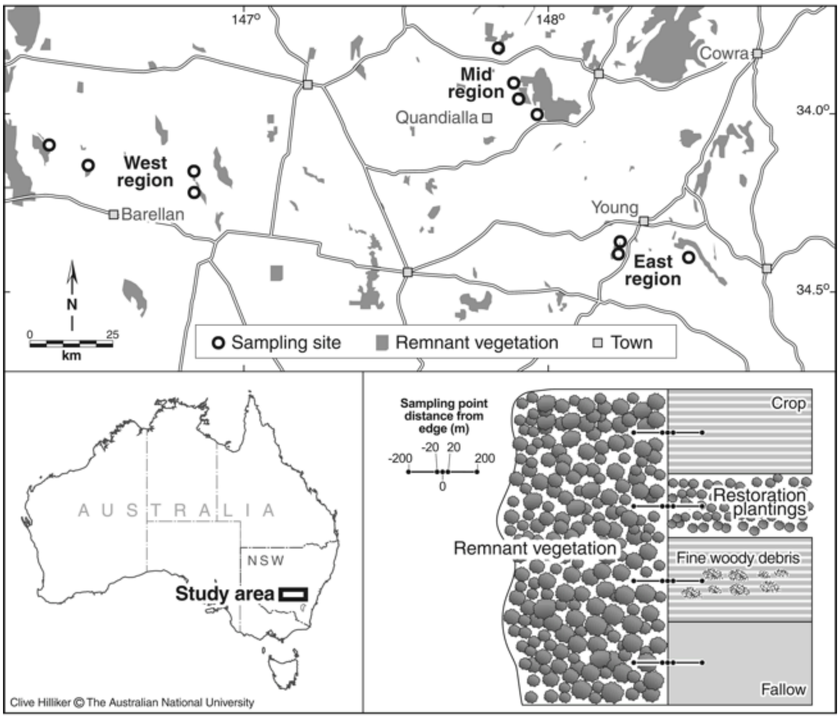


Figure 2. Map showing study sites in New South Wales, south-eastern Australia. Inset shows stylized image of experimental design and pitfall traps placement along four 400 m transects between remnant woodland patch and adjoining farmland habitats.

Beetle sampling

Each sampling point comprised a pair of pitfall traps, which 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). Individual traps from each pair were placed on either side of a drift fence (60 cm long x 10 cm high), which was used to help direct arthropods into traps, and determine directional movement (via differences in abundance on each side of the drift fence). We sampled from the same trap locations during two distinct periods: spring when crops and spring annuals were at peak growth, and summer after crop were harvested (stubble retained) and woody debris treatment applied. We opened a total of 220 pairs of traps (11 replicate sites x 4 transects x 5 trap pairs) for 14 days during spring (October–November 2014), and summer (January–February 2015).

We recognise that pitfall trap data represent a compound measure of abundance, surface activity and species catchability, which may be habitat-dependent (Sunderland 1995). Our study did not aim to survey all species, but rather to compare assemblages between treatments for relatively common species. Pitfall traps provide a consistent and efficient method of studying assemblage differences when results are interpreted carefully (Sunderland 1995). Using linear drift fences and leaving traps open for two weeks was a simple way of increasing the efficiency of captures (Duelli 1997; Weibull et al. 2003).

Arthropods were preserved in 70% ethanol. All adult beetles were removed and sorted to family and genus or species where possible. Beetle taxonomy followed Lawrence and Britton (1994). Where specimens could not be identified to species, abundance and richness measures 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 behaviour of adults at the family and subfamily level (Hunt et al. 2007; Lawrence and Britton 1994). These coarse trophic assignments are useful in providing basic functional grouping information to guide management strategies (Tscharntke et al. 2005a).

Statistical analyses

Samples from each pitfall trap pair were pooled to provide one sample per sampling point. Data from 19 trap pairs were discarded from analysis because at least one trap was damaged by vertebrates. To determine the effects of farmland use, distance from edges, and season (Questions 1 and 2) on beetle assemblages (abundance and species richness of overall beetles and trophic groups), we used generalized linear mixed-effect models (GLMM; Bolker et al. 2009). The main fixed effects tested were ‘farmland use’ (planting, fallow, crop, woody debris), ‘distance’ (as a categorical factor; -200 m, -20 m, 0 m, 20 m, 200 m), ‘time’ (spring, summer) and their interactions (Figure 2). We fitted site, farmland use and trap location as nested random effects (1|site/farmland use/trap location) to account for the non-independent spatial structure and repeated measures of the study design, and used a Poisson error distribution. Model selection was performed using Akaike Information Criterion values adjusted for small sample sizes (AICc). All models within two AICc of the best model were examined (Burnham and Anderson 2002), and the most parsimonious model with fewest parameters were included (Arnold 2010). We 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). We used R 3.2.0 (R Development Core Team 2015), with the ‘lme4’ R (Bates et al. 2015) and ‘MuMIn’ R (Bartoń 2015) packages for GLMM analyses. For the top ranked candidate models, we ran post hoc Tukey–Kramer tests to identify statistically different factor level(s) using the ‘multcomp’ R package (Hothorn et al. 2008).

We assessed edge effect patterns of each candidate GLMM containing an effect of distance or an interaction with distance by (i) determining the “preferred” habitat for each beetle response variable as where mean response values were highest of the patch, farmland or edge; and (ii) assigning edge effect patterns to one of the seven categories (Fig. 1a; adapted from Duelli et al. 1990) after examining pairwise differences along the distance gradient (based on Tukey–Kramer tests; see Table S7 in Paper II: Supplementary Material). (iii) We interpreted the ‘strength’ of edge effects as the relative differences in response variables along the farmland–woodland gradient (Figure 1a). Given the small number of distances from the edge used in our study, we focussed on the relative *magnitude* of edge effects (differences in response values, as per Duelli et al. (1990)) rather than the *extent* of edge effects (how far from edges differences in response values can be observed), as we could not employ continuous functions to compare linear and non-linear edge responses (Ewers and Didham 2006b).

For the movement analyses (Question 3), we used beetle abundance data from individual traps on either side of the drift fence. To infer movement direction, we created a new 'direction bias' metric at each sampling point based on the number of individuals captured in traps on each side of a drift fence. Counts from traps facing the farmland (*F*) and woodland patch (*P*) side of the drift fence were assigned as proportional response variables of (*F*, *P*). To determine if movement direction was influenced by farmland use, distance from edges, season, and/or their interaction, we followed the GLMM model selection approach used for Questions 1 and 2, but modelled direction bias as the response variable assuming binomial distribution. To focus on cross-habitat movements, we ran these models over sampling points close to edges: -20 m, 0 m and 20 m (i.e. excluded -200 m and 200 m distances, which we assumed as being too far from the edge to infer cross-habitat movement). We interpreted predicted response values over 0.5 as having a higher probability of movement towards woodland patches, values under 0.5 as having a higher probability of movement towards farmlands, and 0.5 as an equal probability of movement in either direction.

Results

We recorded 11 360 individual beetles from 53 families and 495 species (Table S1 in Paper II: Supplementary Material). The five most abundant families were Anthicidae (18 species, n=2408), Carabidae (63, n=1617), Staphylinidae (86, n=1533), Curculionidae (53, n=1095) and Tenebrionidae (36, n=895). The five most species rich families were Scarabaeidae (70 species, n=447), Staphylinidae, Carabidae, Curculionidae and Tenebrionidae.

The edge effect patterns found in our results (Table 1) comprised five of the seven categories above (from weak to strong effects): "no edge" (6), "gradual decline" (7), "mutual influence" (4), "positive influence" (3) and "ecotone" (5). We interpreted the "positive influence" (3) and "ecotone" (5) categories as having equally "strongest" negative and positive edge effects respectively; and "no edge" (6) as having no observable edge effect (Figure 1a).

Table 1. Edge responses grouped by (a) species richness and (b) abundance for overall assemblage and trophic groups. Responses shown where there were effects of distance or interaction of distance with farmland use and/or time in the top ranked models (ΔAICc < 2). Edge effect categories (from weak to strong effects): "no edge" (6), "gradual decline" (7), "mutual influence" (4), "positive influence" (3) and "ecotone" (5) (Figure 1a).

	Preferred habitat	**Edge response category**							
(a) Richness responses									
(i) Distance									
Detritivore richness	Farmland	3							
Herbivore richness	Edge	5							
(ii) Distance × Time		*Spring*	*Summer*						
Species richness	Farmland	4	3						
Predator richness	Farmland	7	3						
(b) Abundance responses									
		Crop		*Fine woody debris*		*Fallow*		*Planting*	
(i) Distance × Time × Farmland use		*Spring*	*Summer*	*Spring*	*Summer*	*Spring*	*Summer*	*Spring*	*Summer*
Total abundance	Farmland	3	7	3	5	7	4	7	4
Detritivore abundance	Farmland	4	7	4	4	7	7	6	3
Herbivore abundance	Farmland & remnant	6	6	6	6	6	6	6	6
Predator abundance	Farmland	4	6	4	7	6	7	7	3

Question 1. How do different farmland uses (crop, fallow, planting and woody debris) influence beetle responses with increasing distances from both sides of farmland–woodland edges?

We found significant effects of distance from edges on overall species richness and abundance, and abundance of all trophic groups ($P < 0.001$; Table 1; Tables S2, S4 in Paper II: Supplementary Material). Abundance and species richness of beetle assemblages, detritivores and predators were mostly higher in farmlands than remnant patches, and thus assigned farmland as the "preferred" habitat following Duelli et al. (1990) (Table 1; Figure 3; Figure S2 in Paper II: Supplementary Material).

Abundance of predators, detritivores and overall beetles often varied along a distance from edges through a general decrease from farmlands to remnant woodlands (Table 1). During spring, edge effects for detritivore abundance increased in strength from planting–woodland ("no edge", 6), fallow–woodland ("gradual decline", 7) to crop–woodland ("mutual influence", 4) edge types (Table 1; Figure 3c); while edge effects for predator abundance increased in strength from fallow–woodland ("no edge", 6), planting–woodland ("gradual decline", 7) to crop–woodland ("mutual influence", 4) edge types (Table 1; Figure 3d).

Herbivore richness was higher at edges (0 m) than in interior of farmlands (200 m) and remnant woodlands (200 m) ("ecotone", 5; Table 1; Figure 3b). Detritivore richness was highest in farmlands and decreased from farmlands to remnant woodlands ("positive influence", 3; Table 1; Figure S2c in Paper II: Supplementary Material).

The response of species richness and abundance to edges that changed over time are described in the following section.

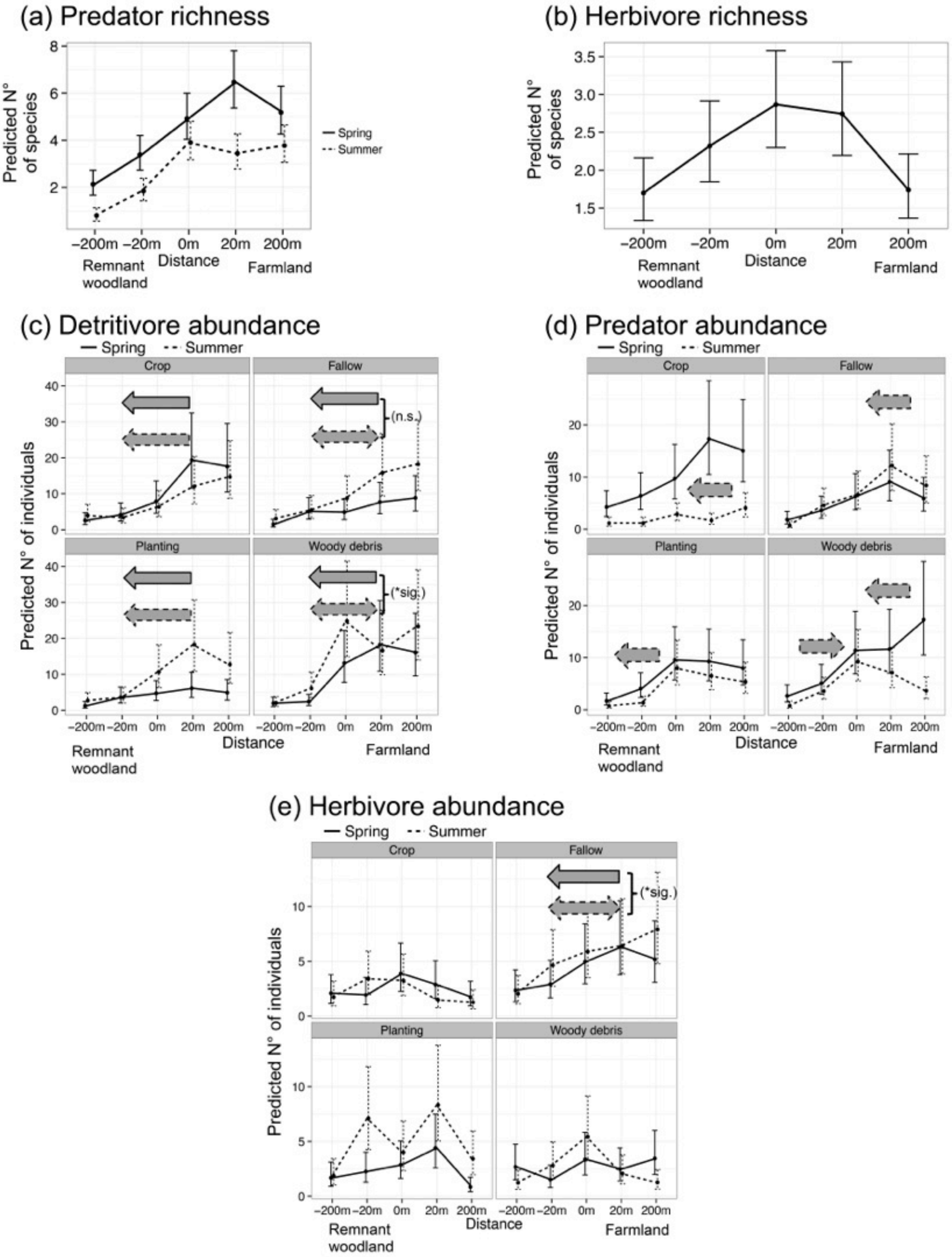


Figure 3. Effects of distance, farmland use and season on predicted (a) species richness of predators, (b) species richness of herbivores, (c)–(e) abundance of detritivores, predators and herbivores. Edge response categories should be interpreted in light of ±95% confidence intervals and pairwise differences (Table 1, Table S7 in Paper II: Supplementary Material); solid and dashed lines show general trends. Solid and dashed arrows show movement trends during spring and summer respectively (significance of directional change shown in parentheses).

Question 2. How do beetle responses to the four types of farmland–woodland edge contrasts change over time?

We found significant interactive effects of ‘distance’ and ‘time’ on the species richness of overall beetles and predators ($P < 0.001$) and interactive effects of ‘distance’, ‘farmland use’ and ‘time’ on the abundance of overall beetles and all trophic groups ($P < 0.001$; Table 1; Tables S2, S4 in Paper II: Supplementary Material).

Overall species richness and predator richness was higher in farmlands than remnant woodlands, and decreased along a transect from farmlands to remnant woodlands (Table 1; Figure 3a; Figure S2a in Paper II: Supplementary Material). Between spring and summer, edge effects for overall species richness increased in strength from “mutual influence” (4) to “positive influence” (3), where there were significant decreases in species richness at all distances except edges (0 m) and -20 m in remnant woodlands (Table 1; Figure S2a in Paper II: Supplementary Material). Predator richness showed “gradual decline” (7) during spring, and stronger “positive influence” (3) during summer. The latter was associated with significant decreases in predator richness between spring and summer at all distances except edges (0 m) (Table 1; Figure 3a).

Between spring and summer, detritivore abundance shifted from “no edge” (6) to stronger “positive influence” (3) along the planting–woodland transect (with significant increases in abundance at 0 m, and 20 m and 200 m in plantings: $P < 0.001$); and shifted from “mutual influence” (4) to weaker “gradual decline” (7) along the crop–woodland transect (with significant decreases in abundance at 20 m in crop fields). Edge response patterns for detritivore abundance did not change between spring and summer along the fallow–woodland (“gradual decline”, 7) and woody debris–woodland (“mutual influence”, 4) transects.

Between spring and summer, edge effects for predator abundance decreased in strength along the crop–woodland transect (“mutual influence”, 4 to “no edge”, 6), associated with significant decreases in predator abundance along entire crop–woodland transect. Edge effects also decreased in strength for predator abundance along the woody debris–woodland transect, but at a lesser extent (“mutual influence”, 4 to “gradual decline”, 7), with significant decreases at 20 m and 200 m in the woody debris. In contrast, edge responses of predator abundance increased in strength along the fallow–woodland (“no edge”, 6 to “gradual decline”, 7) and planting–woodland (“gradual decline”, 7 to “positive influence”, 3) transects (Table 1; Figure 3d).

Herbivore abundance exhibited “no edge” (6) pattern for all habitat edge types during spring and summer. Herbivore abundance fluctuated at irregular sampling distances between spring and summer: significant decrease at 200 m in the woody debris (P = 0.001) along the woody debris–woodland transect, and significant increase at the 200 m, 20 m and -20 m distances (P = 0.001, 0.015 and <0.001 respectively) along the planting–woodland transect (Table 1; Figure 3e).

Question 3. Is there evidence of cross-habitat movement across the farmland–woodland edge, and are temporal changes in movement patterns related to temporal changes in beetle responses to the edge?

Movement patterns for overall beetles (Figure 4a) were similar to detritivores, reflecting the high representation of detritivores in our study (significant interactive effects of farmland use and time; Tables S3, S5 in Paper II: Supplementary Material). Detritivores showed directional movement towards remnant woodlands regardless of adjacent farmland use during spring (Figures 3c, 4b). Between spring and summer, fallowing non-significantly reduced the extent of directional movement of detritivores, while adding woody debris significantly reduced directional movement to no direction bias (Figures 3c, 4b). The weakening in directional movement coincided with edge response patterns of detritivore abundance remaining the same along the fallow–woodland and woody debris–woodland transects (cf. Table 1 and Figures 3c, 4b).

Herbivores showed directional movement from fallow fields towards remnant woodlands in spring, which was significantly different to summer trends of no directional movement at fallow–woodland edges. This movement pattern appeared unrelated to edge response of herbivore abundance, which remained the same over time (“no edge”, 6; cf. Table 1 and Figure 3e, 4c).

Predator movement patterns varied depending on specific distances from edges (significant three-way effects of distance, farmland use and time; Tables S3, S5 in Paper II: Supplementary Material). There were no clear directional movement trends during spring. During summer, predators showed movement towards edges from 20 m within all farmland uses, except for plantings showing no directional movement (Figures 3d, 4d). During summer, predators showed additional movement bias towards edges from -20 m within remnant woodlands along the woody debris–woodland transect. This coincided with a smaller seasonal changes in edge responses of predator abundance along the woody debris–woodland transect (i.e. when compared to crop–woodland edges; cf. Table 1b, Figures 3d, 4d). During summer, planting–woodland edges showed no directional movement of predators in plantings close to edges (20 m) and directional movement of predators away from plantings in woodlands close to edges (-20 m). These movement patterns co-occurred with an increase in the strength of edge effects for predator abundance along the planting–woodland transect from "gradual decline" (7) to "positive influence" (3) between spring and summer (cf. Table 1b, Figures 3d, 4d).

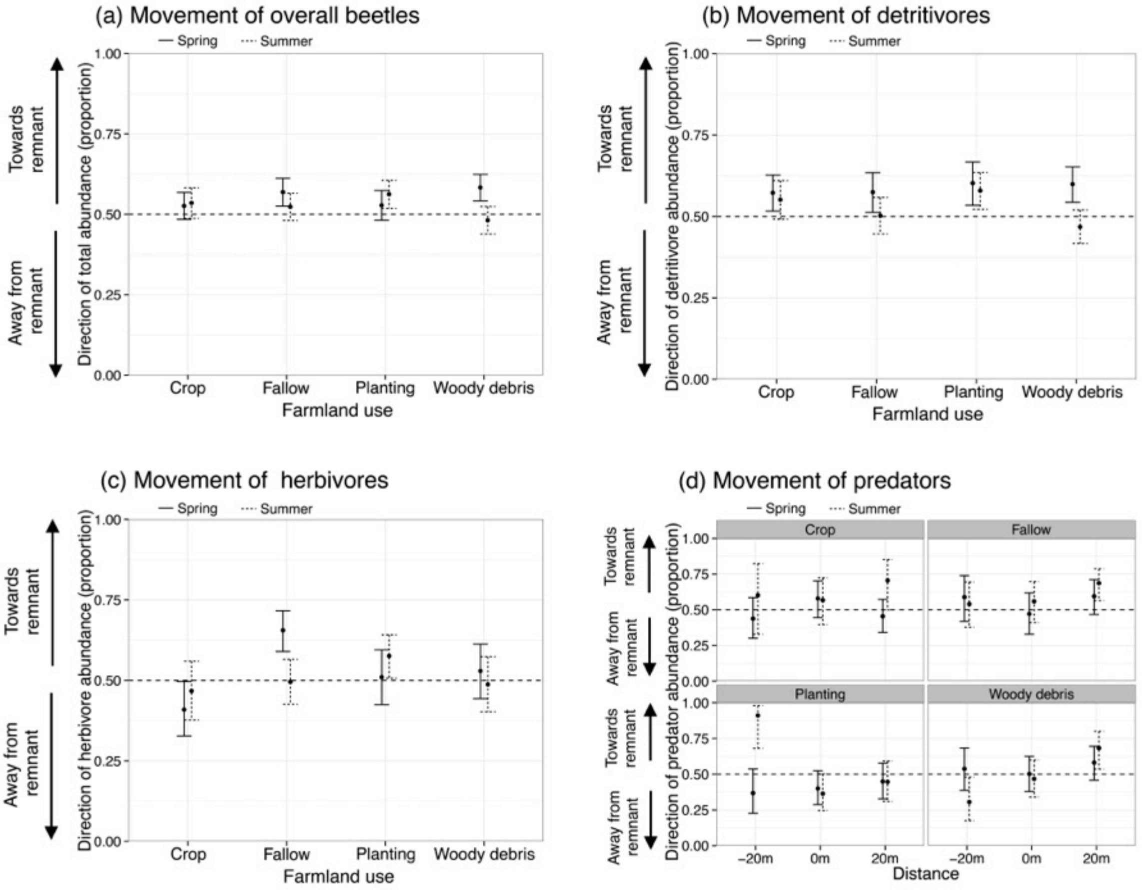


Figure 4. Predicted movement bias between remnant woodlands and different farmland uses based on abundance data for (a) all beetles, (b) detritivores, (c) herbivores, (d) predators. ±95% confidence intervals shown.

Discussion

We examined temporal patterns of edge responses and movement of beetle assemblages between woodland patches and four farmland uses. There were three key findings: (i) interactive effects of distance from the edge, farmland use and season on beetle abundance; (ii) edges were characterized by temporally stable predator richness and higher herbivore richness than adjoining habitats; and (iii) associations between seasonal patterns of edge responses and cross-habitat movement for predator and detritivore abundance. We further discuss our results below, including how farmland uses moderate seasonal edge responses and/or cross-habitat movement of beetles across contrasting farmland–woodland edges.

Interactive effects of distance from the edge, farmland use and time

We found that the abundance of predators and detritivores varied across the edge between farmlands and woodlands, but the edge response patterns, assessed using conceptual models presented in Duelli et al. (1990), depended on farmland use and season. These results are consistent with studies suggesting that arthropod edge responses are strongly influenced by landscape (Campbell et al. 2011; Macfadyen and Muller 2013) and seasonal context (Ries et al. 2004). Drivers of spatio-temporal changes in arthropod abundance in relation to human-modified edges include: seasonal changes in habitat condition, resource availability (e.g. growth, flowering or senescence of annual vegetation) or management practices (e.g. crop harvest); species lifecycle (Murphy et al. 2016); and cross-habitat movement (Rand et al. 2006; Schneider et al. 2016; Tscharntke et al. 2005b), discussed in the following section.

Our hypothesis of stronger edge effects at higher contrast habitat edges (Question 1) (Downie et al. 1996) was supported only for abundance of detritivores and predators during spring (i.e. larger differences in abundance between adjacent habitats at higher contrast crop–woodland edges than lower contrast planting–woodland edges; Table 1), while relationships between edge responses and the degree of edge contrast were inconsistent during summer.

Finding interactive effects of farmland use, distance from edges and season, support our hypothesis of variable edge responses over time (Question 2). Our results suggest that seasonal changes in edge effects and its interaction with adjoining farmland use may contribute to commonly reported inconsistent patterns in edge responses (Didham 2010; Ries and Sisk 2004). Our data did not support our hypothesis of larger temporal changes in edge effects where there were stronger habitat structural contrasts between spring and summer, in that we did not find stronger edge effects at the crop–woodland edge after crop harvest in summer. Instead, seasonal changes in edge patterns depended on farmland–specific shifts in beetle abundance. Directional analyses, explored in the following section, elucidate cross-boundary movements at certain farmland habitat contrasts as a potential mechanism contributing to seasonal variations in edge effects (Rand and Louda 2006).

Edges supported temporally stable predator richness and higher herbivore richness than adjoining habitats

We found that field edges and farmlands supported significantly more beetle species, including predators, than remnant woodlands, which partly support our hypothesis of highest species richness at edges (Question 1). Our finding of a significant decline in species richness between spring and summer at all distances from the edge but not at the edge itself (0 m), suggested that farmland–woodland boundaries may provide important refuge or a population source for beetle diversity. Studies in Europe also have found higher species richness of predators in habitat edges and interior of open habitats (e.g. farmlands, pastures) compared to forest interiors (Magura 2002; Tillman et al. 2012), with habitat heterogeneity at edges specifically supporting more ecological niches (Magura 2002). Predatory species of Carabidae and Staphylinidae, for example, use undisturbed edges for resources (Kromp 1999; Sotherton 1985), or as over-wintering or ovipositioning sites (Holland et al. 2005; Kromp 1999).

Our results highlight that habitat edges can act as source habitats for diverse predator assemblages, or stepping-stones for small-scale dispersal, which may be crucial for species recolonisation and persistence after disturbance events in adjacent habitats (Magura 2002) and/or enhancing pest control at adjoining crop fields (Woodcock et al. 2016a). We did not, however, observe higher predator abundance at edges than adjacent habitats (with the exception of woody debris–woodland edges during summer; Figure 3d), which has been found in some European agroecosystems (Holland et al. 2005; Tillman et al. 2012; Tscharntke et al. 2005b). Instead, only several potential edge-specialists (Kromp and Steinberger 1992) exhibited highest densities at field edges (e.g. *Philonthus* sp. #294, *Notiobia* sp. #293 and *Hypharpax* sp. #137).

Herbivore richness was higher at edges than interior farmland and remnant woodland habitats, which partially supports our hypothesis of highest overall species richness at edges (Question 1), although the predicted number of species was lower than other trophic groups (Figure 3b). Previous studies have observed similar findings to ours but for other taxonomic groups. These kinds of results have been attributed to the mixing of species or resources from bordering habitats or occurrence of edge-specialist that prefer higher heterogeneity of resources at edges (Duelli et al. 1990; Ewers and Didham 2006a; Murphy et al. 2016). In our study area, habitat edges are typically not cultivated and may therefore provide high diversity of vegetation resources and microhabitat niches from overlapping plant communities (Evans et al. 2016; Magura 2002; Ries et al. 2004). Herbivorous beetles may be able to exploit diverse vegetation resources at habitat edges because of host plant specialization of many species (Koricheva et al. 2000) including Curculionidae, which comprised the largest proportion of herbivores in our study. Not finding higher herbivore abundance at field edges than adjacent habitats (Murphy et al. 2016) was, however, unexpected and may be explained by predator spillover effects, discussed in the following section.

Associations between patterns of edge effects and cross-habitat movement

Our study adds new information on cross-habitat movement (Question 3), influenced by differences in farmland use, as a likely mechanism driving temporal and spatial fluctuations in edge responses for some predators and detritivores (Figures 3c, 3d, 4b, 4d). Finding movement patterns at the vicinity of habitat edges (within 20 m) provides further support for the theory of cross-boundary agriculture subsidies (i.e. productive farmlands providing important resources for generalists in other habitats; Rand et al. 2006). We discuss associations between edge responses and cross-habitat movement of each trophic group separately.

Detritivores

We found that directional movement trends from farmlands towards remnant woodlands were widespread for detritivores, where applying woody debris during summer or fallowing increased permeability of edges to cross-habitat movement during summer (and also associated with seasonal stability in edge responses). Our findings are consistent with predictions of high resource productivity in farmlands supporting high densities of generalist species, which result in density-dependent spillover into adjacent habitats (Frost et al. 2015; Rand et al. 2006; Tscharntke et al. 2005b). Significant seasonal differences in movement patterns across the woody debris–woodland edge (compared to other farmland–woodland edges) suggest the addition of litter may provide resources that promote arthropod colonisation of crop fields, likely for mobile species seeking resources during summer. Interestingly, the seasonal changes in movement patterns at the woody debris–woodland and fallow–woodland edges coincided with no seasonal differences in edge responses of detritivore abundance (Table 1; Figures 3c, 4b). This may be explained by the maintenance of detritivore abundance at these edge types over time, although more species-level data are needed to identify the extent to which movement is a causal mechanism of changes in edge effects.

Distinctive seasonal patterns of abundance and movement bias for detritivores (and predators) across planting–woodland edges compared to other farmland–woodland edges suggest that native plantings provided resources for many beetles during summer. We found an increase in detritivore abundance in plantings and edges across planting–woodland edges between spring and summer, which led to a seasonal increase in the strength of edge effects. This increase appeared unrelated to differences in movement patterns across the planting–woodland edge over time (i.e. directional movement towards remnant woodlands remained the same during spring and summer; Table 1; Figures 3c,4b), suggesting that beetles may be colonising plantings from other farmland uses rather than the patch adjacent to plantings during summer.

Predators

Similar to detritivores, we found an increase in edge effect strength for predator abundance between spring and summer across planting–woodland edges, due to maintenance of high predator abundance within plantings. Plantings likely provided suitable habitat during summer, which also led to deeper spillover of predators into remnant woodlands compared to other farmland uses (Table 1, Figures 3d, 4d). It is likely that woodland patch-associated species are driving the seasonal abundance and/or movement patterns observed in our study. We found greater similarities in species composition between patch and plantings during summer (but significant dissimilarities during spring; Table S6 in Paper II: Supplementary Material), which suggests that patch-dependent species could be using plantings during summer as habitat. Lower contrast planting–woodland edges typically have more suitable resources or microclimatic conditions for woodland species (Schneider et al. 2016) compared to higher contrast crop–woodland edges, which in our study, exhibited significant declines in predator abundance at and on both sides of edges (Figure 3d).

For predator abundance, applying woody debris over crop fields reduced the extent of seasonal changes in edge effect patterns at the woody debris–woodland edge compared to the crop–woodland edge. This coincided with possible colonisation of mulched crop fields from remnant woodlands during summer (cf. Table 1, Figures 3d, 4d) which—together with movement towards the edge from 20 m in woody debris (also found across the crop–woodland edge)—led to a non-significant peak in predator abundance at the edge (Figure 3d). This pattern is consistent with findings of some predator species, possibly litter-dependent species, responding positively to mulch applied over crop fields, including edges (Kromp 1999).

Predators showed movement trends towards edges from all adjoining farmland uses except for plantings during summer (also represented by Carabidae). Seasonal movement specifically towards farmland edges also has been reported for predatory coccinellid beetles (Rand and Louda 2006), while active emigration of predators away from farmlands has been found following the senescence of annual vegetation or crop harvest, due to reduced habitat quality and prey resources (Madeira et al. 2016; Rand et al. 2006; Schneider et al. 2016). More work is needed to determine whether there is increased predation pressure or resource competition (with many predatory beetles being omnivorous; Rand and Louda 2006; Schneider et al. 2016) affecting prey assemblages, particularly edge-specialists or woodland species that use edges during summer. We found, for example, weak differences in species composition between edges and crops, suggesting that discrete resource competition may be driving beetle assemblages at the edge–crop interface (Table S6 in Paper II: Supplementary Material).

We found localised movement patterns for predators at specific distances within 20 m from the edge. This is consistent with studies in Europe that have shown many predatory species preferring the vicinity of field edges (within 50 m of edges) due to diverse habitat and foraging resources, and proximity to different habitats needed to complete entire lifecycles (Lovei and Sunderland 1996; Ries et al. 2004; Woodcock et al. 2016a). We could not, however, support our hypothesis (Question 3) of predator movement from remnant woodlands towards farmlands during spring, which were often found for flying arthropods in similar agricultural landscapes, following seasonal availability of resources in cultivated fields (Blitzer et al. 2012; González et al. 2016; Macfadyen et al. 2015; Madeira et al. 2016). It is plausible that ground-dwelling predatory beetles in our agroecosystem are colonising farmlands outside of our sampling period (e.g. earlier during the growing season).

Herbivores

Herbivores exhibited movement trends towards remnant woodlands at fallow–woodland edges during spring, which did not correspond to changes in edge response patterns (Table 1; Figures 3e, 4c). Instead, herbivore abundance always exhibited a “no edge” (6) pattern, which is consistent with predictions of some arthropod species being insensitive to edges (Ries et al. 2004). Based on the resource-based model of edge effects (Ries and Sisk 2004), herbivorous beetles may perceive entire landscape elements as suitable habitat with adequate supplementary resources, although some species may occur in rare landscape elements not included in our study. Cross-habitat movement patterns also suggest that fallow fields may provide important food or breeding resources during spring, which is unsurprising because herbivorous beetles, such as Curculionidae, feed predominantly on pasture grasses (many annual and perennial species being most productive during spring) at adult and larval stages (Lawrence and Britton 1994; Tscharntke and Greiler 1995). Interestingly, we found seasonal fluctuations in herbivore abundance at irregular distances across the planting–woodland and woody debris–woodland edges (Figure 3e), which may be due to species-level responses to localized changes in vegetation resources independent of distance from the edge (Evans et al. 2016). Our results also may be influenced by the pitfall trapping approach, which does not adequately capture specialist feeders on host plants. Targeted taxon-level sampling is needed to better understand the resource requirements of specialist herbivores (Souza et al. 2016).

Our findings suggest that directional pitfall traps are a potentially simple and inexpensive way of collecting landscape-level movement information, given sufficient sampling effort ideally aimed at targeted taxonomic groups. We acknowledge that directional traps do not directly measure movement, and may be confounded with other factors (e.g. emergence from nest sites or under-sampling of flying beetles). Directional traps are commonly used for flight-dispersing arthropods to infer movement (Frost et al. 2015; González et al. 2016; Macfadyen et al. 2015), however more research is needed to evaluate their effectiveness for surface-active arthropods. Finding no directional bias does not preclude the possibility of frequent movement in multiple directions, particularly for highly mobile generalists (Lovei and Sunderland 1996; Weibull et al. 2003). Increasing the frequency and intensity of trapping over time may yield such patterns of mass movement, especially for individual species with adequate data (since aggregating species into trophic groups, as conducted our study, obscures individual responses).

Conclusions and management implications

Our study demonstrated that responses of ground-dwelling beetles across farmland–woodland boundaries are highly dynamic, and influenced by interactive effects of farmland use and seasonal context. This result is noteworthy because surface-active arthropods are a diverse group characterized by fine-scale habitat preferences, and thus often assumed to be affected more by local habitat-level than landscape-level characteristics (Tscharntke et al. 2012). Our findings have implications for the spatial and temporal planning of integrated farm management practices to promote the biodiversity and biodiversity-mediated ecosystem services of ground-dwelling beetles. Cultivated fields can be managed to provide temporary resources and/or mediate (facilitate or impede) cross-habitat movements, and influence assemblages on habitats on both sides of edges. We demonstrated applying fine woody debris over harvested crop fields as a novel way of reducing seasonal variations in edge effects for detritivore abundance, likely by increasing permeability of edges for cross-habitat movement and therefore maintaining high abundance in both adjoining habitats. Native plantings provided important seasonal refuge and resources by supporting high abundance of detritivores and predators, particularly woodland species, during summer.

Edges between woodland patches and intensively managed farmlands need to be considered in conservation management plans because edges support temporally stable predator richness, and higher herbivore richness than adjoining habitats. Establishing buffers from agricultural disturbance around such high contrast field edges with suitable management practices, such as limiting tillage or agrochemical use and improving structural diversity (Magura 2002; Tscharntke et al. 2005a), may help improve the quality of edge resources for beetles in adjoining habitats. However, widespread localised movement of predators from farmlands towards edges during summer may negatively impact edge-dependent prey assemblages, a potential response that requires further study. Our study highlights the importance of studying edge responses together with movement patterns to better understand the processes behind observed edge effects for each functional group. We recommend that future research consider temporal changes in edge responses (Ries et al. 2004), and incorporate measurements of likely mechanisms when studying edge effects (Ruffell and Didham 2016).

Acknowledgements

This work was supported by Central Tablelands Local Land Services (through Australian Government funding), Lake Cowal Foundation and Mount Mulga Pastoral Company. KN was supported by an Australian Government Research Training Program (RTP) scholarship. Thanks to landholders (Day, Foy, Conlan, Hall, Lucas, Nowlan, Aylott, Grimm, Robinson, Crawford, Daley families) for property access. We are grateful to Alicia Ng, Nicholas Shore, Margaret Ning, Phil Pritchard, Dimitrios Tsifakis, Mal Carnegie, Hanh Huynh, Greg Burgess, Hannah Selmes, Yong Ding Li, Jake Lennon, Temma Carruthers-Taylor and Michael Lai for fieldwork assistance; Daniel Martinez-Escobar, Shauna Priest, Imogen Moore and Jake Lennon for lab assistance; Maldwyn John Evans, Kim Pullen, Michael Nash, Lingzi Zhou, Rolf Oberprieler, Margaret Thayer, Vladimir Gusarov and Roberto Pace for beetle identification; Wade Blanchard for statistical advice; and Clive Hilliker for Figure 2 illustration. We thank Raphael Didham, Matt Hill and anonymous reviewers for helpful comments on the manuscript.

Data Availability

The datasets generated during and/or analysed during the current study are available from the CSIRO Data Access Portal.

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Paper III: Dynamic effects of ground-layer plant communities on beetles in a fragmented farming landscape

In Paper III, I draw on additional habitat structure and plant species data to quantify relationships between ground-layer structure, plant species richness and plant composition, and the diversity and composition of beetles from different habitats or seasons. This paper allows me to investigate the extent by which different vegetation attributes might explain the dynamic beetle assemblage patterns observed in Papers I and II.

Ng K, McIntyre S, Macfadyen S, Barton PS, Driscoll DA, Lindenmayer DB, in review, Dynamic effects of ground-layer plant communities on beetles in a fragmented farming landscape, *Biodiversity and Conservation*

Abstract

Vegetation effects on arthropods are well recognized, but it is unclear whether vegetation attributes have consistent effects on arthropod assemblages across dynamically changing agricultural landscapes. Understanding how plant communities influence arthropods under different habitat and seasonal contexts can identify vegetation management options for arthropod biodiversity. We quantified the relationships between vegetation structure, plant species richness and plant species composition, and the diversity and composition of beetles from different habitats and time periods. We asked: (1) What is the relative importance of plant species richness, vegetation structure and plant composition in explaining beetle species richness, abundance and composition? (2) How do plant–beetle relationships vary between different habitats over time? We sampled beetles using pitfall traps and surveyed vegetation in three habitats (woodland, farmland, their edges) during peak crop growth in spring and post-crop harvest in summer. Plant composition better predicted beetle composition than vegetation structure. Both plant richness and vegetation structure significantly affected beetle abundance. The influence of all vegetation attributes often varied in strength and direction between habitats and seasons for all trophic groups. The variable nature of plant–beetle relationships suggests that vegetation management could be targeted at specific habitats and time periods to maximise positive outcomes for beetle diversity. In particular, management that promotes plant richness at edges, and promotes herbaceous cover during summer, can support beetle diversity. Conserving groundcover in all habitats may also improve abundance of all beetle trophic groups. The impacts of existing weed control strategies in Australian crop margins on arthropod biodiversity require further study.

Keywords: Coleoptera; natural enemies; plant–insect interactions; resource concentration hypothesis

Introduction

Vegetation is a well known determinant of arthropod assemblages at both local and regional scales (Joern and Laws 2013). However, the mechanisms by which plant communities influence arthropods are often challenging to identify because different attributes used to characterize plant communities are often highly correlated and difficult to disentangle in observational studies (Koricheva et al. 2000; Perner et al. 2005; Siemann et al. 1998). Consequently, there are numerous competing or overlapping hypotheses that have been posed to explain mechanisms behind complex relationships between plant and arthropod assemblages (Joern and Laws 2013; Siemann et al. 1998). Understanding how plant communities influence arthropods can help identify vegetation management options for arthropod biodiversity.

It is unclear how specific attributes of vegetation communities might influence arthropod assemblages across dynamically changing human-modified landscapes. This is because most studies on plant–arthropod relationships have been conducted within single land-uses, such as agricultural or silvicultural systems (Parry et al. 2015; Perner et al. 2005), or natural woodland and grassland habitats (Parry et al. 2015; Schaffers et al. 2008). The importance of habitat context in structuring plant–arthropod relationships has been previously exemplified by contrasting responses of arthropod diversity to plant diversity between monoculture and polyculture farming systems (Haddad et al. 2001; Siemann 1998). Such hypotheses, however, have rarely been simultaneously tested across multiple habitat types, and also have not considered seasonal dynamics that typically characterise human-modified landscapes. Some agro-ecological studies, however, have found distinct associations between vegetation and arthropod communities between different habitats (e.g. high predator abundance in uncropped areas; Parry et al. 2015; Rouabah et al. 2015) and over time (e.g. arthropod species requiring specific plant resources in different seasons; Landis et al. 2005; Parry et al. 2015). Determining whether different vegetation attributes have consistent or variable effects on arthropod assemblages across multiple habitats or over time may identify subtle mechanisms behind arthropod responses to landscape changes, which might otherwise be masked at broader scales.

Three attributes are often used to characterize plant communities and their effects on arthropod assemblages: plant species composition, plant species richness, and vegetation structure, with the latter two attributes more commonly used in fauna studies (Schaffers et al. 2008). First, individual plant species or combinations of species can provide direct food or habitat resources for many arthropod species (Perner et al. 2005; Schaffers et al. 2008; Siemann 1998). Yet, many studies on plant–arthropod relationships have overlooked plant species composition (Joern and Laws 2013; Schaffers et al. 2008). This is likely due to structural attributes being easier to observe in the field by researchers without specialised botanical expertise (Schaffers et al. 2008). Often community studies have the resources and expertise to focus on only one taxonomic group in detail (i.e. plants *or* invertebrates), with plant species identity mainly considered in work on host plant specialists. Relatively few studies that explicitly analysed plant species composition have identified that plant composition was a better predictor of arthropod assemblages than vegetation structure and other environmental factors like habitat type (Nyafwono et al. 2015; Perner et al. 2005; Schaffers et al. 2008). This is theoretically unsurprising, given that plant composition not only forms the basis of structural characteristics of vegetation communities, but also incorporates other indirect biotic and abiotic influences on arthropod assemblages (Joern and Laws 2013; Schaffers et al. 2008).

Plant species richness is a second commonly used vegetation attribute which represents a diversity of available resources (Perner et al. 2005). Many studies have found positive relationships between plant diversity and the diversity of consumer assemblages. Previous empirical studies have, however, yielded contrasting results (Agrawal et al. 2006; Perner et al. 2005; Siemann 1998; Siemann et al. 1999). Inconsistencies in correlations between plant diversity and arthropod abundance have been linked to site-specific factors such as abiotic conditions, disturbance and productivity (Perner et al. 2005).

Lastly, vegetation structure—the physical architecture of plant communities such as tree canopy and grass cover—is known to directly influence the survival and persistence of arthropod populations by providing microhabitats (e.g. ovipositioning or shelter sites) or altering microclimatic conditions, and indirectly by modifying individual behaviour (e.g. altered movement through different vegetation densities) or species interactions (e.g. hunting efficiency) (Brose 2003; Landis et al. 2005; Siemann 1998). Positive correlations between vegetation-driven structural complexity and animal diversity are well documented in many studies, although contradictory results have been found for some taxonomic groups (Joern and Laws 2013; Tews et al. 2004), including carabid beetles (Brose 2003).

Using a split-plot study design with repeated measures, we quantified relationships between three vegetation attributes (vegetation structure, plant species richness, plant species composition) and the diversity and composition of beetles (including their trophic groups) among three habitat types across a fragmented mixed-farming landscape. The habitat types were remnant woodland patches, adjacent farmland, and their edges, which we sampled during two distinct periods of the farming cycle (spring and summer). We focussed on beetles because they are sensitive to small-scale environmental changes (Gibb and Cunningham 2010) and functionally diverse, with different trophic groups providing distinct ecological functions such as pest control (predators), nutrient cycling (detritivores), and weed control (herbivores) (Grimbacher et al. 2006; Landis et al. 2000). Previously, we found that the composition and diversity of beetle assemblages responded strongly to habitat type (Paper I). Here, we further examined whether responses of overall beetle assemblages and trophic groups were mediated by within-habitat vegetation attributes. Our research questions were: (1) what is the relative importance of plant species richness, vegetation structure and plant species composition in explaining beetle species richness, abundance and composition? (2) How do plant–beetle relationships vary between the different habitats (woodland patch, farmland, and their edges) over two seasons (spring and summer)?

We expected stronger effects of plant species composition on beetle assemblages compared to other vegetation attributes in certain habitats (Prediction I; Figure 1). Plant identity may be particularly important in habitats containing more plant host-specific beetles, such as native vegetation specialist beetles in remnant patches and edge-specialist beetles in field edges (Kromp and Steinberger 1992).

We expected predators to be generally more influenced by vegetation structure than plant species richness and composition, while herbivores would be more influenced by plant species richness or composition than vegetation structure (Prediction II; Figure 1). This is because, regardless of habitat type, many phytophagous species are assumed to be more host plant-dependent than predatory species following a bottom-up approach of biodiversity (Perner et al. 2005; Schaffers et al. 2008; Siemann 1998).

We also expected that plant–beetle relationships would vary between different habitats owing to different mechanisms driving beetle responses (Prediction III; Figure 1). Specifically, more complex perennial habitats (i.e. patches and edges) may exhibit top-down effects according to the “enemies hypothesis” (positive relationship between plant diversity and predator diversity, leading to lower herbivore abundance). In contrast, simplified habitats with a high proportion of annual vegetation (i.e. farmland) may exhibit bottom-up effects following the “resource concentration hypothesis” (negative relationship between plant diversity and herbivore abundance) (Root 1973).

Lastly, we expected strong differences in plant–beetle relationships in all habitats over time (Prediction IV; Figure 1), relating to seasonal changes in plant phenology and/or beetle lifecycle requirements (Parry et al. 2015; Ziesche and Roth 2008).

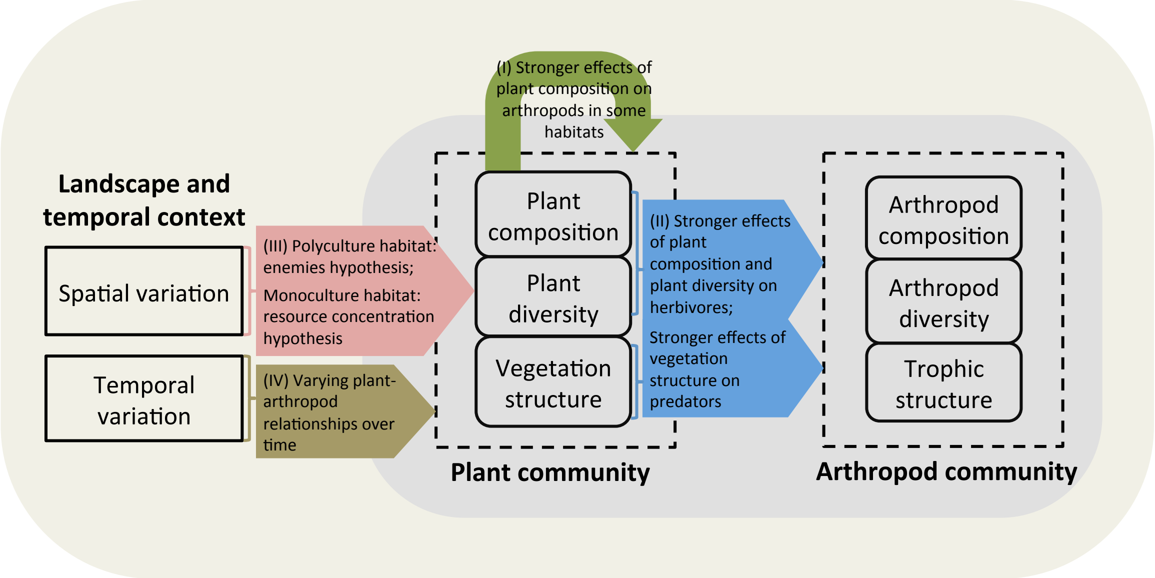

Figure 1. Conceptual model relevant to this study showing factors driving relationships between plant and arthropod communities. We had four initial predictions: stronger effects of plant species composition on beetle assemblages compared to other vegetation attributes in some habitats (I); predators showing stronger associations with vegetation structure, and herbivores with plant species richness (II); varying plant-beetle relationships between different habitats (III) and over time (IV). Our findings underscore the integral role of plant composition (I), as well as spatial (III) and temporal variation (IV) in shaping plant–beetle relationships.

Materials and methods

Study site and sampling design

Our study area was a highly fragmented mixed cropping–grazing landscape within the Lachlan River Catchment, New South Wales, southeastern Australia (location of sites ranging from -34.036 S, 146.363 E; -33.826 S, 147.855 E; to -34.411 S, 148.499 E). Widespread clearing for agriculture has restricted native *Eucalyptus* woodland remnants to infertile, steeper areas. Many remnants also have been modified by livestock grazing, weed invasion, and changed fire regimes (Norris and Thomas 1991).

We selected eleven remnant vegetation patches on the basis that they were *Eucalyptus* woodland communities with high ground-, mid- and over-storey native vegetation complexity (i.e. 'patch' habitat type), and adjoined mixed farm fields which, for the purposes of this study, were pooled as a single 'farmland' habitat type. The farmland types within the fields were: winter wheat crops, fallow fields, fine woody debris applied over harvested wheat crops, and restoration plantings (*Eucalyptus* and native shrubs <7 years old). Farmland and patches differed strongly structurally and floristically. The ground layer in farmland is characterised by lower plant species richness and dominated by exotic annual grasses and forbs (notably *Triticum aestivum, Hypochaeris*, *Lolium,* and *Bromus*), while patches have higher plant species richness and higher proportion of native species (particularly *Acacia*, *Austrostipa*, *Sida* and *Calotis*) (Table 1; Table A2 in Paper III: Supplementary Material). To test if plant–beetle relationships varied between habitats, we selected vegetation attributes that had similar (and therefore comparable) ranges of values within each habitat type (Table 1). This is because some vegetation attributes did not vary between habitats (e.g. trees were always present in patches and mostly absent from farmland).

Our survey design consisted of four 400 m transects running from inside each patch out into the adjoining farmland. We sampled beetles at three locations along each transect: 200 m inside the patch, 200 m inside the farmland, and 0 m at the patch–farmland boundary. We chose 200 m because it represented the interior of smaller farm fields. We included the edge (0 m) as a separate habitat type because edges were previously found to have distinct beetle assemblages (Paper II) and may be affected by farming activities differently to the farm interior (Weibull et al. 2003). We sampled from the same trap location during two distinct periods in terms of plant phenology and agronomic practices in farmland: spring when crops and spring-active species were at peak growth, and summer when crops have been harvested (stubble retained; fine woody debris treatment applied) and summer-active species at peak growth.

Table 1. Vegetation variables recorded in a 20 m by 10 m plot at each pitfall trap location, collected during spring and summer. Raw cover scores were based on the middle percentage values of the following six categories: 0–1%; 1–5%; 5–25%; 25–50%; 50–75%; and 75–100%.

Vegetation variables	**Unit**	**Description**	**Range (mean) in each habitat type**		
			Patch (n=88)	**Edge (n=88)**	**Farmland (n=88)**
Plant species richness	Count	Presence/absence in five 1 × 1 m quadrats placed randomly within plot	Spring: 6 to 33 (16.5) Summer: 1 to 25 (12)	Spring: 5 to 31 (14.5) Summer: 1 to 30 (13.0)	Spring: 2 to 22 (8.9) Summer: 3 to 22 (11.5)
Total herbaceous	Cover score	Sum of cover scores for native	Spring: 10 to 127.5 (51.1) Summer: 10 to 105 (39.4)	Spring: 10 to 105 (68.2) Summer: 10 to 105 (47.5)	Spring: 22.5 to 125.5 (83.3)

cover		forb, native grass, exotic perennial grasses and exotic annual forbs and grasses			Summer: 10 to 130 (63.3)
Litter cover	Cover score	Detached leaf and grass litter	Spring: 2.5 to 85 (34.9) Summer: 15 to 85 (47.7)	Spring: 2.5 to 62.5 (14.6) Summer: 2.5 to 62.5 (30.1)	Spring: 2.5 to 85 (11.0) Summer: 2.5 to 85 (31.7)
Groundstorey vegetation height	Centi-metre	Average height of dominant grasses, forbs, shrubs and other vegetation < 1 m high	Spring: 5 to 60 (25.4) Summer: 1 to 75 (25.3)	Spring: 0 to 60 (22.5) Summer: 1 to 65 (18.3)	Spring: 7 to 85 (45.7) Summer: 1 to 35 (15.7)

Beetle sampling

Each sampling location comprised a pair of pitfall traps, consisting of 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). Individual traps from each pair were placed on either side of a drift fence (60 cm long x 10 cm high) to help direct arthropods into the trap. We opened a total of 132 pairs of traps (11 replicate sites x 4 transects x 3 trap pairs) for 14 days 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). Where specimens could not be identified to species, 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 behaviour of adults at the family and subfamily level (Lawrence and Britton 1994).

Plant surveys

During beetle sampling in spring and summer, the same observer (KN) recorded: (1) six vegetation structural variables (vegetation height and cover of litter, native forb, native grass, exotic perennial grasses, and exotic annual forbs and grasses) within a 20 × 10 m plot centred around the sampling location (Table 1); and (2) the composition of all plant species from five 1 × 1 m quadrats placed randomly within each 20 × 10 m plot. Plant composition data were pooled from these quadrats for each sampling location.

Statistical analyses

Beetle samples from each pitfall trap pair were pooled to provide one sample per sampling location. We used a combination of multivariate techniques and generalized linear mixed-effects modelling (GLMM; Bolker et al. 2009) for analysing univariate variables. We analysed data for the assemblage of beetles and each trophic group separately, and repeated analyses over spring and summer data. We separated our data variables into different analyses because (1) the different data types used in our study (univariate and multivariate variables, respectively) require separate treatments, and (2) plant species richness and plant species composition are intrinsically correlated (and is thus not typically examined concurrently). We classified vegetation structure as univariate (by picking individual metrics) in some analyses and multivariate in others. We transformed all multivariate data to presence/absence and removed singletons of beetle occurrence prior to analyses to reduce the influence of very rare or very abundant species.

Effects of plant composition and vegetation structure (multivariate) on beetle composition (multivariate)

We ran multiple regression on distance matrices (MRM) (Lichstein 2007) to compare relative effects of plant composition, vegetation structure, and geographic distance between sites on beetle composition. The vegetation structural variables were: vegetation height (cm), litter cover (%) and total herbaceous cover (%) (derived from the sum of the cover of forbs and grasses; Table 1), and they were not strongly correlated (< 0.5 Pearson correlation). Beetle and plant composition matrices were based on Bray–Curtis dissimilarities, while vegetation structure and geographic distance were based on Euclidean distances. MRM allows multiple matrices to be used as predictor variables. It creates a multiple regression model for a response matrix against multiple predictor matrices, and uses a permutation procedure to test for statistical significance. Controlling for geographic distance allowed us to compare vegetation effects after having accounted for spatial autocorrelation. We repeated MRM tests for subsets of data within each of the three habitats (patches, edges, farmland), and over time (spring, summer). We assessed the statistical significance of each MRM model based on 999 permutations. We used the ‘ecodist’ package for the MRM tests (Goslee and Urban 2007) in R 3.2.0 (R Development Core Team 2015).

Effects of plant richness and vegetation structure (univariate) on beetle composition (multivariate)

We used Canonical Correspondence Analysis (CCA) (ter Braak and Verdonschot 1995), based on Bray–Curtis dissimilarity matrices, to examine relationships among plant species richness, three measures of vegetation structure (vegetation height, litter cover, and total herbaceous cover) , and beetle species composition. We first ran CCA using habitat type as the constraining factor to quantify the effect of habitat type on overall beetle composition (P = 0.001). We then ran a partial CCA focussed on plant richness and vegetation structure variables by controlling for the effect of habitat as a covariate, and repeated analyses over spring and summer data. We used biplots to identify beetle species that were strongly correlated with variation among our habitat and vegetation variables. We used the ‘vegan’ R package for CCA (Oksanen et al. 2013).

Effects of plant richness and vegetation structure (univariate) on beetle diversity (univariate)

We used GLMM with Poisson errors to determine the effects of plant richness and the three vegetation structural variables on beetle abundance and richness. We included four vegetation variables (plant richness, vegetation height, litter cover, total herbaceous cover) as additive continuous fixed effects and fitted habitat type interactively with each vegetation variable. We ran GLMMs for spring and summer data separately. Transect nested within site was fitted as a random effect to account for the non-independent spatial structure of the study design (particularly variation due to different farmland types adjoining a patch in a site). We performed model selection using Akaike Information Criterion values adjusted for small sample sizes (AICc), and examined the top-ranked candidate model (Burnham and Anderson 2002). We 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). We used the ‘lme4’ (Bates et al. 2015), ‘car’ (Fox et al. 2013) and ‘MuMIn’ (Bartoń 2015) R packages for GLMM analyses.

Results

We collected 393 species of beetles (6632 individuals) from 132 sites during spring and summer. We recorded a total of 276 plant species representing 179 genera and 58 families (Tables A1, A2 in Paper III: Supplementary Material).

Effects of plant composition and vegetation structure on beetle composition

MRM models incorporating plant compositional dissimilarity, vegetation structure, and geographic distance were generally able to predict overall beetle composition ($0.029 < R^2 < 0.229$; Table 2). In all habitats, plant species composition was a significant predictor of overall beetle species composition compared to vegetation structure (i.e. more similar plant communities displayed more similar beetle communities than contrasted vegetation structure). These predictive strengths were stronger during summer than spring, and stronger at edges (summer $R^2 = 0.229$, spring $R^2 = 0.138$), followed by farmland (summer $R^2 = 0.106$, spring $R^2 = 0.078$) and patches (summer $R^2 = 0.029$, spring $R^2 = 0.054$) (Table 2).

The species composition of beetle trophic groups showed mixed responses to plant species composition and vegetation structure depending on habitat and season. In particular, more similar plant species composition was significantly correlated with more similar detritivore species composition in edges during spring and summer ($P = 0.002$; Table 2c), and in patches ($P = 0.001$; Table 2a) and farmland ($P = 0.019$; Table 2b) only during summer. More similar plant species composition was significantly correlated with more similar herbivore species composition in edges during spring ($P = 0.002$) and summer ($P = 0.033$) (Table 2c). More similar plant species composition was significantly correlated with more similar predator species composition in edges during summer ($P = 0.001$; Table 2c), while more similar vegetation structure was significantly (albeit weakly) correlated with more similar predator species composition in patches during summer ($P = 0.043$; Table 2a).

Overall beetle species composition became more dissimilar as geographic distance between samples increased in edges ($\beta > 0.033$; $P < 0.005$) and farmland ($\beta > 0.052$; $P = 0.001$), but not in patches ($\beta = 0.02$; $P > 0.116$). Geographic distance effects on each trophic group depended on habitat and season (details in Table 2).

Table 2. Results of Multiple Regression on Distance Matrices (MRM) model on beetle composition dissimilarity and summary statistics for predictor variables of plant composition dissimilarity, vegetation structure dissimilarity and geographic distance, in (a) patch, (b) farmland and (c) edge habitats.

Model ~ Predictor variables	**Model R^2**	**Coefficient**	**P**	**Model R^2**	**Coefficient**	**P**
(a)	**Patch habitat**					
	Spring			**Summer**		
Overall beetle composition	0.029			0.054		
Intercept		0.600	0.997		0.503	0.924
Plant composition dissimilarity		0.094	**0.042**		0.192	**0.009**
Vegetation structure		0.005	0.547		-0.031	**0.016**
Geographic distance		0.015	0.116		0.016	0.293
Detritivore composition	0.007			0.059		
Intercept		0.804	0.777		0.418	1.000
Plant composition dissimilarity		0.078	0.430		0.443	**0.001**
Vegetation structure		-0.012	0.459		-0.015	0.447
Geographic distance		0.028	0.210		0.054	**0.028**
Herbivore composition	0.002			0.015		
Intercept		0.782	0.665		0.643	0.882
Plant composition		0.052	0.707		0.263	0.068
Vegetation structure		-0.009	0.690		-0.032	0.162
Geographic distance		0.016	0.520		-0.009	0.760
Predator composition	0.012			0.025		
Intercept		0.717	0.980		0.721	0.240
Plant composition dissimilarity		0.112	0.153		0.048	0.847
Vegetation structure		0.025	0.065		-0.080	**0.043**
Geographic distance		-0.002	0.893		-0.005	0.907

(b)	**Farmland habitat**					
	Spring			**Summer**		
Overall beetle composition	0.078			0.106		
Intercept		0.594	1.000		0.584	0.996
Plant composition dissimilarity		0.071	**0.032**		0.191	**0.007**
Vegetation structure		0.015	0.134		-0.008	0.399
Geographic distance		0.052	**0.001**		0.057	**0.001**
Detritivore composition	0.042			0.082		
Intercept		0.437	1.000		0.369	0.986
Plant composition dissimilarity		0.104	0.058		0.304	**0.019**
Vegetation structure		0.028	0.119		-0.023	0.272
Geographic distance		0.050	**0.015**		0.079	**0.003**
Herbivore composition	0.024			0.016		
Intercept		0.665	0.971		0.732	0.976
Plant composition		0.056	0.435		0.073	0.399
Vegetation structure		0.016	0.436		0.027	0.044
Geographic distance		0.078	**0.012**		0.029	0.091
Predator composition	0.036			0.033		
Intercept		0.642	0.996		0.831	0.718
Plant composition dissimilarity		0.067	0.130		0.005	0.938
Vegetation structure		0.010	0.462		-0.005	0.677
Geographic distance		0.049	**0.002**		0.060	**0.002**

(c)	Edge habitat					
	Spring			Summer		
Overall beetle composition	0.138			0.229		
Intercept		0.549	1.000		0.474	1.000
Plant composition dissimilarity		0.238	**0.002**		0.333	**0.001**
Vegetation structure		0.017	0.056		0.014	0.084
Geographic distance		0.033	**0.005**		0.042	**0.001**
Detritivore composition	0.068			0.144		
Intercept		0.446	1.000		0.437	1.000
Plant composition dissimilarity		0.417	**0.002**		0.298	**0.002**
Vegetation structure		0.006	0.732		<0.001	0.991
Geographic distance		0.016	0.475		0.095	**0.001**
Herbivore composition	0.042			0.008		
Intercept		0.599	1.000		0.746	0.977
Plant composition		0.282	**0.002**		0.144	**0.033**
Vegetation structure		0.018	0.177		<0.001	0.972
Geographic distance		0.017	0.359		0.002	0.905
Predator composition	0.025			0.097		
Intercept		0.676	0.951		0.489	1.000
Plant composition dissimilarity		0.067	0.450		0.354	**0.001**
Vegetation structure		0.014	0.240		0.015	0.083
Geographic distance		0.033	**0.041**		0.030	**0.040**

Effects of plant richness and vegetation structure on beetle composition

Beetle composition showed distinct clustering among habitat types (Figure 2). Partial CCA (after accounting for habitat type) showed that both plant richness and all vegetation structural variables had significant effects on overall beetle composition during spring ($P < 0.004$). During summer, effects of litter cover on overall beetle species composition were weakly significant ($P = 0.049$). Partial CCA also revealed significant effects of: total herbaceous cover on detritivore composition during spring ($P = 0.007$), plant richness on herbivore composition during summer ($P = 0.016$), and plant richness ($P = 0.044$) and total herbaceous cover ($P = 0.014$) on predator composition during spring (Table A3 in Paper III: Supplementary Material).

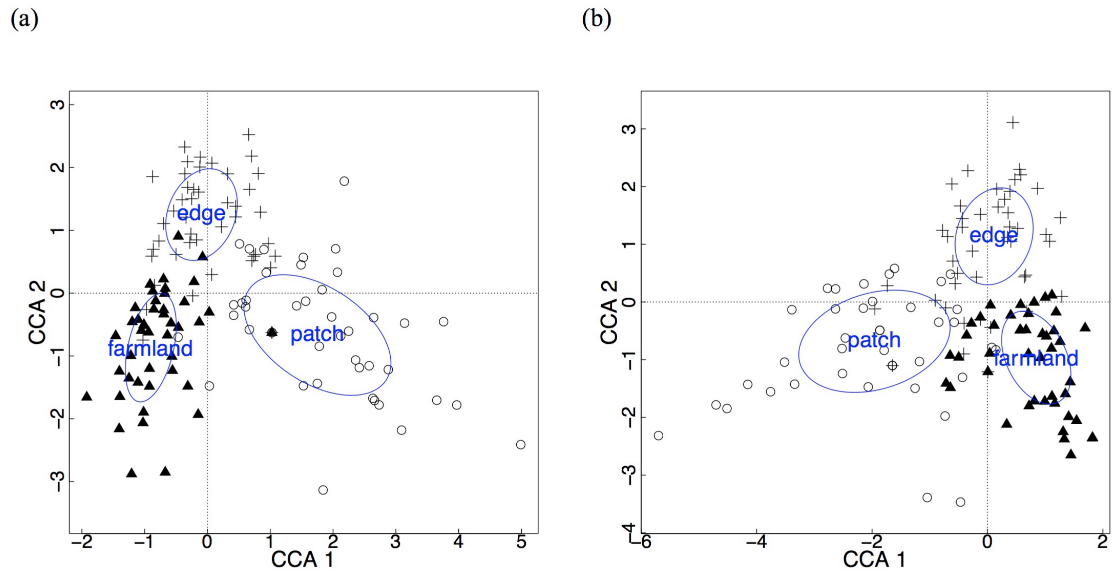

Figure 2. Canonical correspondence analysis (CCA) ordination showing beetle composition for spring (a) and summer (b) with respect to habitat. Ellipses indicate one standard deviation from the centroid of each habitat group.

Effects of plant richness and vegetation structure on beetle diversity

We found significant interactions between habitat and plant richness in the top-ranked models for the abundance of overall beetles, herbivores (summer only), detritivores, and predators (P < 0.001). Plant richness and vegetation structure variables (litter cover, total herbaceous cover and/or vegetation height) were always included in the top-ranked models for the abundance of overall beetles, predators, detritivores, and herbivores (Table 3; Table A4 in Paper III: Supplementary Material; model details in Tables A5, A6). In farmland during summer, herbivore abundance significantly decreased with plant richness (P < 0.001), while predator abundance significantly increased with plant richness. However, in patches during summer, herbivore abundance significantly decreased with plant richness (P < 0.001), and there were no effects of plant richness on the abundance and richness of predators (Table 3).

During spring, regardless of habitat type, litter cover had a significant positive effect on detritivore abundance (P = 0.022), while vegetation height had a significant positive effect on predator abundance (P < 0.001). During summer, respective effects of litter cover on detritivore abundance (significantly positive effect in edges, negative in farmland; P < 0.001) and vegetation height on predator abundance (significantly negative effect in patches; P = 0.004) varied depending on habitat type (Table 3).

Vegetation structure variables often had interactive effects with habitat for beetle abundance, where the direction or strength of effects within a habitat often changed between spring and summer for the abundance of overall beetles and each trophic group. For example, total herbaceous cover had a significant positive effect during spring and negative effect during summer on predator abundance in patches and farmland. In contrast, total herbaceous cover had a significant negative effect on predator abundance at edges during spring ($P < 0.001$), and a significant positive effect during summer ($P < 0.001$) (Table 3).

During summer, overall species richness had a significant positive association with total herbaceous cover, without interactive effects of habitat ($P = 0.007$) (Table A4 in Paper III: Supplementary Material).

Edges were characterised by mostly significant positive associations between plant richness and abundance of all trophic groups (Table A6 in Paper III: Supplementary Material).

Table 3. Summary of top-ranked generalized linear mixed-effect models testing responses of species richness and abundance of beetle trophic groups to the effects of plant species richness, vegetation structure (litter cover, total herbaceous cover, vegetation height), and interaction with habitat, if applicable. Direction and significance of responses are shown (+/- ‘0.05’; ++/-- ‘0.01’; +++/--- ‘0.001’; n.s. omitted). Habitats are p = patch, f = farmland and e = edge. Significant terms (P < 0.05) in bold.

	Spring					Summer				
Response	Model terms	Direction	Chisq	Df	Pr(Chisq)	Model terms	Direction	Chisq	Df	Pr(Chisq)
Detritivore richness	*Best model: None*					*Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*				
						Habitat*Vegetation height	e(-)	3.4	1	0.067
Detritivore abundance	*Best model: Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*					*Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*				
	Litter cover	+	5.2	1	**0.022**	Habitat*Plant richness	p(---); e(++)	19.1	2	**<0.001**
	Habitat*Plant	p(---); e(+++);	91.2	2	**<0.001**	Habitat*Litter	e(+++);	104.1	2	**<0.001**

	richness	f(++)				cover	f(---)			

	Habitat*Vegetation height	p(-);
		e(++)
			8.5	2	**0.014**	Habitat*Vegetation height	p(+++);
							e(---);
							f(+++)
								38.1	2	**<0.001**

	Habitat*Total herbaceous cover	e(--);
		f(+++)
			44.7	2	**<0.001**	Habitat*Total herbaceous cover	p(---);
							e(+++);
							f(---)
								19.1	2	**<0.001**

Herbivore richness	_Best model: None_					_Best model: None_				
Herbivore abundance	_Best model: Habitat * Litter + Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height_					_Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Vegetation height_				

	Plant richness	+	4.1	1	**0.043**	Habitat*Plant richness	p(---);
							e(+++);
							f(--)
								34.9	2	**<0.001**

	Habitat*Litter cover	p(+++);
		e(-);
		f(+)
			39.4	2	**<0.001**	Habitat*Litter cover	p(--);
							e(+);
							f(---)
								20.3	2	**<0.001**

	Habitat*Vegetation height	e(+); f(--)	30.7	2	**<0.001**	Habitat*Vegetation height	e(--); f(+++)	12.8	2	**0.002**

	Habitat*Total herbaceous cover	p(++);
		e(---);
		f(+++)
			23.0	2	**<0.001**					

Predator richness	_Best model: None_					_Best model: None_				
Predator abundance	_Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Vegetation height_					_Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Vegetation height_				
	Vegetation height	+++	32.8	1	**<0.001**	Habitat*Plant richness	f(+++)	68.0	2	**<0.001**

	Habitat*Plant richness	p(---);
		e(+++);
		f(-)
			36.6	2	**<0.001**	Habitat*Litter cover	p(---);
							e(+++);
							f(---)
								51.6	2	**<0.001**

	Habitat*Litter cover	p(+++); e(--)	20.4	2	**<0.001**	Habitat*Vegetation height	p(--)	17.4	2	**<0.001**

	Habitat*Total herbaceous cover	p(+++);
		e(---);
		f(+++)
			70.7	2	**<0.001**	Habitat*Total herbaceous cover	p(--);
							e(+++);
							f(---)
								18.5	2	**<0.001**

Discussion

We quantified the relationships between attributes of the ground-layer plant community (structure, species richness, species composition) and the diversity and composition of beetles in three habitat types (remnant woodland patches, farmland and their edges), during peak crop growth in spring and post-crop harvest in summer. We found that: (1) plant composition better predicted beetle composition than vegetation structure; (2) plant species richness and vegetation structure both significantly affected overall beetle abundance; and (3) the influence of these vegetation attributes varied depending on habitat and time, for all trophic groups (key findings in Figure 3). We discuss our results in relation to predictions from a conceptual model summarising our findings (Figure 1). Importantly, our study highlights the integral role of plant composition (Prediction I), as well as habitat (Prediction III) and temporal (Prediction IV) context in mediating vegetation effects on beetle assemblages across dynamic, modified landscapes (Figure 1). These three elements appear to override habitat-independent predictions of predators showing stronger associations with vegetation structure and herbivores with the species richness or composition of plant communities (Prediction II).

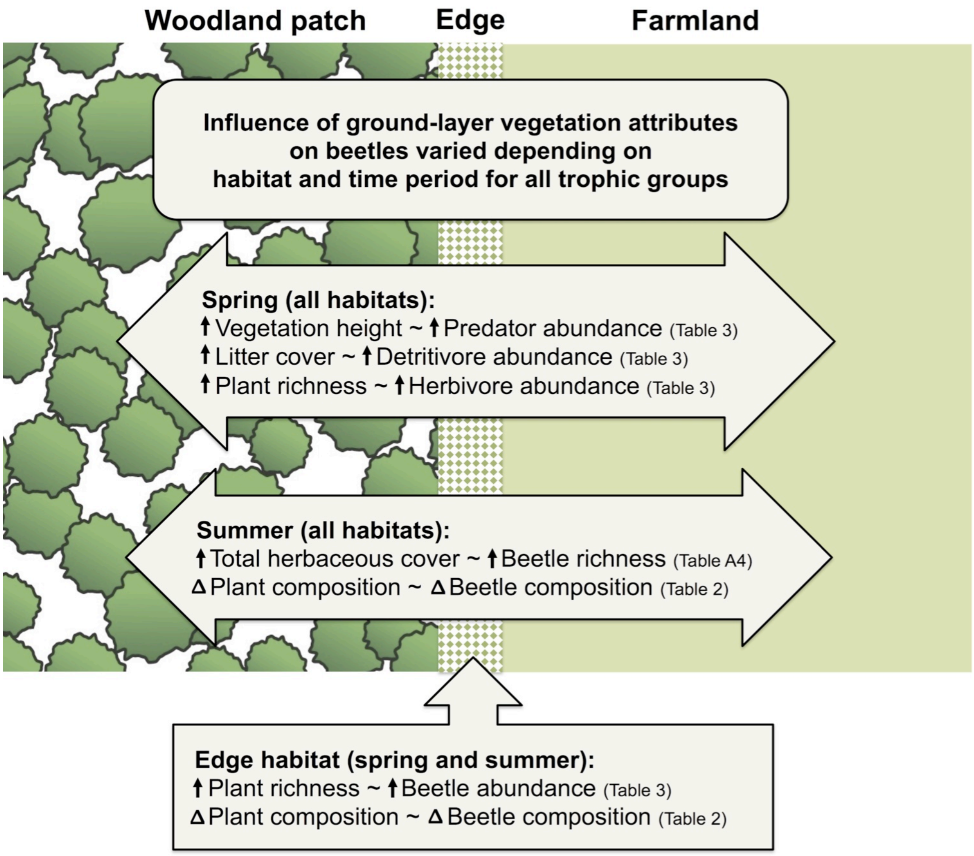

Figure 3. Visual summary of our study's key findings, showing the direction of beetle responses to the effects of different vegetation attributes (details in main text).

Stronger influence of plant composition on beetle composition than vegetation structure

We identified plant composition as a stronger predictor of beetle composition than vegetation structure in all habitats during both seasons. This is mainly consistent with our Prediction I of stronger effects of plant composition compared to other vegetation attributes in some habitats. Our prediction of beetles in farmlands being more habitat generalists and less affected by plant composition, compared to woodland patches and edges, was not supported (Table 2). Our findings are consistent with studies that explicitly compared the effects of plant composition and other vegetation attributes on arthropod composition (Koricheva et al. 2000; Müller et al. 2011; Perner et al. 2005; Schaffers et al. 2008). Schaffers et al. (2008) used a predictive co-correspondence approach to demonstrate that plant composition best predicted the composition of several arthropod groups, including beetles, compared to vegetation structure and environmental condition. Similar studies concluded that the identity or combination of plant species was more important than other vegetation attributes in determining the abundance of most arthropods (Koricheva et al. 2000; Perner et al. 2005). This is because plant species composition directly mediates vegetation structure, microclimate and environmental factors (Joern and Laws 2013; Koricheva et al. 2000; Müller et al. 2011; Perner et al. 2005; Schaffers et al. 2008), and potentially influences microhabitat selection preferences of individual beetle species (Buse 1988; Niemelä and Spence 1994). Importantly, our findings provide evidence of the overriding effects of plant composition on arthropod composition both in natural and managed habitats occurring in modified landscapes. These effects are likely masked in zoological studies relying on coarser measurements of vegetation structure, because environmental influences at smaller spatio-temporal scales are not adequately characterised.

We also identified higher species dissimilarity with increasing geographic distance for overall beetle composition in farmland and edges, but not in remnant patches. This suggests that beetles in remnant patches may be dispersal-limited woodland specialists (Driscoll et al. 2010). Beetles in farmland and edges may be more affected by the distance decay of similarity due to natural dispersal processes among sites, or high environmental heterogeneity in mixed-farmland contributing to niched-based species sorting (Soininen et al. 2007; Tews et al. 2004). We also found differences in geographic distance effects on beetle trophic groups between habitats and seasons. This indicates spatio-temporal turnover in beetle assemblages (Driscoll et al.

2010; Tews et al. 2004), likely linked to fluctuations in heterogeneity or connectivity of habitat resources in agricultural landscapes (e.g. summer aggregation of detritivorous *Latridius* sp. 437 in edges and *Ommatophorus* sp. 98 in patches; see Paper II) (Duflot et al. 2016). Most of the variation in beetle composition was, however, still attributed to differences in plant composition after accounting for geographic distance (Table 2).

Beetle responses to plant species richness and vegetation structure

Both plant species richness and vegetation structure significantly influenced the abundance of all beetle trophic groups to some extent (Table 3). These results do not support Prediction II of predators showing stronger associations with vegetation structure, and herbivores with plant species richness. Instead, our findings are consistent with studies showing that multiple vegetation characteristics contribute to species habitat preferences and structuring of different trophic groups (Lassau et al. 2005; Nyafwono et al. 2015; Tews et al. 2004). Plant species richness is commonly linked to the diversity of available resources for arthropods (Perner et al. 2005), while vegetation structure is more likely to be linked to biophysical resources such as food, shelter and ovipositioning sites (Landis et al. 2005). These vegetation measures may, however, be auto-correlated (Lassau et al. 2005; Perner et al. 2005), with plant diversity effects on arthropod abundance potentially indirectly mediated by vegetation structure (Buse 1988; Koricheva et al. 2000). Further manipulative experiments would be useful in disentangling effects of individual vegetation attributes and other confounding factors, such as species interactions, plant productivity, soil characteristics, or microclimate (Niemelä and Spence 1994; Perner et al. 2003; Siemann et al. 1999).

Our data did not support the “enemies hypothesis” in patches, and “resource concentration hypothesis” in farmland (Prediction III; Root 1973). Conversely, we found plant–beetle relationship consistent with the “natural enemies” hypothesis in farmland during summer (positive relationship between plant richness and predator abundance; negative relationships between plant richness and herbivore abundance) and with the “resource concentration” hypothesis in patches (negative relationships between plant richness and herbivore abundance; no effects of plant richness on predator diversity) (Table 3). These contradictory findings may be related to Prediction I of stronger effects of plant composition compared to other vegetation attributes in some habitats. First, a higher proportion of dense annual crop or weeds in farmlands (Table A2 in Paper III: Supplementary Material), albeit lower in diversity, may provide preferred plant-mediated resources for predatory beetles, such that an increase in plant richness is associated with a high number of host plants which have positive effects on predator abundance (Joern and Laws 2013; Koricheva et al. 2000; Tews et al. 2004). Positive associations between predatory beetles and plant richness also may be linked to relatively high habitat heterogeneity across our mixed-farmlands (which spanned a number of contrasting land-uses from crops to fallow fields) contributing to reduced predation risks on beetles, compared to woodland patches (enemy-free space hypothesis; Brose 2003). Second, our woodland patches are characterised by more diverse native-dominant plant communities (Table A2 in Paper III: Supplementary Material) but sparser plant growth forms than farmland. Decreasing herbivore abundance with increasing plant richness may be due to more strenuous conditions to locate host plants (Agrawal et al. 2006; Root 1973) for beetles adapted to a small number of host plants in woodlands (Niemelä and Spence 1994), or increased predation risks in more open habitats (hunting efficienty hypothesis; Brose 2003).

Spatially and temporally dynamic vegetation effects on beetles

Plant composition

We found that the influence of plant composition on beetle composition was stronger in summer than in spring, and stronger in edges followed by farmland and patches (Table 2). Differences in the effects of plant composition on beetles across different habitats and time supports our Prediction III of varying plant–beetle relationships between different habitats, and Prediction IV corresponding to differences in plant–beetle relationships over time. Pronounced seasonal and habitat effects on plant–beetle relationships can be explained by a combination of changes in plant host use at different stages of beetle lifecycles, changes in plant phenology and succession (e.g. growth, flowering or senescence of annual vegetation) (Landis et al. 2005; Lassau et al. 2005; Parry et al. 2015; Rouabah et al. 2015), as well as changing environmental conditions (e.g. seasonal fluctuations in temperature and humidity) (Landis et al. 2000; Niemelä and Spence 1994). We suggest that individual plant species might be particularly important in providing food or habitat resources for beetles during hot and dry summer conditions when plant resources are likely in short supply (including reduced crop biomass). Field edges may provide temporally stable foraging and nesting sites for many beetles due to low disturbance and cross-habitat mixing of diverse plant resources (Holland et al. 2005; Rouabah et al. 2015).

Trophic groups were differently affected by plant and geographic factors between different habitats and time periods. This result is consistent with studies showing varying responses of trophic groups to vegetation resources depending on spatial and temporal differences (Lassau et al. 2005; Niemelä and Spence 1994; Tews et al. 2004; Woodcock and Pywell 2010). It is noteworthy that we found correlations between plant and beetle composition for all trophic levels under certain habitats and seasons, because herbivores are often assumed to be more sensitive to plant composition than predators (Buse 1988; Siemann 1998; Siemann et al. 1998; Woodcock and Pywell 2010). For beetle composition, we also could not fully support our Prediction II of predators being more influenced by vegetation structure and herbivores by plant composition. Instead, we found that herbivore composition (represented by a large proportion of Curculionidae in our data) was significantly affected by plant composition only at edges, while during summer, predator composition was significantly affected by plant composition at edges and by vegetation structure in patches (Table 2). Plausible explanations for the mixed responses of herbivores and predators to plant composition or vegetation structure include the following. First, significant effects of plant composition on herbivore composition in edges can be related to higher plant diversity associated with edge effects (Ewers and Didham 2006b). This is supported by our data showing that, during summer, there was higher plant species richness at edges than patches and farmland (Table 1), and positive correlations between plant species richness and herbivore abundance at edges (Table 3). A higher diversity of host plants often supports compositionally different and higher herbivore numbers due to the host specificity of many herbivores (Kromp and Steinberger 1992; Woodcock and Pywell 2010). Second, associations between predator composition and the composition or structure of plants is consistent with literature suggesting that many predatory arthropods use ephemeral floral food resources directly in field edges (e.g. nectar, pollen; Landis et al. 2005; Ramsden et al. 2015; Woodcock et al. 2016a), as well as use plant-mediated resources indirectly (e.g. increased plant-associated prey and correlations with productivity or structural complexity; Joern and Laws 2013; Koricheva et al. 2000; Tews et al. 2004). Our data identified that remnant patches might specifically provide structural refuge (e.g. ovipositioning or aestivation sites; Landis et al. 2000) for predatory beetles during the austral summer (e.g. *Diaphoromerus* sp. 456).

Plant species richness and vegetation structure

Like plant composition, effects of vegetation structure and plant richness on beetle trophic groups often varied with habitat type, and the strength or direction of effects was seasonally variable. This was exemplified by changes between spring and summer in the direction of the relationship between total herbaceous cover and predator abundance in all habitats (Table 3). Our findings suggest that conservation strategies aimed at manipulating vegetation structure need to be targeted at appropriate taxonomic, spatial and temporal levels, because a structural change which benefits a trophic group in one habitat type during spring may have adverse consequences for different trophic groups or habitats, or when applied during different seasons.

During spring, litter and vegetation height was positively associated with the abundance of detritivores and predators, respectively, regardless of habitat type, but their effects were habitat-specific during summer (Table 3). A positive effect of litter on detritivore abundance during spring is consistent with studies showing the benefits of coarse woody debris for many species of saproxylic beetles (Barton et al. 2009; Gibb et al. 2006). We found contrasting effects of litter on detritivore abundance in different habitat types during summer (positive effects in edges, negative in farmland; Table 3). This may be linked to differences in the quality of litter over time (e.g. litter from more diverse vegetation at edges may provide preferred food sources compared to litter dominated by annual grasses in farmland) (Woodcock and Pywell 2010). Positive effects of vegetation height on predator abundance during spring may be explained by increased structural refugia from predation, prey resources and soil moisture availability associated with higher vertical habitat complexity (Dennis et al. 1998; Lassau et al. 2005; Rouabah et al. 2015). Conversely, we found negative effects of vegetation height on predator abundance, specifically in remnant patches during summer (Table 3). This suggests that vegetation height might have an entirely different influence in this context (e.g. impeding movement and searching ability of scarce food resources) (Siemann et al. 1998).

During summer, beetle species richness was positively affected by total herbaceous cover (Table A4 in Paper III: Supplementary Material). Positive correlations between the percentage cover of plant species and species richness of surface-active arthropods also were found in Woodcock and Pywell (2010). This finding was attributed to higher diversity of structural variation of different growth forms, which provide increased ecological niches to support higher arthropod diversity (Joern and

Laws 2013; Siemann et al. 1998; Woodcock and Pywell 2010). Finding effects of total herbaceous cover on beetle species richness specifically during summer may be due to direct (e.g. reduced plant resources), or indirect seasonal effects (higher cover providing increased soil moisture and protection from adverse microclimatic conditions) of vegetation in our study landscape (Landis et al. 2005; Lassau et al. 2005; Perner et al. 2003).

Edges exhibited temporally stable patterns of plant–beetle relationships compared to patches and farmland, through positive relationships between plant richness and abundance for all trophic groups. Studies focussed on edge effects have found that field edges can support higher arthropod populations than adjoining habitats (particularly farmland), which have been linked to increased structural refuges and diversity of plant or prey foraging resources from overlapping habitats (Landis et al. 2005; Magura 2002; Ramsden et al. 2015; Rouabah et al. 2015; Woodcock et al. 2016a).

Implications for beetle biodiversity management

Our findings underscore the highly dynamic influence of vegetation on beetle assemblages across a modified landscape, and is represented by the conceptual model used in our study (Figure 1): plant-beetle relationships can be better understood by deconstructing their associations at a fine spatial and temporal scale (e.g. between growing season, within farm fields, field margins or patches), and considering multiple vegetation attributes – particularly plant species composition. We suggest that more collaboration between plant and insect ecologists is needed to enable collection of high quality species-level data in community-based studies on plant-arthropod relationships.

Conservation and management strategies based on altering vegetation structure or plant species richness need careful consideration, because changes focused on improving the habitat for a given trophic group (e.g. natural enemies) may negatively impact the abundance of other trophic groups providing important ecosystem services, or have adverse effects at other time periods. Our findings indicate that managing plant species composition at edges (compared to remnant patches and farmland), and during summer (compared to spring), are effective ways of altering the composition of beetle trophic groups (Figure 3). More research, however, is needed to determine how different species use vegetation resources across the landscape at different times of the year (Joern and Laws 2013; Souza et al. 2016; Woodcock and Pywell 2010) – this information is severely lacking for most beetle species outside of Europe.

Our study has several general findings that could be used to maximise positive outcomes for beetle diversity and the ecosystem services associated with different trophic groups (Figure 3). First, in all habitats in spring, management that leads to increased vegetation height supports predators, increased litter cover supports detritivores, and higher plant richness supports herbivores. Second, enhanced total herbaceous cover during summer (e.g. through fallowing, revegetation or reducing grazing), can increase overall beetle species richness. Third, promoting plant richness at the edge between woodland and farmland can improve overall beetle abundance (Figure 3). Arthropod conservation approaches are currently focused on protecting extant native vegetation in Australia (Parry et al. 2015), but our study shows that management of vegetation along edges and field margins could be altered to support beetles in Australian landscapes. Approaches employed in well-established European agri-environment schemes to manage floral resources in field edges for arthropod diversity (Rouabah et al. 2015; Woodcock et al. 2016a) could be relevant to Australian agroecosystems. In Australian croplands, current weed control practices at edges focus on the use of broad-spectrum herbicides or soil tillage (Preston 2010; Preston et al. 2017). More research is needed to determine whether the timing and tactics of existing weed control strategies have off-target negative impacts on beetle biodiversity particularly through the loss of plant diversity at edges, which provide habitat resources for beetles.

Acknowledgements

This work was supported by Central Tablelands Local Land Services (through Australian Government funding), Lake Cowal Foundation and Mount Mulga Pastoral Company. KN was supported by an Australian Government Research Training Program (RTP) scholarship. Thanks to landholders (Day, Foy, Conlan, Hall, Lucas, Nowlan, Aylott, Grimm, Robinson, Crawford, Daley families) for property access. We thank volunteers (particularly Alicia Ng, Nicholas Shore, Margaret Ning, Mal Carnegie and Dimitrios Tsifakis) for fieldwork assistance; Daniel Martinez-Escobar lab assistance; Maldwyn John Evans, Kim Pullen, and Michael Nash for beetle identification; Margaret Ning, Mikla Lewis, David Albrecht, Rainer Rehwinkel, Nicki Taws for plant identification; Wade Blanchard and Yong Ding Li for statistical advice.

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Paper IV: Disentangling the effects of farmland use, habitat edges and vegetation structure on ground beetle morphological traits

Little is known about how species traits of insects vary across different land-uses and their edges, with most studies focussing on single habitat types and overlooking edge effects. A traits perspective may help uncover mechanisms shaping assemblages responses to landscape modification. In Paper IV, I disentangled the effects of farmland use, edge effects and vegetation structure on the morphological traits of all species of the ground beetle (Carabidae) family.

Ng K, Barton PS, Blanchard W, Evans MJ, Lindenmayer DB, Macfadyen S, McIntyre S, Driscoll DA, in review, Disentangling the effects of farmland use, habitat edges and vegetation structure on ground beetle morphological traits, *Oecologia*

Abstract

Habitat fragmentation and modification due to agriculture are major drivers of biodiversity change, and may influence species differently depending on their traits. It is unclear how species traits of insects vary across different land-uses and their edges, with most studies focussing on single habitat types and overlooking edge effects. We examined variation in morphological traits of ground beetles (Coleoptera:Carabidae) on both sides of edges between woodlands and four adjoining but contrasting farmland uses in an agricultural landscape. We asked: (1) How do traits differ between woodlands and farmland uses (crop, fallow, restoration planting, woody debris applied over crop), and do effects depend on increasing distances from the farmland–woodland edge? (2) Does vegetation structure explain observed effects of farmland use and edge effects on these traits? We found that carabid species varied in body size and shape, including traits associated with diet, robustness, and visual ability. Smaller-sized species were associated with woodlands and larger-sized species with farmlands. Farmland use further influenced these associations, with woodlands adjoining plantings supporting smaller species, and fallows and crops supporting larger species. Vegetation structure was associated with body size, flying ability and body shape, and helped explain the effects of farmland use and distance from edges on body size. Our findings emphasise that habitat complexity is a fundamental driver of variation in body size and dispersal-related traits in modified landscapes. We highlight the important role of vegetation structure, farmland use and edge effects in filtering the morphological traits of carabid assemblages across a fragmented agricultural landscape.

Keywords: fourth-corner analysis; size-grain hypothesis; soft traits; textural-discontinuity hypothesis

Introduction

Habitat fragmentation and modification due to agriculture are major drivers of biodiversity change globally (Didham 2010; Haddad et al. 2015). It is generally accepted that environmental changes resulting from habitat modification may influence species differently depending on their traits (Davies et al. 2000; Duflot et al. 2014; Gibb and Parr 2010; Tscharntke et al. 2012). Trait-based approaches are particularly useful in generalising predictions of arthropod community responses (Gibb et al. 2015; McGill et al. 2006) because the taxonomy and ecology of many species are poorly known (Cardoso et al. 2011; Gibb et al. 2015; Yates et al. 2014). Information gained from traits can thus provide additional insights into the mechanisms influencing arthropod responses to environmental change over and above that gained by examining species identities only (Barton et al. 2011a; Magura et al. 2017; Ribera et al. 2001; Yates et al. 2014).

Morphological traits, such as dispersal ability, foraging efficiency, as well as feeding and sensorial capacity, strongly influence how they interact with their environment (Barton et al. 2011a; Moretti et al. 2017; Weiser and Kaspari 2006; Wood et al. 2015). Morphological traits are useful for studying arthropod assemblages such as beetles, where detailed biological information on diet, life-history, behaviour, and physiology (Moretti et al. 2017) are often completely unknown. For example, body size is one of the most studied animal morphological traits because it is easy to measure, and strongly influences how organisms interact with their environment (Allen et al. 2006; McGill et al. 2006; Moretti et al. 2017; Peters 1986). Larger species are predicted to be more prone to extinction from habitat fragmentation and modification (Davies et al. 2000; Kotze and O'Hara 2003) with habitats experiencing high disturbance selecting for smaller species with higher dispersal ability, while less disturbed habitats are more suitable for larger species with lower dispersal ability (Lovei and Sunderland 1996; Ribera et al. 2001). Yet, studies have found mixed responses of body size to habitat disturbance, including negative (Ribera et al. 2001; Winqvist et al. 2014), positive (Gibb and Parr 2013; Kaspari 1993; Rouabah et al. 2015) and neutral (Gibb and Parr 2013; Wiescher et al. 2012) relationships. These contradictory effects on body size might be due to some larger species having greater longevity (Davies et al. 2000) or dispersal abilities, while some larger species have lower population densities with increased disturbance (Tscharntke et al. 2012).

There are large knowledge gaps on how species traits might differ across contrasting land-uses, as well as across the edges between them (Evans et al. 2016; Öckinger et al. 2010). Most trait-based studies focus on single habitat types (e.g. woodlands, grasslands, or specific crop fields) and do not explicitly consider the spatial heterogeneity that typically characterize human-modified landscapes (Allen et al. 2006; Gibb et al. 2015; Wood et al. 2015). Intensively farmed areas, in particular, are often assumed to be homogenous habitats (Driscoll et al. 2013), but there are subtle differences within each land-use or field type. These include vegetation structure (Rouabah et al. 2015), management regimes (Ribera et al. 2001) and edge-mediated changes in microhabitat conditions (Evans et al. 2016), which can all affect habitat suitability for different species and therefore combinations of traits (Rouabah et al.

2015). While considerable research has been done on the effects of edges on the taxonomic diversity and composition of arthropod assemblages (e.g. Magura 2017; Ries et al. 2004), the use of trait-based approaches in edge-effects studies remains scant but promising (but see Barnes et al. 2014; Evans et al. 2016). Disentangling the various effects of land-use changes, edge effects and vegetation structure on the traits of species making up each assemblage could help to reveal specific mechanisms shaping assemblages responses to landscape modification (Evans et al. 2016; McGill et al. 2006).

In this study, we examined the variation in morphological traits of ground beetles (Coleoptera: Carabidae) between woodland patches and adjoining, contrasting farmland uses in a fragmented farming landscape. We focused on ground beetles because they are speciose, and sensitive to small- and large-scale changes in habitat conditions (Cardoso et al. 2011; Thiele 1977). They also have important functional roles in delivering biological pest control services (most species being predators in Australia; Gibb et al. 2017), as well as providing food resources to other fauna (Cardoso et al. 2011; Duflot et al. 2014; Lovei and Sunderland 1996). We asked the following questions: (1) How do traits differ between woodlands and farmland uses (crop, fallow, restoration planting, woody debris applied over crop), and do effects depend on increasing distances from the farmland–woodland edge? (2) Does vegetation structure explain observed effects of farmland use and edge effects on these traits?

Environmentally stable later successional habitats (e.g. interior of woodlands or in undisturbed habitat edges) generally favour larger and more robust species with longer development times (Chown and Gaston 2010; Lovei and Sunderland 1996; Ribera et al. 2001; Thiele 1977). Conversely, more disturbed habitats (e.g. cultivated cropland) tend to favour smaller and less robust species due to their faster development and shorter generation times (Barton et al. 2011; Blake et al. 1994; Kaspari 1993; Ribera et al. 2001). However, a variety of factors other than disturbance, such as structural complexity, food availability and microclimate, can result in idiosyncratic responses of body size to habitat type (Barton et al. 2011; Ribera et al. 2001; Wiescher et al. 2012). For example, smaller species may be favoured in structurally complex habitats because their movements are less impeded by dense vegetation. Conversely, structurally simple and productive habitats (e.g. farmlands) may support larger species due to better resistance to desiccation, or positive effects of higher food resources and temperatures on growth rates (Chown and Gaston 2010; Holling 1992; Kaspari and Weiser 1999; Siemann et al. 1999).

As for traits relating to dispersal and body shape, species with weaker dispersal ability (e.g. wingless or with shorter legs) may be favoured in woodland habitats. Species with greater dispersal ability, on the other hand, may be favoured in farmland monoculture habitats due to higher predation risks on weaker dispersers where vegetation is less structurally complex (Chown and Gaston 2010). Beetles with feeding traits adapted for larger prey (i.e. increased head width) have been associated with more productive farmland habitats than with less productive remnant habitats (Laparie et al. 2010). Open farmland habitats might also contain more visual hunters with larger eye protrusion and surface area than more complex woodland habitats (Fountain-Jones et al. 2015; Talarico et al. 2011).

Methods

Study area

Our study was conducted in a fragmented cropping–grazing landscape within the Lachlan River Catchment, New South Wales, southeastern Australia. Widespread clearing for agriculture has restricted native *Eucalyptus* woodlands to infertile steeper areas. Many remnants have also been modified by livestock grazing, weed invasion, and altered fire regimes (Norris and Thomas 1991). The study sites were clustered in three regions (east, mid and west), which spanned approximately 250 km along a decreasing elevation and rainfall gradient (Figure S1 in Paper IV: Supplementary Material).

Experimental design

We selected eleven woodland patches as our study sites on the basis that they were *Eucalyptus* woodland communities with high ground-, mid- and over-storey native vegetation complexity, and adjoined four farmland uses: (1) winter wheat crop, (2) fallow (rested from crop rotation or sown-pasture rotation), (3) plantings of native trees and shrubs (<7 years old), and (4) winter wheat crop over which eucalypt-based fine woody debris was applied (a treatment to promote ground cover resources for ground-dwelling arthropods). Our experimental design consisted of four 400 m transects running from inside each woodland patch out into each adjoining farmland. To quantify potential edge effects on beetle species traits, we sampled beetles at five locations along each transect: 200 m and 20 m inside woodlands, 200 m and 20 m inside farmlands, and at the woodland–farmland edge (0 m) (Figure S1 in Paper IV: Supplementary Material). The 200 m distance represented the interior of smaller farm fields.

Beetle sampling

Each sampling location comprised a pair of pitfall traps, consisting of 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). Individual traps from each pair were placed on either side of a drift fence (60 cm long x 10 cm high) to help direct arthropods into traps. We opened a total of 220 pairs of traps for 14 days during spring (Oct–Nov 2014), and repeated sampling during summer (January–February 2015). Arthropods were preserved in 70% ethanol. All adult ground beetles (Carabidae) were removed and identified to morphospecies and subfamily, 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.

Vegetation surveys

The same observer (KN) recorded seven ground-layer vegetation structural variables within a 20 × 10 m plot centred around each pitfall location during beetle sampling. The variables were: vegetation height, and cover of litter, bare ground, native forb, native grass, exotic perennial grasses, and exotic annual forbs and grasses. We calculated total herbaceous cover (%) from the sum of forb and grass cover (Table S1 in Paper IV: Supplementary Material). We selected these vegetation variables because they had similar and therefore comparable ranges of values within each habitat type (Table S1 in Paper IV: Supplementary Material). Other vegetation variables did not vary between habitats (e.g. trees were always present in woodlands and mostly absent from farmland).

Morphological trait measurements

We measured twelve morphological traits from all 62 ground beetle species caught in our study (Table 1), focussing on traits that reflected differences in species' size, shape, and other life-history attributes among species in the carabid assemblage. We chose these traits based on their likely functional role as described in the literature (Table 1). We measured up to six individuals per species, using individuals from different regions and of differing sex where possible, to account for geographical variability and sexual dimorphism. We took photographs of individuals using a digital camera mounted on a stereomicroscope, and measured traits using the "ImageJ" software (Rasband 2007).

Total body length, a useful approximation of body size (Ribera et al. 2001), was calculated by summing the lengths of the head, pronotum and elytra (which were unaffected by preservatives).

Table 1. Morphological traits of ground beetles measured in this study.

Morphological trait	Type	Description	Functional role
Wing occurrence	Nominal	Presence or absence of wings	Dispersal ability (Driscoll and Weir 2005; Kotze and O'Hara 2003).
Head width	Continuous	Maximum dorsal head width, including eyes	Feeding and foraging ability, e.g. preferred prey size (Kaspari and Weiser 1999).
Head length	Continuous	Maximum dorsal head length, excluding mandibles	
Pronotum width	Continuous	Maximum dorsal pronotum width	Robustness, microhabitat choice (Barton et al. 2011a; Ribera et al. 1999), dispersal, visual ability (narrow shape allows greater elytra spread and rear visual field; Forsythe 1987).
Pronotum length	Continuous	Maximum dorsal pronotum length	
Pronotum depth	Continuous	Maximum pronotum depth	
Elytra width	Continuous	Maximum dorsal elytra width	Robustness (Ribera et al. 1999).
Elytra length	Continuous	Maximum dorsal elytra length	
Rear femur length	Continuous	Maximum length of rear femur	Dispersal ability and foraging range (Kaspari and Weiser 1999; Ribera et al. 1999).
Metatrochanter length	Continuous	Maximum length of metatrochanter	Running or pushing ability (Forsythe 1987)
Eye protrusion	Continuous	Difference between maximum head width with eyes, and maximum head width without eyes	Activity period, hunting and dispersal behaviour (Forsythe 1987; Gibb and Parr 2013; Weiser and Kaspari 2006).
Mandible protrusion	Continuous	Difference between maximum head length with mandibles, and maximum head length without mandibles	Diet preferences (Gibb et al. 2015).
Body length	Continuous	Sum of head length, pronotum	Disturbance tolerance (Ribera et

	length and elytra length as a measure of body size	al. 2001), reproduction (Kotze and O'Hara 2003), feeding rate (Rusch et al. 2015), and prey preference (Radloff and Du Toit 2004).

Data analyses

Beetle samples from each pitfall trap pair, and across the two time periods, were pooled to provide one sample per sampling location. We used the average trait values across all individuals for each species, and log-transformed trait values prior to analysis.

Descriptive analyses: beetle species traits and composition, and vegetation structure

Beetle traits. Many morphological traits of animals are correlated with each other and with body size (Peters 1986). To identify traits that varied independently of each other, and from body size, we conducted principal component analysis (PCA, based on covariance among traits) on twelve different linear measures of each beetle species (Table 1). PCA (and ordination methods in general) is a useful way to characterize species in 'morphospace' because it reduces data dimensionality by creating new compound axes of variation that contain meaningful functional and allometric information (Ribera et al. 1999; Weiser and Kaspari 2006). We $\log_{10}$ transformed all trait measures prior to PCA, and used the component variables that explained over 5% of the morphological variation in subsequent analysis. Wing occurrence was excluded from PCA because it is a nominal variable.

Beetle composition. To determine how species identity might influence trait–environment relationships, we examined whether species composition of ground beetles differed depending on habitat type and distance from edges. We fitted a multivariate generalized linear model for species occurrence, using the following predictor variables in relation to our paired woodland–farmland study design: adjoining 'farmland use' (planting, fallow, crop, woody debris), 'distance' from the edge (categorical factor: -200 m, -20 m, 0 m, 20 m, 200 m), interaction between 'farmland use' and 'distance', and vegetation structure (Table S1). We analysed data using the 'manyglm' function in the 'mvabund' R package (Wang et al. 2016) in R 3.2.0 (R Development Core Team 2015). We also examined how individual species responded to environmental factors by fitting a single multispecies model (SDM) using the 'traitglm' function in 'mvabund' without traits. We used the same criteria and formulae as the fourth-corner analysis (detailed below) for the ‘manyglm’ and ‘traitglm’ functions.

Vegetation structure. We examined effects of habitat type and distance from edges on vegetation structure, using generalized linear mixed-effect models (GLMM; Bolker et al. 2009). The main fixed effects tested were ‘farmland use’, ‘distance’, and their interactions. We controlled for possible effects of region (three levels: east, mid, west) by including it as an additive fixed effect, although it was not of primary interest in this study. We fitted farmland use nested within site as a random effect to account for the study design’s non-independent spatial structure, and used a Poisson error distribution. We ran Wald tests to determine statistical significance of fixed effects. We used R 3.2.0 (R Development Core Team 2015), with the ‘lme4’ (Bates et al. 2015), and ‘car’ (Fox et al. 2013) R packages for the GLMM analyses.

Predictive analyses: Fourth-corner modelling

We used fourth-corner analyses (Brown et al. 2014; Warton et al. 2015) to quantify relationships between morphological traits and environmental variables of farmland use (Question 1) and vegetation structure (Question 2). Fourth-corner approaches provide a way of analysing relationships between a species trait matrix (Q) and an environmental variable matrix (R) by way of a species abundance/occurrence matrix (L) (Legendre et al. 1997). We used the ‘traitglm’ function in the ‘mvabund’ R package (Wang et al. 2016). This function fits a fourth-corner model to predict abundance/occurrence across multiple taxa (L) as a function of environmental variables (R) and traits (Q). R-Q interactions represents the fourth corner, and the coefficients quantify how environmental responses across taxa vary with traits (Brown et al. 2014; Wang et al. 2016).

We fitted multivariate generalized linear fourth-corner models (with a binomial distribution) for species occurrence (absence/presence) as a function of the species traits matrix, environmental variable matrix and their interactions. We used absence–presence data to reduce the influence of very rare or abundant species (Ribera et al. 2001). We fitted models for each species traits separately: $\log_{10}$(body length), and three PCA component variables Dim.2, Dim.3, and Dim.4. We used body length as a direct measure of body size instead of the first component of our PCA (Dim.1) that also represented body size to enable higher repeatability and comparison with other studies (Barton et al. 2011a; Ribera et al. 2001).

We fitted two models per trait variable in relation to questions (1) and (2) respectively:

(I) *farmland use:distance:trait* + *region:trait*; and

(II) *bare.ground.cover:trait* + *litter.cover:trait* + *total.herbaceous.cover:trait* + *vegetation.height:trait* + *region:trait*.

Farmland use comprised four categorical levels (planting, fallow, crop, woody debris), distance of five levels (-200 m, -20 m, 0 m, 20 m, 20 m), region of three levels (west, mid, east), and vegetation structural variables were continuous (rescaled to have a mean of zero and standard deviation of 1). *Region:trait* was included as an additive term to account for possible effects of regional variation. We ran model selection by applying a LASSO penalty (i.e. method='glm1path' that uses cross validation to choose the amount of smoothing, **λ**) which penalises coefficients that do not reduce BIC to zero (Tibshirani 1996). We conducted inferences on the direction of associations based on the fitted model's coefficients. Note that this method does not allow comparison of the magnitude of differences between treatments because determining reliable standard errors from LASSO is mathematically non-trivial (Lockhart et al. 2014). We inspected diagnostic plots to check that model assumptions were met.

To determine how much vegetation structure might be correlated with and therefore account for trait responses to 'farmland use' and 'distance', we also ran models (III) that additively combined terms from the first two models (I) and (II) above. Only body size exhibited significant terms for both parts of the fitted combined model (III) (while there were no differences in associations for the other response variables across the three models). So, for body size, we compared coefficients of the combined model (III) with model (I) to inspect whether vegetation structure contributes to some of the variation in body size across 'farmland use' and/or 'distance'.

Results

We collected 1566 individual ground beetles, which comprised 62 morphospecies (47 with wings, 15 without wings) (Table S2 in Paper IV: Supplementary Material). The body size of all species ranged from 1.43 to 40.5 mm long (Table S3 in Paper IV: Supplementary Material), with Scaritinae, Carabinae and Helluoninae representing the largest three subfamilies and Pseudomorphinae, Bembidiinae and Amblystominae representing the smallest three.

Beetle species traits and composition, and vegetation structure

Beetle composition and vegetation structure. We identified significant effects of farmland use, distance from edges, and vegetation structure on beetle composition (Table S4, Figure S2 in Paper IV: Supplementary Material). This indicated that species differed among our sites, and that traits would also differ. Farmland use and distance from edge also had significant interactive effects on vegetation structure, indicating beetle habitat differed among our sites (Figure S3 in Paper IV: Supplementary Material).

Beetle traits. The PCA identified four main dimensions in which the morphological traits of ground beetles varied. The first component (Dim.1) explained 64.5% of the morphological variance, and was a consistent measure of change from large to small overall body size (Table 2). The remaining three components Dim.2, Dim.3, and Dim.4 combined explained 24.5% of the variance. Dim.2 was positively associated with head width and pronotum length (which we interpreted as being associated with diet; Table 2). Dim.2 loadings thus represented a gradient from species with narrow heads and short pronotum (*Adelotopus* sp. C389, *Harplaner* sp. C529) to species with wide heads and long pronotum (e.g. *Amblystomus* sp. C252, *Pericompsus* sp. C164) (Figure 1a). Dim.3 was positively association with elytra width (interpreted as measure of robustness; Table 2), and represented a gradient from narrow elytra (*Calosoma schayeri*, *Scaraphites lenaeus*, *Amblystomus* sp. C252) to wide elytra (e.g. *Cainogenion* sp. C439, *Pericompsus* sp. C164) (Figure 1b). Dim.4 was positively associated with eye protrusion (interpreted as a measure of visual ability; Table 2), representing a gradient of species with less protruding eyes (*Agoninae* sp. C710, *Mecyclothorax punctipennis*) to species with highly protruding eyes (*G. melbournensis*, *Scopodes boops*) (Figure 1c).

Table 2. Summary of principal components analysis conducted on log-transformed trait values. High loadings are shown in bold.

	Dim.1 (body size)	Dim.2 (diet)	Dim.3 (robustness)	Dim.4 (visual ability)
Percentage variation explained	64.50	11.79	6.77	5.91
Correlation with morphological traits				
Head width	0.33	**0.80**	0.07	-0.29
Head length	**0.95**	0.12	-0.14	-0.04
Pronotum width	**0.93**	-0.11	-0.08	-0.16

Pronotum length	0.30	**0.78**	0.27	0.29
Pronotum depth	**0.94**	-0.12	-0.05	-0.08
Elytra width	0.56	-0.26	**0.69**	-0.05
Elytra length	**0.96**	-0.10	-0.04	-0.06
Rear femur length	**0.96**	-0.07	0.12	-0.02
Metratrochanter length	**0.94**	-0.13	0.10	-0.02
Body length	**0.98**	-0.06	-0.07	-0.06
Eye protrusion	0.64	-0.06	-0.06	**0.71**
Mandible protrusion	**0.68**	0.18	-0.44	0.00

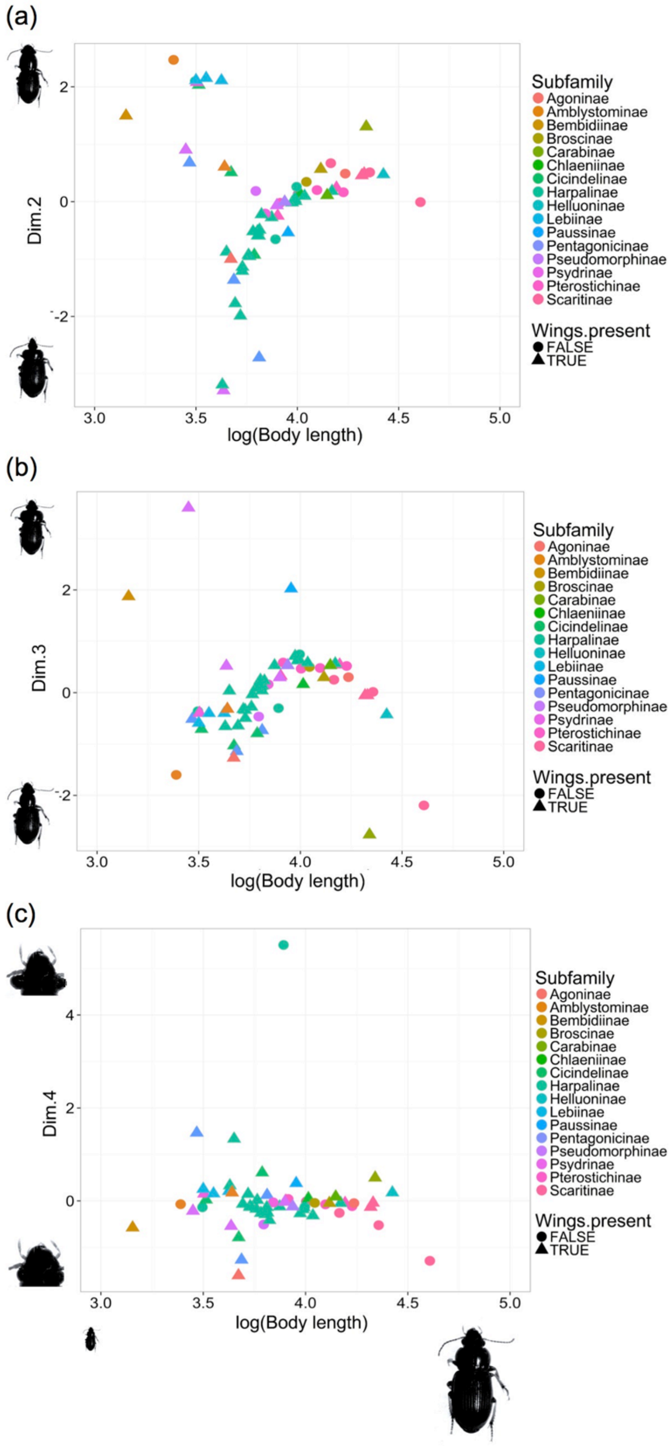
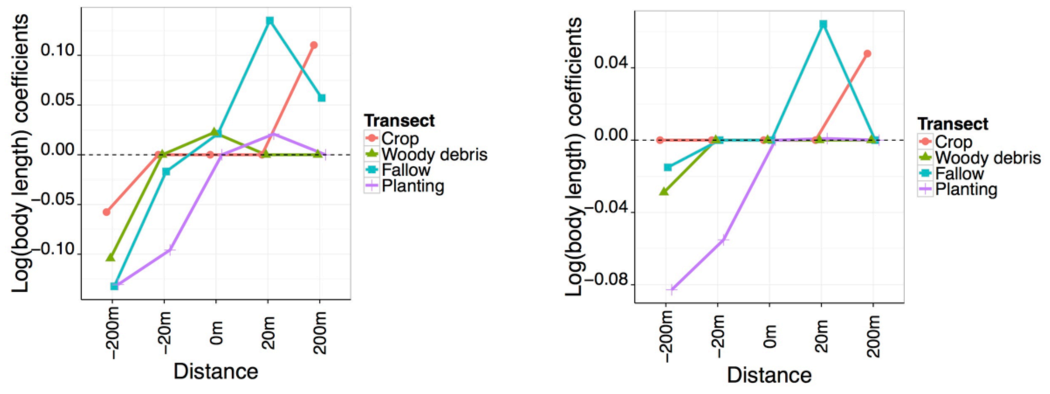


Figure 1. Relative position of ground beetle species in morphological space showing log(body length) against coefficients of PCA dimensions Dim.2 (diet: increasing head width and pronotum length) (a), Dim.3 (robustness: increasing elytra width) (b), Dim.4 (visual ability: increasing eye protrusion) (c).

Question (1) How do traits differ between woodlands and farmland uses (crop, fallow, restoration planting, woody debris applied over crop), and do effects depend on increasing distances from the farmland–woodland edge?

Fourth-corner analyses showed associations between interactions of ‘farmland use’ and ‘distance’ with body size (β-values in Figure 2a), but not for other body shape-related morphological traits (represented by PCA component variables Dim.2, Dim.3 and Dim.4) and wing presence (i.e. farmland use’ × ‘distance’ effects: β = 0). Winged beetles were negatively associated with -200m in the woodland interior (‘distance’ effect only: β = -0.30).

When not accounting for vegetation structure [model (I)], there was a general pattern of higher occurrence of smaller species in woodlands and higher occurrence of larger species in crop and fallow farmland uses (Figure 2a). Smaller-sized beetle species were associated with interior (-200 m) of woodlands for all adjoining farmland types (-0.13 < β < -0.06), and near edges (-20 m) of woodlands adjoining plantings (β = 0.096) and fallows (β = -0.017). Larger-sized beetles were associated with interior (200m) of fallows (β = 0.057) and crops (β = 0.11), and near edges (20 m) of fallows (β = 0.14) and plantings (β = 0.021). Larger body sizes also were associated with edges (0 m) of woodland–fallow (β = 0.057) and woodland–woody debris (β = 0.022) habitats (Figure 2a).


(a) Model (I): Farmland use × distance × log(body length)

(b) Model (III): Farmland use × distance × log(body length) + vegetation structure × log(body length)

Figure 2. Coefficients of fourth-corner interaction showing Relationships between log(body length) and the interaction between farmland use and distance. Significant relationships are non-zero values, with direction of relationships shown as positive or negative values. Distance -200m and -20m refers to the woodland, 0m the edge, and

200m and 20m the farmland adjoining the woodland. Lines show general trends only, and cannot be used to infer magnitude of differences between treatments. Fitted models as follows: excluding vegetation structural variables (a), accounting for vegetation structural variables (b).

Question (2) Does vegetation structure explain observed effects of farmland use and edge effects on these traits?

Vegetation structure accounted for some of the interactive effects of ‘farmland use’ and ‘distance’ on body size [combined model (III); cf. Figures 2a,b]. After accounting for all four vegetation variables (vegetation height, litter cover, bare ground cover and total herbaceous cover), larger-sized beetles were associated with the edges (20 m) of fallows (β = 0.06) and with interior (200 m) of crops (β = 0.05). Smaller-sized beetles were still associated with -20m (β = -0.05) of woodlands adjoining plantings, and interior (-200 m) of woodlands adjoining fallow, woody debris and plantings, but not crops (Figure 2b).

Regardless of farmland use [model (II)], body size was negatively related to litter cover (β = -0.05), and positively related to bare ground cover (β = 0.02) and total herbaceous cover (β = 0.03) (Figure 3a).

There were varying associations between body-shape related traits and different vegetation structural variables (Figure 3a). Dim.2 (diet) was positively related to vegetation height (β = 0.04), and negatively associated with total herbaceous cover (β = -0.03). Dim.3 (robustness) was negatively associated with bare ground cover (β = -0.008). Dim.4 (visual ability) was negatively associated with litter cover (β = -0.05) and positively associated with vegetation height (β = 0.03) (Figure 3a).

Wingless beetles were associated with increased vegetation height (β = 0.09) and decreased litter cover (β = -0.23). Winged beetles were associated with increased bare ground cover (β = 0.05), increased total herbaceous cover (β = 0.32), and decreased litter cover (β = -0.003) (Figure 3b).

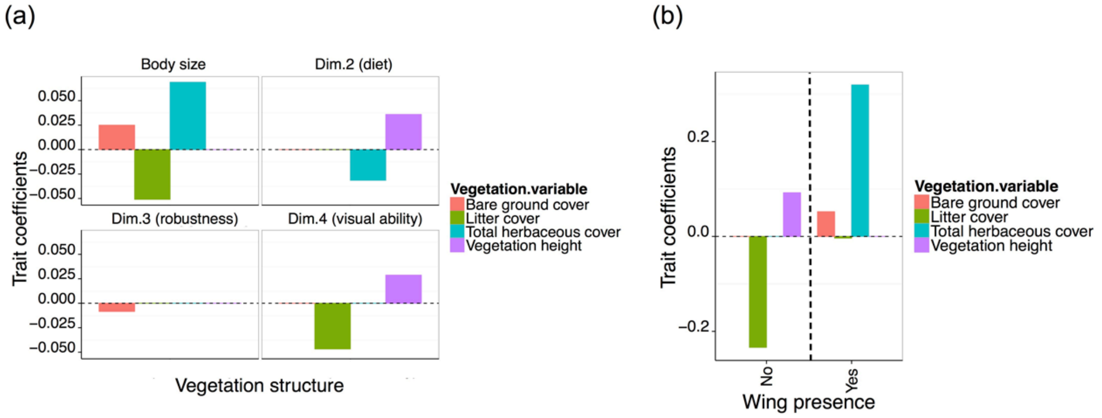


Figure 3. Coefficients of fourth-corner interaction showing associations between vegetation structure and ground beetle traits of: body length and PCA dimensions Dim.2 (diet), Dim.3 (robustness) and Dim.4 (visual ability) summarising traits (a), and wing presence (b).

Discussion

We set out to disentangle the influence of farmland use, edge effects, and vegetation structure on the morphological traits of ground beetles. In our study landscape, ground beetle species varied in their body size, and shape-related traits associated with diet, robustness and visual ability. There were two key findings: (1) smaller-sized species were associated with woodlands and larger-sized species with farmlands, where there were mediating effects of farmland use on the strength of these associations; (2) vegetation structure was associated with traits relating to body size, flying ability and body shape, and helped explain some of the effects of farmland use and distance from edges on body size.

Farmland use and edge effects

Body size

We found higher occurrence of smaller beetles in the interior of woodlands, regardless of adjoining farmland type, and larger beetles in crop and fallow fields (Figure 2a). This result is consistent with the textural-discontinuity hypothesis, which predicts that animal body size would exhibit discontinuous distribution following the discontinuity in the habitat structure of the landscape (Fischer et al. 2008; Holling 1992). This hypothesis predicts that smaller-bodied species are more dominant in structurally complex landscapes with fine-grained heterogeneity, and larger-bodied species are dominant in simpler landscapes with coarse-grained heterogeneity (Fischer et al. 2008; Holling 1992).

The size-grain hypothesis also predicts more smaller species in more complex, less disturbed habitats (Kaspari and Weiser 1999), and has been specifically linked to movement mechanisms (Fischer et al. 2008; Kaspari and Weiser 1999). This hypothesis predicts that smaller species (often with proportionately shorter legs) have a functional advantage of being able to move through fine-grained environments while movements of larger species are impeded (Gibb and Parr 2010; Kaspari and Weiser 1999). Conversely, it predicts that larger species are favoured in simpler, more disturbed habitats due to advantages from their higher robustness and dispersal ability (particularly greater leg length) in using open environments (Barton et al. 2011a; Gibb and Parr 2010; Kaspari and Weiser 1999). In open habitats larger species are therefore generally able to move rapidly for foraging or escaping predation (Kaspari and Weiser 1999), and can withstand higher desiccation stress from adverse climatic conditions (Barton et al. 2011a; Kaspari 1993; Ribera et al. 2001). Besides movement, relationships between body size and habitat complexity also could be explained by other mechanisms operating at different spatial or temporal scales (Allen et al. 2006; Fischer et al. 2008). This includes inter-specific and community interactions, or broader-level biogeographic and phylogenetic constraints (Allen et al. 2006), relationships between resource use and habitat complexity (Fischer et al. 2008), and the amount of direct or cross-habitat supplementary resources (Ries et al. 2004).

Flying ability

The majority of species in our data were winged, but we found lower occurrence of winged species in the interior of woodlands. This result supports predictions of flying ability strongly influencing beetle responses to disturbance in fragmented landscapes (Driscoll and Weir 2005). We suggest that although cursorial movement of ground beetles are more widespread in temperate (Thiele 1977), farmed areas (Hanson et al. 2016), if required, many species can overcome disturbance through flight to a more suitable environment (Thiele 1977). Flying species have likely persisted in this fragmented landscape due to their ability to colonise scattered habitat patches, thereby accessing a wider range of available resources (Driscoll and Weir 2005; Ribera et al. 2001; Tscharntke et al. 2005a; Tscharntke et al. 2012). Our species-level data also suggest that species in woodlands might be dispersal-limited woodland specialists (e.g.

abundant small, flightless *Amblystomus* sp. C252), and susceptible to further habitat loss (Ribera et al. 2001; Tscharntke et al. 2005a).

Our species composition data showed that trends of larger species in farmlands might be influenced by the abundance of a few moderate-sized (body length: 5 to 7mm), winged species in crops (*Clivina* sp. C032 and *M. punctipennis*), and fallows (*Hypharpax* sp. C114 and *G. multipunctatus*). These species may be able to thrive in cultivated areas because their flying capacity enables them to exploit ephemeral resources across farmlands (Blake et al. 1994; Thiele 1977).

Vegetation structural effects

Body size

Interestingly, associations between vegetation structure and body size in our data also broadly support the textural-discontinuity (Holling 1992) and size-grain hypotheses (Kaspari and Weiser 1999) at small microhabitat scales. We found that larger body sizes were associated with lower litter cover and higher bare ground (Figure 3a), which are vegetation metrics commonly used to characterise low habitat heterogeneity and high disturbance (Eyre et al. 2013; Ribera et al. 2001; Rouabah et al. 2015). These findings are also consistent with the hunting efficiency hypothesis, which predicts that larger predators would prefer more open microhabitats (Brose 2003). We found that total herbaceous cover was positively associated with body size (Figure 3a). This suggests that total herbaceous cover might be a better indicator of the amount of available food or habitat resources than the level of vertical or horizontal habitat complexity (Kaspari and Weiser 1999; Parr et al. 2003).

When considered as additive effects, adding all of the vegetation variables explained most of the edge responses of body size to different farmland types (cf. Figure 2a,b). These results support previous studies on the influences of multiple vegetation attributes on ground beetle traits, through changes in habitat complexity, disturbance (Ribera et al. 2001; Thiele 1977), or resource availability (Eyre et al. 2013; Rouabah et al. 2015). For example, we found larger species associated with low litter in fallows (i.e. lower structural complexity), most likely caused by livestock grazing in fallows (cf. Figure 2a, and Figure S3d, Figure S4a in Paper IV: Supplementary Material). We also identified significant interactive effects of farmland use and distance from edges on all vegetation structural variables (Table S5 in Paper IV: Supplementary Material). Therefore, the ground beetle trait responses we observed could be interpreted as being secondary effects of the response of vegetation structure to farmland use and edge effects.

While vegetation structure was able to explain some of the underlying differences in ground beetle body size, there was remaining variation in the relationship between body size and the interactive effects of farmland use and distance from edges (cf. Figure 2a,b). This unexplained variability might be due to land management (e.g. soil tillage or pesticide use; Winqvist et al. 2014) or environmental factors (e.g. microclimate, Kaspari 1993; soil moisture, Thiele 1977) not measured in our study. Here, we highlight three notable patterns of body size associations with farmland use and edge effects that could not be fully explained by vegetation structure. The mechanisms behind these observations are likely to be highly complex, so our interpretations of these associations remain speculative.

First, we still found larger species in crops and fallows than woodlands after accounting for effects of vegetation structure. This is a surprising result because, irrespective of vegetation structure, larger species have been found to be more vulnerable to increased habitat disturbance in intensively farmed areas, due to their longer development times and lower reproduction rates (Blake et al. 1994; Lovei and Sunderland 1996; Ribera et al. 2001). In agroecosystems, disturbance and primary productivity are thought to be key determinants of ground beetle activity and assemblage patterns (Eyre et al. 2013; Ribera et al. 2001; Thiele 1977). While productive farmlands can provide plentiful foraging resources, the availability of resources are short-lived in frequently disturbed agroecosystems and thus not accessible to higher trophic levels (Blake et al. 1994; Ribera et al. 2001). This has led to higher activity of larger ground beetle species in farms with high productivity and low to medium management intensity in England (Eyre et al. 2013). Farmlands in our study region are perhaps better characterised as having low to moderate levels of disturbance, due to the soil conservation practices in the area (i.e. reduced tillage and increased stubble retention; Llewellyn et al. 2012). Given that body size is positively associated with predation rates (Rusch et al. 2015), increased intensification of cultivation practices in this region may be to the detriment of larger ground beetle species and have profound implications for pest control in farmlands. Other ecosystem functions, such as the availability of large beetle prey for birds may also be affected (Blake et al. 1994).

Second, we found that vegetation structure could account for the occurrence of smaller species in the interior of woodlands adjacent to crops, but not in the interior of woodlands adjacent to plantings, fallow and the woody debris treatment (cf. Figures

2a,b). This result is comparable to literature on the effects of surrounding farmlands on beetle assemblages within non-cropped or native habitat patches (Driscoll et al. 2013; Eyre et al. 2016; Tscharntke et al. 2012). For example, Eyre et al. (2016) found that surrounding crop cover significantly affected ground beetle abundance in non-crop habitats, with more larger, non-flying species where crop management intensity was reduced. Vegetation structure might be a discernible explanatory factor filtering towards smaller-sized species in woodlands adjoining crops (e.g. following the textural-discontinuity hypothesis previously discussed) because long-term cropping in our study region could be regarded as an established component of the landscape (Eyre et al. 2016). In comparison, plantings, fallow rotation, and the woody debris treatment might be regarded as relatively novel, less disturbed landscape components that might therefore contributed to additional biotic or abiotic factors. For example, long-distance spillover of competitive or predatory fauna from these adjoining farmlands into the woodland interior (perhaps due to higher edge permeability; Rand et al. 2006) might have led to a reduction in larger ground beetles.

Third, we found that vegetation structure did not account for the occurrence of smaller species near woodland edges adjacent to plantings (cf. Figures 2a,b). For this pattern, we speculate that increased bird activity in plantings (Munro et al. 2007) might have led to their spillover into adjacent woodlands and increases in foraging rates of large beetles at all distances within the woodlands. More work is needed to investigate whether restoration plantings might act as ecological traps (Battin 2004) for larger-sized beetles in agricultural landscapes.

Body shape

We found interpretable links between the structuring of body-shape related traits and three ecological functions in our PCA, which supports previous beetle morphometric studies (Barton et al. 2011a; Ribera et al. 1999; Winqvist et al. 2014). The largest morphological variations in Carabidae are typically linked to specialized modes of nutrition (e.g. species of snail predators exhibiting narrow heads; Thiele 1977). The compound axes Dim.2 was related to diet (increasing head width), Dim.3 to robustness (increasing elytra width), and Dim.4 to visual ability (increasing eye protrusion).

We found that vegetation structure was a good predictor of body shape-related traits associated with diet (Dim.2), robustness (Dim.3) and visual ability (Dim.4), whereas we did not find interactive effects between these traits and farmland use or distance from edges. Our findings suggest that – regardless of land-use context –

vegetation variables measured in our study adequately captured changes to environmental conditions that explained body shape-related trait responses. These results support studies on the key influence of small-scale changes in vegetation structure on morphological traits (Barton et al. 2011a; Gibb and Parr 2013; Rouabah et al. 2015; Winqvist et al. 2014). Our results highlight the importance of considering multiple shape-related traits beyond body size in trait-based studies (Barton et al. 2011a; Öckinger et al. 2010). Body size may be confounded with other life-history traits that directly influence how species physically exploit or interact with the environment (Davies et al. 2000; Moretti et al. 2017; Rusch et al. 2015), whereas other continuous traits may better reflect species' land-use preferences (McGill et al. 2006).

Higher values of Dim.2 (diet) with higher vegetation height and lower total herbaceous cover (Figure 3a) may be explained by two different processes. First, greater occurrence of species with wider heads (e.g. *Egadroma* sp. C086, *Pericompsus* sp. C164, and *Simodontus* sp. C039; Figure 1; Table S4, Figure S2 in Paper IV: Supplementary Material) may be due to the availability of larger prey associated with increased productivity of taller vegetation (Forsythe 1987; Weiser and Kaspari 2006). Second, species with wider heads (e.g. *Amblystomus* sp. C252; Figure 1; Table S4, Figure S2 in Paper IV: Supplementary Material) may be disadvantaged in physically navigating through more complex microhabitats where there is higher total herbaceous cover (Gibb et al. 2015).

We identified a negative association between Dim.3 (robustness) and bare ground cover (Figure 3a). This result was inconsistent with our prediction of more robust species in simpler and more disturbed areas (Barton et al. 2011a; Kaspari and Weiser 1999; Wiescher et al. 2012). Our species composition data shows that this result may be related to an increase in narrow-shaped *Notiobia* sp. C293 with increased bare ground, although we also found increased occurrence of a relatively robust *G. multipunctatus* with increased bare ground (Figure 1; Table S4, Figure S2 in Paper IV: Supplementary Material). It could be that elytra width also represent life-history traits outside of robustness for different species, such as some species with wider elytra having stronger flying ability, and other narrower bodied species being associated with faster running speeds which might be an advantage in open habitats (Gibb et al. 2015).

Positive associations between Dim.4 (visual ability) and vegetation height (Figure 3a) is consistent with a study that found ants adapted to having increased sensory abilities (including larger eye widths) in more complex habitats due to perceptually demanding conditions in these habitats (Yates et al. 2014). For beetles, however, simpler microhabitats have previously been found to contain more diurnal visual hunters with larger eye protrusion and surface area than in complex microhabitats (Fountain-Jones et al. 2015; Talarico et al. 2011). Negative associations between Dim.4 (visual ability) and litter cover may also be related to significant decreases in the occurrence of *G. melbournensis* with higher litter cover (Figure 2; Table S4, Figure S4 in Paper IV: Supplementary Material).

Flying ability

We found higher occurrence of wingless species in areas with increased vegetation height, and higher occurrence of winged species in areas with increased bare ground (Figure 3b). These results may be related to studies that found less flight-capable species of ground beetles (Shibuya et al. 2014) and plant-hoppers (Kotze and O'Hara 2003) in denser vegetation, which were attributed to more stable habitat conditions favouring species with lower mobility (Shibuya et al. 2014). We suggest that flightless species might be particularly disadvantaged in dynamically changing, cultivated farmlands due to reduced vegetation structural complexity at local scales.

Conclusions

We found compelling evidence of environmental filtering of the morphological traits of ground beetles in response to land-use change in a fragmented agricultural landscape. Species traits relating to body size and shape were strongly influenced by changes in vegetation structure, which have consequences for assemblage composition and diversity. In farmlands and their adjoining woodlands, body size was further affected by farmland use and edge effects after accounting for vegetation structure. In particular, woodlands (i.e. in the interior and near edges) adjoining restoration plantings supported smaller ground beetle species, whereas fallows and crops generally supported larger species. This additional variation in body size might be due to effects of on-farm management and other abiotic or biotic factors on life-history traits not measured in our study. Our findings further emphasise the important role of habitat complexity in driving morphological traits at multiple spatial scales (Carrié et al. 2017; Fischer et al. 2008), and this is possibly linked to the textural-discontinuity (Holling 1992) and size-grain (Kaspari and Weiser 1999) hypotheses. Our work also demonstrates the value of using multiple body size and body shape related traits at both local (e.g. microhabitat structure) and landscape scales (e.g. multiple land-uses, edge effects), to provide additional insights into the ecological processes underpinning community assembly.

Our findings indicate potential implications of land-use changes on trait-mediated ecological functions of carabid species across both managed and unmanaged parts of fragmented farming landscapes. This includes, for example, predation of differently sized invertebrate prey by beetles, or the availability of varying beetle sizes as food for other arthropod and vertebrate predators, in areas of contrasting land use. We suggest maintaining adequate heterogeneity in land-uses and vegetation structural attributes (e.g. by incorporating low-intensity land-uses or reducing weeds that might lead to homogenised vegetation) as a way of supporting a range of different species sizes and traits across the landscape, which may promote higher landscape-level diversity and increased variety of ecological functions (Rouabah et al. 2015; Wood et al. 2015).

Acknowledgements

This work was supported by Central Tablelands Local Land Services (through Australian Government funding), Lake Cowal Foundation and Mount Mulga Pastoral Company. KN was supported by an Australian Government Research Training Program (RTP) scholarship. Thanks to landholders (Day, Foy, Conlan, Hall, Lucas, Nowlan, Aylott, Grimm, Robinson, Crawford, Daley families) for property access. We thank volunteers for fieldwork (particularly Alicia Ng, Nicholas Shore, Margaret Ning, Mal Carnegie and Dimitrios Tsifakis) and lab assistance (particularly Daniel Martinez-Escobar); Kim Pullen, and Michael Nash for carabid identification.

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Paper I: Supplementary materials

Table S1. Summary of beetles sampled in spring and summer 2014 (trophic group, family, and top four common species shown)

	Remnant patch (pooled) - paired with four farmland uses; see Figure 1)		**Planting matrix**		**Fallow matrix**		**Woody debris matrix**		**Crop matrix**	
	No. species	**Abundance**	**No. species**	**Abundance**	**No. species**	**Abundance**	**No. species**	**Abundance**	**No. species**	**Abundance**
1. Detritivore	**42**	**287**	**16**	**195**	**13**	**501**	**15**	**378**	**15**	**319**
?UNKNOWN	1	1	0	0	0	0	0	0	0	0
ADERIDAE	1	2	0	0	0	0	0	0	0	0
ANOBIIDAE	3	7	2	6	1	1	0	0	1	1
ANTHICIDAE	5	178	4	122	6	367	5	296	4	250
ANTHRIBIDAE	0	0	0	0	0	0	0	0	0	0
BIPHYLLIDAE	0	0	0	0	0	0	0	0	0	0
BRENTIDAE	0	0	0	0	0	0	0	0	0	0
DERMESTIDAE	0	0	0	0	0	0	1	2	0	0
GEORISSIDAE	2	3	0	0	0	0	0	0	0	0
HYDROPHILIDAE	0	0	1	1	0	0	0	0	0	0
LUCANIDAE	1	1	0	0	0	0	0	0	0	0
MELANDRYIDAE	1	1	0	0	0	0	0	0	0	0
MORDELLIDAE	2	3	0	0	0	0	0	0	0	0
NITIDULIDAE	5	11	0	0	0	0	1	1	2	2

PHLOEOSTICHIDAE	0	0	0	0	0	0	0	0	0	0
SCARABAEIDAE	0	0	1	2	1	4	2	7	2	22
SILPHIDAE	0	0	0	0	0	0	0	0	0	0
SILVANIDAE	1	1	0	0	0	0	0	0	0	0
TENEBRIONIDAE	18	77	8	64	4	128	6	72	5	42
THROSCIDAE	0	0	0	0	0	0	0	0	0	0
TROGIDAE	1	1	0	0	1	1	0	0	1	2
ZOPHERIDAE	1	1	0	0	0	0	0	0	0	0
2. Fungivore	**16**	**43**	**11**	**68**	**5**	**16**	**12**	**146**	**10**	**89**
CIIDAE	0	0	1	1	0	0	0	0	0	0
CLAMBIDAE	0	0	0	0	0	0	0	0	0	0
CORYLOPHIDAE	7	15	3	30	1	2	4	94	2	14
CRYPTOPHAGIDAE	3	5	2	24	2	10	2	22	2	56
DISCOLOMATIDAE	0	0	1	1	0	0	0	0	0	0
ENDOMYCHIDAE	0	0	0	0	0	0	0	0	0	0
LATRIDIIDAE	5	18	3	11	1	3	4	22	4	16
MYCETOPHAGIDAE	0	0	0	0	0	0	1	7	1	2
SPHINDIDAE	0	0	0	0	0	0	1	1	1	1
STAPHYLINIDAE	1	5	1	1	1	1	0	0	0	0
3. Herbivore	**69**	**226**	**20**	**66**	**35**	**296**	**23**	**67**	**15**	**53**
BUPRESTIDAE	1	1	0	0	0	0	0	0	0	0
BYRRHIDAE	5	12	0	0	3	7	1	1	0	0

CERAMBYCIDAE	0	0	0	0	0	0	0	0	0	0
CHRYSOMELIDAE	3	4	2	5	4	10	1	5	1	1
CURCULIONIDAE	24	134	7	30	14	258	6	28	6	21
ELATERIDAE	14	28	6	23	8	14	9	27	5	28
LAEMOPHLOEIDAE	0	0	0	0	0	0	0	0	0	0
LANGURIIDAE	0	0	0	0	0	0	0	0	0	0
LYCIDAE	0	0	0	0	0	0	1	1	0	0
SCARABAEIDAE	21	46	5	8	5	6	5	5	3	3
SCRAPTIIDAE	1	1	0	0	1	1	0	0	0	0
4. Predator	**58**	**205**	**41**	**239**	**45**	**226**	**41**	**302**	**49**	**343**
BOTHRIDERIDAE	0	0	0	0	0	0	0	0	0	0
CARABIDAE	22	77	22	44	25	171	22	211	33	254
CLERIDAE	0	0	0	0	0	0	0	0	0	0
COCCINELLIDAE	4	4	1	2	2	6	2	2	0	0
CUCUJIDAE	0	0	0	0	0	0	0	0	0	0
HISTERIDAE	0	0	0	0	1	1	1	1	0	0
MELYRIDAE	2	5	1	1	0	0	1	1	1	1
STAPHYLINIDAE	30	119	17	192	17	48	15	87	15	88
TROGOSSITIDAE	0	0	0	0	0	0	0	0	0	0
Grand Total	**185**	**761**	**88**	**568**	**98**	**1039**	**91**	**893**	**89**	**804**
5. Common species										
Cubicorhynchus maculatus (COL140)		32		4		16		1		2

Floydwernerius gushi (COL004)	160	105	315	220	197
Oxypodini sp #3 (COL003)	58	98	10	43	50
Omonadus hesperi (COL022)	10	15	45	73	50

Table S2. Summary of initial generalized linear mixed models for species richness and abundance of (a) overall beetles, (b) trophic groups and (c) common families, as predicted by transect type, habitat, time, region or patch size. Significant values (P < 0.05) in bold (patch size was discarded from final models because the variation it explained was not significant).

	Species richness				Abundance			
Response	Model terms	Chisq	Df	Pr(>Chisq)	Model terms	Chisq	Df	Pr(>Chisq)
(a)								
Overall beetles	transect	3.10	3	0.377	transect	0.44	3	0.932
	habitat	86.99	1	**<0.001**	habitat	38.77	1	**<0.001**
	time	20.09	1	**<0.001**	time	0.91	1	0.340
	patchsize	0.11	1	0.742	patchsize	0.15	1	0.695
	region	21.08	2	**<0.001**	region	10.31	2	**0.006**
	transect * habitat	2.35	3	0.503	transect * habitat	1.36	3	0.715
	transect * time	3.98	3	0.264	transect * time	2.83	3	0.419
	habitat * time	2.63	1	0.105	habitat * time	0.01	1	0.927
	transect * habitat * time	6.08	3	0.108	transect * habitat * time	0.91	3	0.824
(b)								
Predators	transect	0.80	3	0.850	transect	1.98	3	0.577
	habitat	2.25	1	0.134	habitat	0.05	1	0.816
	time	1.32	1	0.251	time	0.98	1	0.322
	patchsize	0.00	1	0.961	patchsize	0.02	1	0.891
	region	2.90	2	0.235	region	3.07	2	0.215
	transect * habitat	0.08	3	0.994	transect * habitat	1.04	3	0.793
	transect * time	1.63	3	0.652	transect * time	0.32	3	0.956
	habitat * time	1.74	1	0.187	habitat * time	0.52	1	0.471
	transect * habitat * time	1.58	3	0.664	transect * habitat * time	2.92	3	0.404
Detritivores	transect	1.63	3	0.653	transect	0.45	3	0.930
	habitat	0.00	1	0.980	habitat	0.01	1	0.932
	time	0.19	1	0.664	time	0.40	1	0.529
	patchsize	0.52	1	0.470	patchsize	0.00	1	0.987
	region	5.17	2	0.075	region	7.96	2	**0.019**
	transect * habitat	1.59	3	0.661	transect * habitat	0.43	3	0.933

	transect * time	1.22	3	0.749	transect * time	1.06	3	0.786
	habitat * time	0.05	1	0.823	habitat * time	0.12	1	0.733
	transect * habitat * time	0.11	3	0.991	transect * habitat * time	0.04	3	0.998
Herbivores	transect	5.55	3	0.136	transect	0.50	3	0.919
	habitat	0.07	1	0.792	habitat	0.47	1	0.495
	time	3.19	1	0.074	time	2.19	1	0.139
	patchsize	1.17	1	0.279	patchsize	0.01	1	0.928
	region	4.22	2	0.121	region	2.50	2	0.286
	transect * habitat	2.67	3	0.445	transect * habitat	1.88	3	0.597
	transect * time	2.08	3	0.557	transect * time	0.56	3	0.905
	habitat * time	0.03	1	0.872	habitat * time	0.43	1	0.512
	transect * habitat * time	3.14	3	0.371	transect * habitat * time	0.60	3	0.897
(c)								
Carabidae	transect	6.33	3	0.096	transect	3.54	3	0.316
	habitat	32.89	1	**<0.001**	habitat	12.25	1	**<0.001**
	patchsize	0.84	1	0.359	patchsize	0.01	1	0.911
	region	9.15	2	**0.010**	region	0.40	2	0.821
	transect * habitat	4.42	3	0.219	transect * habitat	0.56	3	0.905
Staphylinidae	transect	2.73	3	0.435	transect	0.67	3	0.880
	habitat	14.43	1	**<0.001**	habitat	4.04	1	**0.044**
	patchsize	1.08	1	0.298	patchsize	0.13	1	0.714
	region	5.87	2	0.053	region	0.94	2	0.626
	transect * habitat	2.66	3	0.448	transect * habitat	1.03	3	0.794
Curculionidae	transect	7.33	3	0.062	transect	2.89	3	0.409
	habitat	0.55	1	0.460	habitat	0.00	1	0.977
	patchsize	0.00	1	0.976	patchsize	0.27	1	0.602
	region	1.24	2	0.538	region	2.00	2	0.368
	transect * habitat	11.43	3	**0.010**	transect * habitat	1.87	3	0.601
Anthicidae	transect	9.03	3	**0.029**	transect	2.08	3	0.556
	habitat	33.73	1	**<0.001**	habitat	11.11	1	**0.001**
	patchsize	0.12	1	0.730	patchsize	0.28	1	0.600
	region	14.84	2	**0.001**	region	7.79	2	**0.020**
	transect * habitat	0.71	3	0.872	transect * habitat	0.80	3	0.849
Tenebrionidae	transect	0.35	3	0.951	transect	0.95	3	0.814

habitat	9.16	1	**0.002**	habitat	4.26	1	**0.039**
patchsize	0.00	1	0.975	patchsize	0.58	1	0.446
region	1.89	2	0.389	region	1.44	2	0.486
transect * habitat	4.07	3	0.254	transect * habitat	1.13	3	0.770

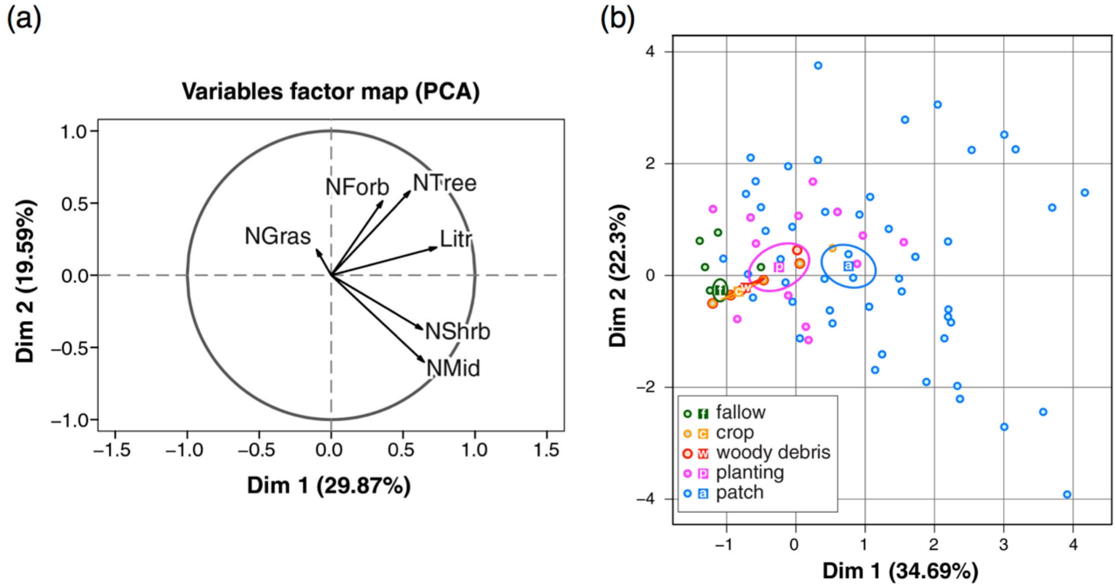


Figure S1. Results of principal components analysis (PCA) of vegetation structure variables, showing structural differences between the remnant patch and farmland matrix. (a) Principal components Dim 1 and Dim 2 make up 49.82% of explained variation. NShrb = native shrub, NMid = native midstorey, NTree = native tree, Litr = litter, NGras = native grass, NForb = native forb; and (b) Graphical display of principal components Dim 1 and Dim 2 grouped by the different farmland matrix (crop, woody debris, fallow, planting) and remnant patch habitat types

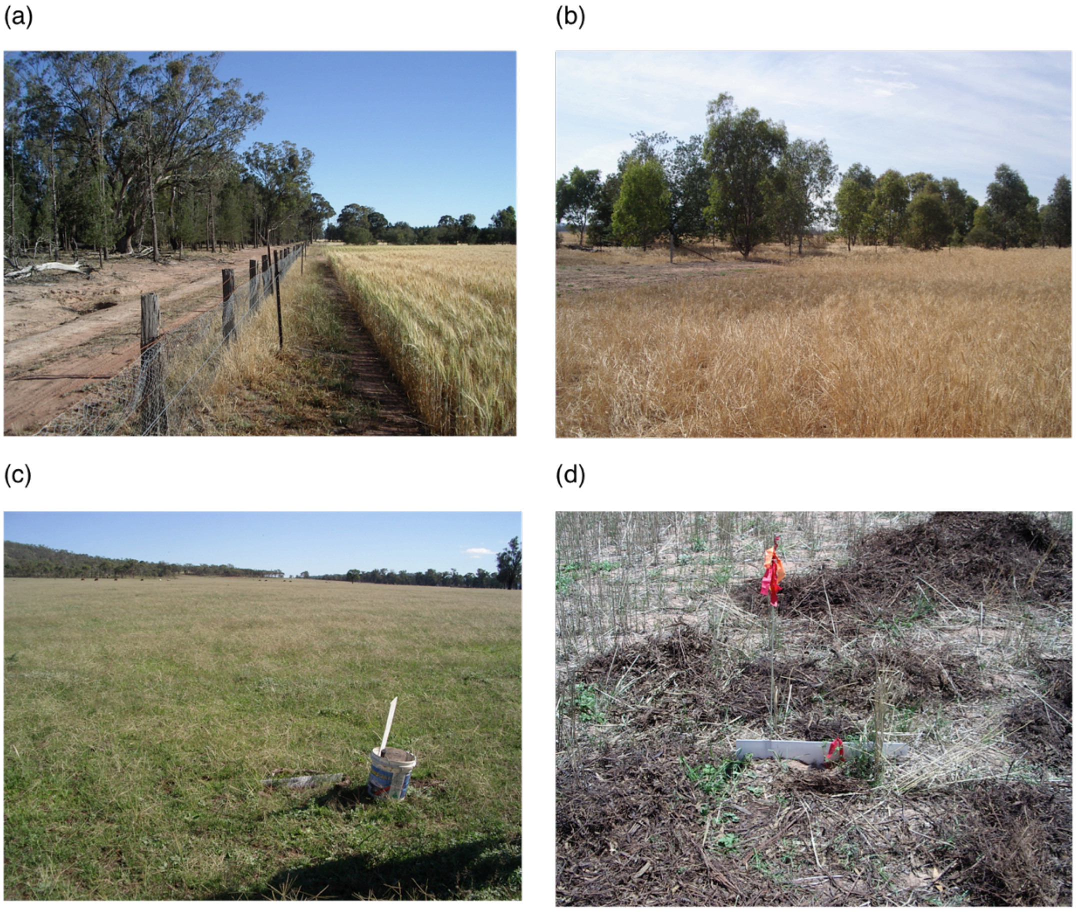


Figure S2. Photographs of five landscape elements in study area (a) remnant patch and adjacent crop: (b) restoration plantings of native trees and shrubs, (c) fallow, (d) woody debris application

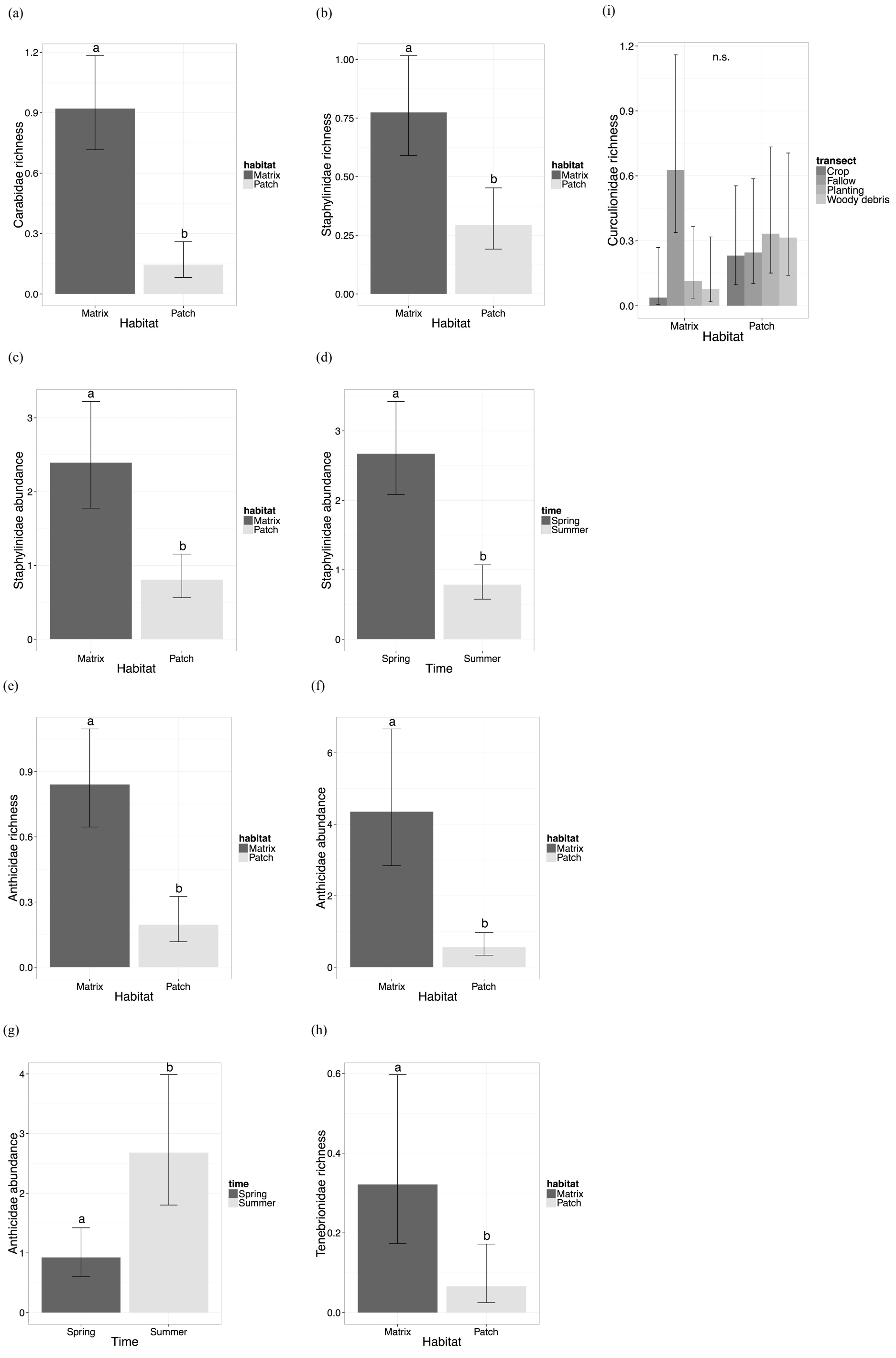


Figure S3. Predicted responses of (a) Carabidae richness to habitat, (b) Staphylinidae richness to habitat, (c)-(d) Staphylinidae abundance to habitat and time, (e) Anthicidae richness to habitat, (f)-(g) Anthicidae abundance to habitat and time, (h) Tenebrionidae richness to habitat, and (i) Curculionidae richness to habitat (P-values in Table 1). Patch refers to remnant vegetation, while matrix refers to four farmland uses adjoining the remnant (crop, fallow, planting, woody debris). 95% confidence intervals around predictions shown. Different letters indicate significantly different results (Tukey-Kramer test)

Paper II: Supplementary materials

Table S1. Summary of beetles sampled in spring 2014 and summer 2014–15, by (a) trophic group and (b) family

	Total		Woodland patch		Planting		Fallow		Woody debris		Crop		Edge	
	No. species	No. individuals	No. species	No. individuals	No. species	No. individuals	No. species	No. individuals	No. species	No. individuals	No. species	No. individuals	No. species	No. individuals
(a) Trophic group														
Detritivores	141	5448	103	795	36	694	25	948	38	1045	31	835	76	1131
Herbivores	185	2099	119	617	55	255	50	508	41	135	34	106	98	478
Predators	169	3815	97	632	68	460	60	531	55	563	73	671	88	958
(b) Family														
?UNKNOWN	1	1	1	1	0	0	0	0	0	0	0	0	0	0
ADERIDAE	5	10	3	6	1	1	0	0	0	0	0	0	2	3
ANOBIIDAE	9	60	7	29	3	4	1	1	1	4	1	1	5	21
ANTHICIDAE	18	2408	13	315	4	308	7	618	6	193	5	471	10	503
ANTHRIBIDAE	1	1	1	1	0	0	0	0	0	0	0	0	0	0
BIPHYLLIDAE	2	5	2	3	0	0	0	0	0	0	0	0	1	2
BOTHRIDERIDAE	2	2	2	2	0	0	0	0	0	0	0	0	0	0
BRENTIDAE	1	1	0	0	0	0	0	0	0	0	0	0	1	1
BUPRESTIDAE	5	9	1	2	0	0	3	3	0	0	0	0	3	4
BYRRHIDAE	7	96	7	24	1	5	5	28	2	12	2	4	4	23
CARABIDAE	63	1617	39	212	32	114	36	391	26	151	38	390	34	359

CERAMBYCIDAE	2	2	0	0	0	0	0	0	0	0	0	0	2	2
CHRYSOMELIDAE	20	111	13	28	6	11	6	11	1	7	4	5	9	49
CIIDAE	3	4	3	3	1	1	0	0	0	0	0	0	0	0
CLAMBIDAE	1	1	0	0	0	0	0	0	0	0	0	0	1	1
CLERIDAE	1	1	0	0	0	0	0	0	0	0	0	0	1	1
COCCINELLIDAE	11	58	6	17	2	6	2	7	3	5	0	0	8	23
CORYLOPHIDAE	9	582	8	26	4	143	3	8	4	163	3	34	4	208
CRYPTOPHAGIDAE	5	213	3	15	2	35	2	11	3	41	2	73	5	38
CUCUJIDAE	1	1	0	0	0	0	0	0	0	0	0	0	1	1
CURCULIONIDAE	53	1095	37	248	18	136	16	397	11	56	12	40	25	218
DERMESTIDAE	4	7	2	3	0	0	0	0	2	3	0	0	1	1
DISCOLOMATIDAE	1	1	0	0	1	1	0	0	0	0	0	0	0	0
ELATERIDAE	24	264	17	51	9	47	8	23	14	45	9	47	14	51
ENDOMYCHIDAE	2	4	0	0	0	0	0	0	1	1	0	0	2	3
GEORISSIDAE	2	3	2	3	0	0	0	0	0	0	0	0	0	0
HISTERIDAE	2	37	1	1	0	0	1	1	1	2	2	33	0	0
HYDROPHILIDAE	2	4	1	1	1	1	0	0	0	0	0	0	2	2
LANGURIIDAE	2	5	0	0	1	1	0	0	0	0	0	0	2	4
LATRIDIIDAE	9	177	6	37	4	14	3	6	6	43	4	28	7	49
LUCANIDAE	1	4	1	3	0	0	0	0	0	0	0	0	1	1
LYCIDAE	2	4	0	0	1	1	0	0	1	1	0	0	1	2
MELANDRYIDAE	2	2	1	1	0	0	0	0	0	0	0	0	1	1
MELYRIDAE	4	30	2	9	3	4	0	0	1	6	2	8	1	3
MORDELLIDAE	4	18	4	15	0	0	0	0	0	0	0	0	3	3
MYCETOPHAGIDAE	2	21	1	1	0	0	0	0	1	14	1	2	1	4

NITIDULIDAE	9	29	7	19	0	0	0	0	2	2	3	3	4	5
PHLOEOSTICHIDAE	1	1	0	0	0	0	0	0	0	0	0	0	1	1
SCARABAEIDAE	70	447	45	161	20	59	12	42	14	26	9	38	38	121
SCRAPTIIDAE	1	5	1	2	0	0	1	1	0	0	0	0	1	2
SILPHIDAE	1	1	0	0	0	0	0	0	0	0	0	0	1	1
SILVANIDAE	3	3	2	2	0	0	0	0	0	0	0	0	1	1
SPHINDIDAE	1	5	1	1	0	0	0	0	1	1	1	1	1	2
STAPHYLINIDAE	86	1533	49	405	32	286	23	110	25	276	32	214	43	242
TENEBRIONIDAE	36	895	27	212	13	159	5	184	7	78	7	87	17	175
THROSCIDAE	1	2	1	1	0	0	0	0	0	0	0	0	1	1
TROGIDAE	1	14	1	3	0	0	1	1	1	1	1	7	1	2
TROGOSSITIDAE	1	1	0	0	0	0	0	0	0	0	0	0	1	1
ZOPHERIDAE	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Total	495	9796	319	1864	159	1337	135	1843	134	1131	138	1486	262	2135

Table S2. Summary of top ranked models (ΔAICc < 2) testing responses of (a) beetle species richness and total abundance; and (b) species richness and abundance of trophic groups to the effects of distance (dst), farmland use (frm), and time (tim). Competing models shown below top rank model. Int = model intercept, Df = degrees of freedom, LogLik = log likelihood, AICc = Akaike Information Criterion for small samples, ΔAICc = change in AICc

Response	Predictors	Int	Df	LogLik	AICc	ΔAICc
(a) Overall						
Species richness	dst × tim + tim × frm	1.39	19	-1213.6	2467.1	0
Total abundance	dst × frm × tim	2.06	43	-2540.1	5175.7	0
(b) Trophic groups						
Detritivore abundance	dst × frm × tim	1.38	43	-1817.9	3731.3	0
Detritivore species richness	dst + tim × frm	0.44	15	-960.9	1952.9	0
Herbivore abundance	dst × frm × tim	0.54	43	-1274.5	2644.5	0
Herbivore species richness	dst + tim × frm	0.26	15	-848.3	1727.8	0
	dst + frm	0.35	11	-852.8	1728.2	0.41
Predator abundance	dst × frm × tim	0.15	43	-1560.1	3215.7	0
Predator species richness	dst × tim + tim × frm	-0.42	19	-973.5	1986.8	0

Table S3. Summary of top ranked models (ΔAICc < 2) testing responses of movement direction probability (subset of data at three distances -20 m, 0 m, 20 m) for (a) total abundance; and (b) abundance of trophic groups to the effects of distance (dst), farmland use (frm), and time (tim). Competing models shown below top rank model. Int = model intercept, Df = degrees of freedom, LogLik = log likelihood, AICc = Akaike Information Criterion for small samples, ΔAICc = change in AICc.

Response (-20m, 0m, 20m)	Predictors	Int	Df	LogLik	AICc	ΔAICc	Weight
(a) Overall							
Direction of total abundance	tim × frm	0.17	11	-748.2	1519.5	0	
(b) Trophic groups							

Direction of detritivore abundance	tim × frm	0.21	11	-517.1	1057.2	0	1
Direction of herbivore abundance	frm	-0.08	7	-353.0	720.5	0	0.484
	(none)		4	-356.6	721.4	0.92	0.306
	tim + frm	-0.13	8	-352.8	722.2	1.66	0.211
Direction of predator abundance	dst × tim × frm	0.41	27	-422.6	905.6	0	0.717
	tim + frm	0.17	8	-445.4	907.4	1.86	0.283

Table S4 Summary of best generalized linear mixed models showing edge responses of beetle assemblages by species richness and abundance of (a) all beetles and (b) trophic groups. Significant values ($P < 0.05$) shown in bold.

Response	Model terms	Chisq	Df	Pr(>Chisq)
(a)				
Total abundance	Distance	246.91	4	**<0.001**
	Time	3.40	1	0.065
	Farmland use	3.29	3	0.348
	Farmland use × Distance	15.98	12	0.192
	Farmland use × Time	471.16	3	**<0.001**
	Distance × Time	13.06	4	**0.011**
	Farmland use × Distance × Time	127.40	12	**<0.001**
Species richness	Distance	127.38	4	**<0.001**
	Time	15.88	1	**<0.001**
	Farmland use	1.50	3	0.682
	Distance × Time	14.58	4	**0.006**
	Time × Farmland use	18.45	3	**<0.001**
(b)				
Detritivore abundance	Distance	191.02	4	**<0.001**
	Time	161.17	1	**<0.001**
	Farmland use	7.61	3	0.055
	Farmland use × Distance	19.43	12	0.079
	Farmland use × Time	187.83	3	**<0.001**
	Distance × Time	20.11	4	**<0.001**

	Farmland use × Distance × Time	80.23	12	**<0.001**
Detritivore richness	Distance	105.46	4	**<0.001**
	Time	0.53	1	0.465
	Farmland use	10.91	3	**0.012**
	Time × Farmland use	13.99	3	**0.003**
Herbivore abundance	Distance	28.90	4	**<0.001**
	Time	29.45	1	**<0.001**
	Farmland use	15.39	3	**0.002**
	Farmland use × Distance	30.74	12	**0.002**
	Farmland use × Time	42.66	3	**<0.001**
	Distance × Time	34.55	4	**<0.001**
	Farmland use × Distance × Time	42.83	12	**<0.001**
Herbivore richness	Distance	35.70	4	**<0.001**
	Time	0.07	1	0.798
	Farmland use	12.73	3	**0.005**
	Time × Farmland use	9.02	3	**0.029**
Predator abundance	Distance	134.36	4	**<0.001**
	Time	204.34	1	**<0.001**
	Farmland use	3.30	3	0.347
	Farmland use × Distance	8.95	12	0.707
	Farmland use × Time	258.26	3	**<0.001**
	Distance × Time	20.75	4	**<0.001**
	Farmland use × Distance × Time	90.55	12	**<0.001**
Predator richness	Distance	145.38	4	**<0.001**
	Time	84.06	1	**<0.001**
	Farmland use	2.08	3	0.556
	Distance × Time	19.66	4	**0.001**
	Time × Farmland use	19.13	3	**<0.001**

Table S5 Summary of best generalized linear mixed models showing directional movement responses based on abundance of all beetles and trophic groups. Significant values (P < 0.05) shown in bold.

Response	Model terms	Chisq	Df	Pr(>Chisq)
Direction of total abundance	Farmland use	1.31	3	0.726
	Time	0.80	1	0.371
	Farmland use × Time	20.23	3	**<0.001**
Direction of detritivore abundance	Farmland use	3.90	3	0.272
	Time	9.74	1	**0.002**
	Farmland use × Time	11.53	3	**0.009**
Direction of herbivore abundance	Farmland use	7.72	3	0.052
	Time	0.47	1	0.494
Direction of predator abundance	Farmland use	12.87	3	**0.005**
	Distance	4.78	2	0.092
	Time	1.51	1	0.219
	Farmland use × Distance	5.85	6	0.441
	Farmland use × Time	3.58	3	0.311
	Distance × Time	3.93	2	0.140
	Farmland use × Distance × Time	20.60	6	**0.002**

Table S6. Pairwise comparisons of beetle species composition dissimilarity (Bray-Curtis) between habitat types, based on permutational multivariate analysis of variance (PERMANOVA). Significant values (P < 0.05) shown in bold. P-values adjusted using a sequential Bonferroni procedure are also shown (*).

	Spring				Summer			
Habitat pairs	F	R2	P	P adjusted	F	R2	P	P adjusted
Fallow vs. Woody debris	1.09	0.05	0.348	1.000	1.37	0.07	0.151	1.000
Fallow vs. Crop	1.50	0.07	0.063	0.945	1.66	0.08	0.06	0.900
Plantings vs. Woody debris	1.27	0.06	0.175	1.000	1.73	0.08	0.051	0.765

Plantings vs. Fallow	1.34	0.07	0.115	1.000	0.74	0.04	0.791	1.000
Plantings vs. Crop	1.32	0.06	0.165	1.000	1.82	0.08	**0.024**	0.360
Patch vs. Woody debris	2.69	0.05	**0.001**	**0.015**	2.99	0.06	**0.002**	**0.030**
Patch vs. Fallow	2.02	0.04	**0.002**	**0.030**	1.92	0.04	**0.008**	0.120
Patch vs. Plantings	1.98	0.04	**0.002**	**0.030**	1.01	0.02	0.441	1.000
Patch vs. Edge	2.98	0.04	**0.001**	**0.015**	2.47	0.03	**0.003**	**0.045**
Patch vs. Crop	3.07	0.06	**0.001**	**0.015**	2.31	0.05	**0.006**	0.090
Edge vs. Woody debris	1.32	0.02	0.104	1.000	1.53	0.03	0.088	1.000
Edge vs. Fallow	1.04	0.02	0.409	1.000	1.31	0.02	0.144	1.000
Edge vs. Plantings	1.29	0.02	0.125	1.000	1.01	0.02	0.401	1.000
Edge vs. Crop	1.62	0.03	**0.025**	0.375	1.77	0.03	**0.034**	0.510
Crop vs. Woody debris	0.34	0.02	0.999	1.000	1.14	0.06	0.3	1.000

(*) Description of statistical analyses and results for PERMANOVA Table S6

Differences in beetle species composition between the remnant patch, four farmland uses and edges were examined using permutational multivariate analysis of variance (PERMANOVA), based on Bray-Curtis dissimilarities. We ran 999 permutations, and stratified within site and farmland use to account for the nested sampling design of farmland uses within sites. Singleton species were excluded, and we ran comparisons for spring and summer separately. P-values were also adjusted using sequential Bonferroni corrections to account for multiple comparisons. We used the 'vegan' R package for PERMANOVA analyses. PERMANOVA results can help with interpretation of species richness responses.

Beetle composition was significantly different between remnant woodland patches and other farmland habitats ($P < 0.008$), except for the patch and plantings where beetle composition was non-significant during summer ($P = 0.044$). This reflects agricultural land use change, which has significantly modified vegetation structure through introduction of exotic crops and pastures. Beetle composition was also significantly different between the crop and edge during spring ($P = 0.025$) and summer ($P = 0.034$), and between the plantings and crop during summer ($P = 0.024$), however these differences were non-significant after Bonferroni corrections (Table S6).

Table S7. Tukey-Kramer tests showing pairwise comparisons along the distance gradient. Different letters between treatments for each response indicate significantly different results. -200m and -20m refer to distances in woodlands, 200m and 200m in farmlands, and 0m at edges.

			Tukey test results					**Assigned category**	**Assignment notes**
(a) Richness response									
(i) Distance			-200m	-20m	0m	20m	200m		
Detritivore richness			a	b	c	c	c	3 (positive influence)	0m significantly higher than -20m (interpret as spillover into woodlands)
Herbivore richness			a	ab	b	b	a	5 (ecotone)	0m significantly higher than interiors -200m and 200m
(ii) Distance × Time			-200m	-20m	0m	20m	200m		
Species richness		Spring	b	bd	df	f	df	4 (mutual influence)	Overlaps in confidence interval on either side of edge (-20m, 0m vs. 0m, 20m), and declining trend along entire transect i.e. 200m significantly higher than -200m
		Summer	a	bc	ef	cde	cde	3 (positive influence)	0m significantly higher than -20m (interpret as spillover into woodlands)
Predator richness		Spring	b	c	ce	e	de	7 (gradual decline)	200m sig. higher than -200m, while declines between these mostly gradual
		Summer	a	b	cd	c	c	3 (positive influence)	0m significantly higher than -20m (interpret as spillover into woodlands)
(b) Abundance responses									
(i) Distance × Time × Farmland use			-200m	-20m	0m	20m	200m		
Total abundance	Crop	Spring	aij	bcdejn	kmovw	wAEGLP	vwM	3 (positive influence)	0m significantly higher than -20m (interpret as spillover into woodlands)
		Summer	ae	agh	bcdehjpqr	cdehjnos	fgjnosxyzAB	7 (gradual decline)	200m sig. higher than -200m, while declines between

									these mostly gradual
	Woody debris	Spring	aef	aij	mnorvFG	orvw	vwB	3 (positive influence)	0m significantly higher than -20m (interpret as spillover into woodlands)
		Summer	a	bcdehjnos	uwzEHKO	morvw	mnorsIJKLM	5 (ecotone)	0m significantly higher than interiors -200m and 200m
	Fallow	Spring	ad	bcdehjlm	dehjovw	mnorvGH	josw	7 (gradual decline)	200m sig. higher than -200m, while declines between these mostly gradual
		Summer	ad	cdehjnotuv	jovw	twyFJNQ	vxCEIQ	4 (mutual influence)	Equal overlaps in confidence interval on either side of edge (-20m, 0m vs. 0m, 20m), with also a declining trend along entire transect i.e. 200m being significantly higher than -200m
	Planting	Spring	ab	aijk	ehjovw	ehjowC	cdehjov	7 (gradual decline)	200m sig. higher than -200m, while declines between these mostly gradual
		Summer	ac	bcdehjno	jovw	psvDNOP	ilnqwDE	4 (mutual influence)	Overlaps in confidence interval on either side of edge (-20m, 0m vs. 0m, 20m), and declining trend along entire transect i.e. 200m significantly higher than -200m
Detritivore abundance	Crop	Spring	adegh	adeghijkln	fhrsxy	uvxyBC	prsxy	4 (mutual influence)	Overlaps in confidence interval on either side of edge (-20m, 0m vs. 0m, 20m), and declining trend along entire transect i.e. 200m significantly higher than -200m
		Summer	adeghijkl	adeghkl	cehrsu	lprszA	nopqrstxy	7 (gradual decline)	200m sig. higher than -200m, while declines between these mostly gradual
	Woody debris	Spring	ade	agh	jprsx	rsxy	opqrsty	4 (mutual influence)	Overlaps in confidence interval on either side of edge (-20m, 0m vs. 0m, 20m), and declining trend along entire transect i.e. 200m significantly higher than -

									200m
		Summer	adef	bdrsu	yAEHJ	opqrstxy	xzDHI	4 (mutual influence)	Overlaps in confidence interval on either side of edge (-20m, 0m vs. 0m, 20m), and declining trend along entire transect i.e. 200m significantly higher than -200m
	Fallow	Spring	abc	adeghp	adehijklq	ehrxy	hsxy	7 (gradual decline)	200m sig. higher than -200m, while declines between these mostly gradual
		Summer	adeghk	aehrs	grsxy	opqstCDEFG	rwBFIJ	7 (gradual decline)	200m sig. higher than -200m, while declines between these mostly gradual
	Planting	Spring	a	adeghklm	adeghijlo	cehsvw	adeghjklt	6 (no edge)	200m non-significantly different to -200m, and all adjacent points along transect non-significantly different
		Summer	adegh	adeghijkl	kprsxy	rxyG	imprsxy	3 (positive influence)	0m significantly higher than -20m (interpret as spillover into woodlands)
Herbivore abundance	Crop	Spring	bdefg	bdeg	bdh	bdh	bde	6 (no edge)	200m non-significantly different to -200m, and all adjacent points along transect non-significantly different
		Summer	bde	bdh	bdh	bcd	bd	6 (no edge)	Same as above
	Woody debris	Spring	bdh	bcd	bdh	bdh	beh	6 (no edge)	Same as above
		Summer	bd	bdh	ceh	bdefg	ad	6 (no edge)	Same as above
	Fallow	Spring	bdh	bdh	dh	eh	dh	6 (no edge)	Same as above
		Summer	bdefg	dh	ceh	eh	fh	6 (no edge)	Same as above
	Planting	Spring	bde	bdef	bdh	defg	ab	6 (no edge)	Same as above
		Summer	bdeg	gh	bdh	h	dh	6 (no edge)	Same as above

Predator abundance	Crop	Spring	adefhijkl	efjkm	hjkm	mn	lmn	4 (mutual influence)	Overlaps in confidence interval on either side of edge (-20m, 0m vs. 0m, 20m), and declining trend along entire transect i.e. 200m significantly higher than -200m
		Summer	bc	bd	bfi	bf	acdefhijk	6 (no edge)	200m non-significantly different to -200m, and all adjacent points along transect non-significantly different
	Woody debris	Spring	bfh	cdefhijkm	ijkm	km	mn	4 (mutual influence)	Overlaps in confidence interval on either side of edge (-20m, 0m vs. 0m, 20m), and declining trend along entire transect i.e. 200m significantly higher than -200m
		Summer	ab	bfhijk	hijkm	fjn	bfhijk	7 (gradual decline)	Farmland (i.e. 20m point) sig. higher than -200m, while declines between these mostly gradual. Note 200m and -200m points are not significantly different here, but this pattern is not suitable categorised as 6 (no edge).
	Fallow	Spring	bfg	bfhijk	efjkm	hijkm	efjkm	6 (no edge)	200m non-significantly different to -200m, and all adjacent points along transect non-significantly different
		Summer	b	cdefhijkm	fjkm	jm	hijkm	7 (gradual decline)	200m sig. higher than -200m, while declines between these mostly gradual
	Planting	Spring	bf	acdfhijkl	hijkm	hijkm	ghijkm	7 (gradual decline)	200m sig. higher than -200m, while declines between these mostly gradual
		Summer	ab	be	ghijkm	fjkm	cdefhijkm	3 (positive influence)	0m significantly higher than -20m (interpret as spillover into woodlands)

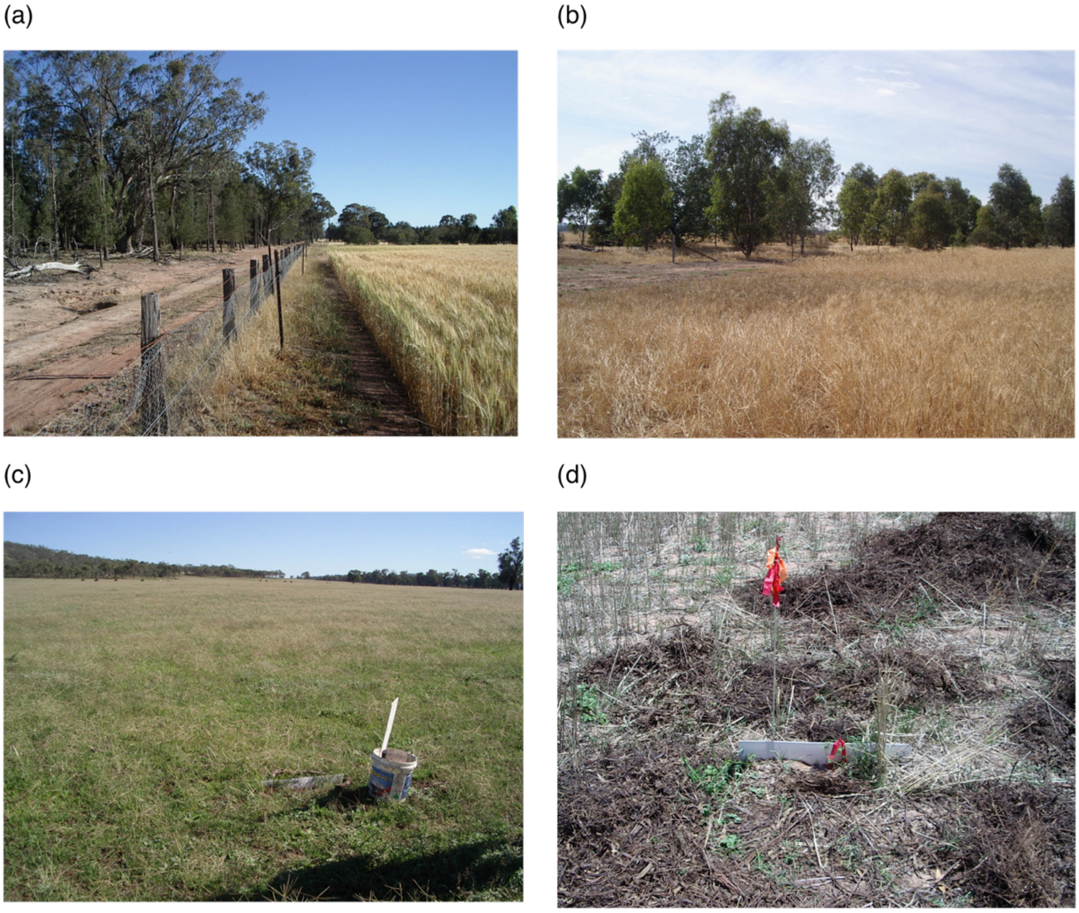
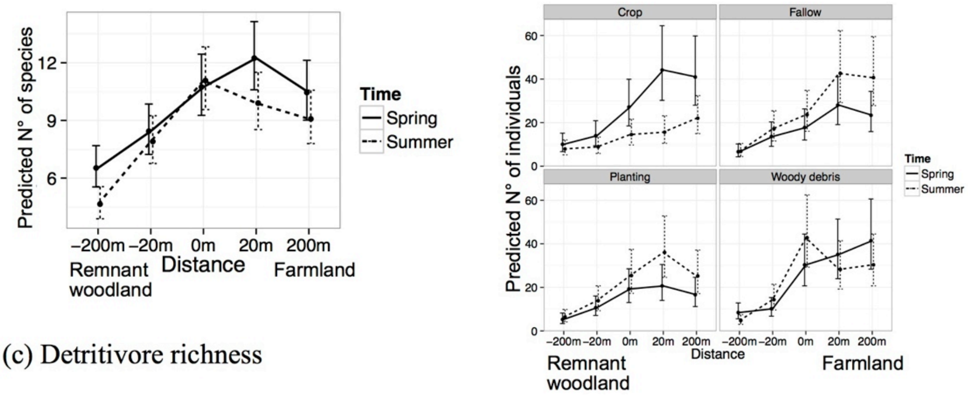


Figure S1. Photographs of five landscape elements in study area (a) remnant vegetation patch and adjacent crop, (b) plantings of native trees and shrubs, (c) fallow, (d) fine woody debris application



(a) Species richness

(b) Total abundance

(c) Detritivore richness

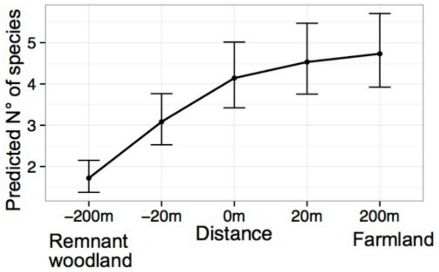


Figure S2. Relationship between distance, farmland use and season for (a) species richness, (b) total abundance, (c) species richness of detritivores. ±95% confidence intervals shown; solid and dashed lines show general trends.

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Table A1. Summary of beetles sampled in spring 2014 and summer 2014–15, by (a) trophic group and (b) family

	Total		Woodland patch		Farmland		Edge	
	No. individuals	No. species	No. individuals	No. species	No. individuals	No. species	No. individuals	No. species
(a) Trophic group								
Detritivores	3175	781	301	142	1741	320	1133	319
Herbivores	1194	539	221	152	487	142	486	245
Predators	2263	829	197	129	1118	346	948	354
(b) Family								
?UNKNOWN	1	1	1	1	0	0	0	0
ADERIDAE	5	4	2	2	0	0	3	2
ANOBIIDAE	36	26	7	6	8	5	21	15
ANTHICIDAE	1725	269	151	38	1062	133	512	98
BIPHYLLIDAE	2	1	0	0	0	0	2	1
BRENTIDAE	1	1	0	0	0	0	1	1
BUPRESTIDAE	5	4	1	1	0	0	4	3
BYRRHIDAE	43	31	12	10	8	6	23	15
CARABIDAE	1142	389	72	48	685	182	385	159
CERAMBYCIDAE	2	2	0	0	0	0	2	2

CHRYSOMELIDAE	74	36	4	4	21	13	49	19
CIIDAE	1	1	0	0	1	1	0	0
CLAMBIDAE	1	1	0	0	0	0	1	1
CLERIDAE	1	1	0	0	0	0	1	1
COCCINELLIDAE	37	28	5	5	9	5	23	18
CORYLOPHIDAE	363	61	15	13	140	24	208	24
CRYPTOPHAGIDAE	155	50	5	5	112	25	38	20
CUCUJIDAE	1	1	0	0	0	0	1	1
CURCULIONIDAE	734	247	134	81	337	57	263	109
DERMESTIDAE	3	2	0	0	2	1	1	1
DISCOLOMATIDAE	1	1	0	0	1	1	0	0
ELATERIDAE	171	91	27	18	93	45	51	28
ENDOMYCHIDAE	3	2	0	0	0	0	3	2
GEORISSIDAE	3	2	3	2	0	0	0	0
HISTERIDAE	2	2	0	0	2	2	0	0
HYDROPHILIDAE	3	3	0	0	1	1	2	2
LAEMOPHLOEIDAE	10	1	0	0	0	0	10	1
LANGURIIDAE	4	2	0	0	0	0	4	2
LATRIDIIDAE	119	76	18	13	52	29	49	34
LUCANIDAE	2	2	1	1	0	0	1	1
LYCIDAE	3	2	0	0	1	1	2	1
MELANDRYIDAE	2	2	1	1	0	0	1	1

MELYRIDAE	11	9	4	3	4	4	3	2
MORDELLIDAE	6	6	3	3	0	0	3	3
MYCETOPHAGIDAE	13	10	0	0	9	6	4	4
NITIDULIDAE	19	18	11	10	3	3	5	5
PHLOEOSTICHIDAE	1	1	0	0	0	0	1	1
SCARABAEIDAE	224	149	42	37	61	35	121	77
SCRAPTIIDAE	4	4	1	1	1	1	2	2
SILPHIDAE	1	1	0	0	0	0	1	1
SILVANIDAE	2	2	1	1	0	0	1	1
SPHINDIDAE	4	4	0	0	2	2	2	2
STAPHYLINIDAE	1098	415	121	76	420	155	557	184
TENEBRIONIDAE	567	177	75	41	308	68	184	68
THROSCIDAE	1	1	0	0	0	0	1	1
TROGIDAE	24	8	1	1	3	3	20	4
TROGOSSITIDAE	1	1	0	0	0	0	1	1
ZOPHERIDAE	1	1	1	1	0	0	0	0
Total	6632	2149	719	423	3346	808	2567	918

Table A2. Summary of plants sampled in spring 2014 and summer 2014–15 (site occurrence, grouped by habitat type). Taxonomy based on NSW Flora Online (http://plantnet.rbgsyd.nsw.gov.au, accessed January 2017). Exotic species indicated with asterisk (*).

Plant species		Woodland patch	Farmland	Edge
_1._	_Acacia decora_	8	2	0
_2._	_Acacia doratoxylon_	4	0	0
_3._	_Acacia genistifolia_	4	0	0
_4._	_Acacia_ sp.	6	2	2
_5._	_Acacia deanei_	2	0	0
_6._	_Acaena agnipila_	2	0	0
_7._	*_Acetosella vulgaris_	4	10	10
_8._	_Actinobole uliginosum_	6	0	2
_9._	*_Aira elegantissima_	0	0	2
_10._	*_Aira_ spp.	10	6	6
_11._	_Alternanthera nana_	10	8	10
_12._	*_Anagallis arvensis_	2	2	6
_13._	*_Aphanes arvensis_	0	2	2
_14._	*_Arctotheca calendula_	28	22	60
_15._	_Aristida behriana_	14	6	8
_16._	_Aristida ramosa_	6	0	4
_17._	_Aristida_ spp.	10	6	10
_18._	_Arthropodium minus_	34	2	0
_139._	_Hyalosperma semisterile_	0	2	0
_140._	_Hybanthus monopetalus_	20	0	2
_141._	_Hydrocotyle laxiflora_	0	8	2
_142._	_Hypericum gramineum_	0	4	4
_143._	*_Hypericum perforatum_	4	0	0
_144._	*_Hypochaeris glabra_	72	20	48
_145._	*_Hypochaeris radicata_	10	10	26
_146._	_Indigofera adesmiifolia_	2	0	0
_147._	_Isotoma axillaris_	0	0	2
_148._	_Juncus bufonius_	0	14	6
_149._	_Juncus capitatus_	0	0	2
_150._	_Juncus_ spp.	0	0	2
_151._	_Juncus subsecundus_	12	10	22
_152._	_Kickxia commutata_	0	2	0
_153._	*_Lactuca serriola_	0	6	0
_154._	_Lamarckia aurea_	0	0	2
_155._	_Laxmannia gracilis_	8	0	0
_156._	*_Lepidium africanum_	10	22	10

19.	*Asperula conferta*	2	0	0
20.	*Atriplex spinibractea*	2	4	22
21.	*Austrostipa blackii*	8	2	2
22.	*Austrostipa densiflora*	8	2	4
23.	*Austrostipa elegantissima*	0	2	2
24.	*Austrostipa scabra*	76	32	104
25.	*Austrostipa* spp	0	0	2
26.	*Austrostipa verticillata*	4	4	14
27.	*Austrostipa elegantissima*	2	0	0
28.	**Avena sativa*	0	20	2
29.	**Avena* spp.	4	8	8
30.	*Bertya cunninghamii*	2	0	0
31.	*Boerhavia dominii*	2	8	16
32.	*Bothriochloa macra*	12	4	14
33.	*Brachychiton populneus* ssp. *populneus*	0	2	0
34.	*Brachyloma daphnoides*	4	0	0
35.	**Brassica napus*	0	6	0
36.	**Briza minor*	2	2	2
37.	**Bromus catharticus*	0	0	2
38.	**Bromus diandrus*	14	24	10
39.	**Bromus hordeaceus*	22	36	32
40.	**Bromus rubens*	0	4	6
157.	*Lepidosperma laterale*	2	0	0
158.	*Leptospermum* sp.	14	0	0
159.	*Lissanthe strigosa*	8	4	6
160.	**Lolium perenne*	14	14	16
161.	**Lolium rigidum*	22	50	56
162.	*Lomandra confertifolia*	2	0	2
163.	*Lomandra filiformis*	14	4	2
164.	*Lomandra filiformis* ssp. *coriacea*	8	0	4
165.	*Lomandra multiflora*	4	0	0
166.	*Lomandra patens*	4	0	0
167.	**Lupinus angustifolius*	0	10	0
168.	*Luzula densiflora*	0	0	2
169.	*Lythrum hyssopifolia*	2	0	0
170.	*Maireana enchylaenoides*	12	4	32
171.	*Maireana excavata*	8	0	14
172.	*Maireana humillima*	0	0	6
173.	*Maireana microphylla*	6	0	8
174.	**Malva parviflora*	2	14	6
175.	**Marrubium vulgare*	0	8	4
176.	**Medicago laciniata*	0	4	0
177.	**Medicago sativa*	12	2	0
178.	**Medicago polymorpha*	0	4	6

41.	Brunonia australis	2	0	0
42.	Bulbine semibarbata	54	2	28
43.	Bursaria spinosa	4	0	0
44.	Bursaria spinosa ssp. spinosa	2	0	0
45.	Calandrinia eremaea	26	0	14
46.	Callitris glaucophylla	34	6	18
47.	Calochilus spp.	2	0	0
48.	Calostemma purpureum	6	0	0
49.	Calotis cuneifolia	48	8	32
50.	Calotis sp.	6	0	4
51.	Calytrix tetragona	10	0	2
52.	Carex breviculmis	2	0	0
53.	Carex inversa	22	10	6
54.	Carex spp.	6	0	2
55.	*Carthamus lanatus	4	8	2
56.	Cassinia arcuata	10	0	0
57.	Cassinia quinquefaria	10	0	0
58.	Cassinia sp.	2	0	0
59.	*Centaurea melitensis	4	4	4
60.	*Centaurium spp.	0	0	2
61.	Chamaesyce drummondii	16	44	30
62.	Cheilanthes sieberi ssp. sieberi	106	12	28
179.	*Medicago unknown 1	2	4	8
180.	*Medicago unknown 2	2	2	0
181.	*Medicago truncatula	2	0	0
182.	Melaleuca uncinata	6	0	6
183.	Microlaena stipoides	44	12	54
184.	Microtis sp.	4	0	0
185.	Minuria leptophylla	14	4	0
186.	Mirbelia pungens	2	0	0
187.	*Moenchia erecta	0	0	4
188.	*Onopordum acanthium	2	0	2
189.	Oxalis perennans	0	0	6
190.	Oxalis sp.	54	38	32
191.	*Panicum capillare	4	36	18
192.	Panicum effusum	10	12	32
193.	Panicum queenslandicum var. queenslandicum	0	4	2
194.	Panicum sp.	6	2	0
195.	*Parentucellia latifolia	0	0	2
196.	Parsonsia eucalyptophylla	6	0	0
197.	Paspalidium sp.	4	6	22
198.	*Paspalum dilatatum	0	2	0
199.	Pentaschistis airoides	34	4	28
200.	Persicaria prostrata	2	0	0

63.	**Chenopodium album*	0	6	0
64.	*Chenopodium desertorum*	10	12	24
65.	*Chloris truncata*	2	16	26
66.	**Chondrilla juncea*	6	24	8
67.	*Chrysocephalum apiculatum*	12	0	0
68.	*Chrysocephalum semipapposum*	4	2	0
69.	**Cirsium vulgare*	10	10	2
70.	**Citrullus lanatus*	0	26	18
71.	*Clematis microphylla*	0	4	0
72.	*Convolvulus angustissimus*	0	2	0
73.	*Convolvulus erubescens*	0	8	2
74.	*Convolvulus* unknown 1	2	0	2
75.	*Convolvulus* unknown 2	2	0	6
76.	**Conyza bonariensis*	8	22	6
77.	**Conyza* sp.	6	6	12
78.	*Crassula decumbens* var. *decumbens*	0	10	6
79.	*Crassula sieberiana*	42	30	42
80.	**Cucumis myriocarpus*	2	8	2
81.	**Cyclospermum leptophyllum*	0	2	0
82.	*Cymbonotus preissianus*	4	0	0
83.	*Cynodon dactylon*	8	12	24
84.	**Cynodon incompletus*	0	0	2
201.	*Petrorhagia nanteuilii*	2	2	4
202.	**Phalaris* sp.	2	16	8
203.	*Philotheca brevifolia*	0	0	4
204.	*Phyllanthus fuernrohrii*	4	4	0
205.	*Phyllanthus hirtellus*	4	0	0
206.	*Phyllanthus virgatus*	2	0	0
207.	*Plantago gaudichaudii*	4	0	0
208.	*Plantago varia*	6	0	0
209.	*Poa* spp.	4	0	0
210.	*Poa tenera*	2	0	0
211.	**Polycarpon tetraphyllum*	8	0	2
212.	**Polygonum arenastrum*	0	14	0
213.	*Pomaderris* sp.	2	0	0
214.	*Pomax umbellata*	2	0	0
215.	*Poranthera microphylla*	4	0	0
216.	**Portulaca oleracea*	0	10	16
217.	**Proboscidea louisiana*	0	4	0
218.	*Pseudognaphalium luteoalbum*	0	12	2
219.	*Ptilotus indivisus*	0	0	2
220.	*Ptilotus sessilifolius*	2	0	0
221.	*Rhodanthe diffusa ssp diffusa*	6	0	0
222.	*Rhodanthe floribunda*	0	0	2

85.	*Dactyloctenium radulans*	0	0	2
86.	*Daucus glochidiatus*	40	2	4
87.	*Desmodium* sp.	6	0	8
88.	*Dianella* sp.	10	4	4
89.	*Dichelachne* spp.	6	0	0
90.	*Dichondra repens*	22	2	6
91.	*Dichopogon* sp.	4	2	0
92.	*Digitaria brownii*	0	2	12
93.	*Digitaria diffusa*	4	0	0
94.	**Digitaria sanguinalis*	0	4	4
95.	*Digitaria* unknown 1	2	0	0
96.	*Digitaria* unknown 2	2	0	0
97.	*Dillwynia sericea*	2	0	0
98.	*Dodonaea boroniifolia*	2	0	0
99.	*Dodonaea viscosa* subsp. *Cuneata*	0	2	0
100.	*Dysphania pumilio*	24	60	54
101.	*Echinochloa colona*	0	6	2
102.	*Echium plantagineum*	18	30	30
103.	*Einadia nutans*	18	8	26
104.	*Einadia* spp.	16	4	12
105.	**Eleusine tristachya*	2	2	2
106.	*Elymus scaber*	68	10	44
223.	*Rhodanthe laevis*	2	0	2
224.	*Rhyncharrhena linearis*	6	0	0
225.	*Rumex brownii*	34	16	14
226.	*Rytidosperma pallidum*	4	0	0
227.	*Rytidosperma* unknown 1	118	18	60
228.	*Rytidosperma* unknown 2	8	4	12
229.	*Rytidosperma* unknown 3	10	2	16
230.	*Rytidosperma* unknown 4	2	0	4
231.	*Rytidosperma* unknown 5	0	0	2
232.	*Salsola australis*	0	8	22
233.	*Schoenus apogon*	2	0	0
234.	*Sclerolaena bicornis* var. *horrida*	0	0	4
235.	*Sclerolaena diacantha*	4	0	12
236.	*Sclerolaena muricata*	10	0	12
237.	*Senna artemisioides* ssp. *petiolaris*	4	0	0
238.	*Senna* sp.	0	0	2
239.	*Sida corrugata*	52	38	72
240.	*Sida filiformis*	0	0	2
241.	**Silene gallica*	8	0	2
242.	**Silybum marianum*	2	2	2
243.	**Sisymbrium* spp.	2	2	38
244.	*Solanum esuriale*	2	6	10

107.	*Enteropogon acicularis*	60	46	90
108.	*Epilobium* spp.	2	0	0
109.	*Eragrostis brownii*	0	6	4
110.	**Eragrostis cilianensis*	0	50	36
111.	*Eragrostis elongata*	0	2	4
112.	*Eragrostis lacunaria*	14	0	8
113.	*Eragrostis parviflora*	0	4	10
114.	*Eragrostis* spp.	0	4	0
115.	*Eremophila deserti*	2	0	0
116.	*Eremophila longifolia*	16	2	14
117.	*Eriochloa pseudoacrotricha*	0	12	8
118.	**Erodium cicutarium*	0	0	4
119.	*Erodium crinitum*	10	12	20
120.	*Eucalyptus* spp.	2	6	6
121.	*Euchiton involucratus*	0	4	0
122.	*Euchiton sphaericus*	0	6	2
123.	*Fimbristylis dichotoma*	4	0	0
124.	**Galium divaricatum*	6	0	2
125.	**Gamochaeta* spp.	0	2	0
126.	*Glycine* sp.	8	2	0
127.	*Glycine canescens*	10	0	0
128.	*Glycine tabacina*	2	0	0
245.	**Solanum nigrum*	2	12	10
246.	**Solanum triflorum*	0	4	0
247.	*Solenogyne dominii*	4	0	0
248.	**Sonchus oleraceus*	30	36	24
249.	**Stellaria media*	0	8	8
250.	*Stuartina muelleri*	32	4	14
251.	*Stypandra glauca*	18	0	0
252.	*Thyridolepis mitchelliana*	28	0	2
253.	*Trachymene* sp.	4	0	0
254.	*Tragus australianus*	0	4	12
255.	**Tribulus terrestris*	0	18	24
256.	*Tricoryne elatior*	4	4	4
257.	**Trifolium angustifolium*	10	16	4
258.	**Trifolium arvense*	14	20	34
259.	**Trifolium campestre*	6	2	4
260.	**Trifolium glomeratum*	18	28	52
261.	**Trifolium striatum*	12	0	6
262.	**Trifolium* sp.	14	20	16
263.	**Trifolium subterraneum*	14	20	16
264.	**Trifolium vesiculosum*	0	12	0
265.	*Triptilodiscus pygmaeus*	20	2	2
266.	**Triticum aestivum*	0	62	6

129.	*Gonocarpus elatus*	46	0	14	*267.*	*Velleia paradoxa*	12	4	6
130.	*Goodenia hederacea*	12	0	0	*268.*	*Vittadinia cuneata*	34	22	16
131.	*Goodenia pinnatifida*	4	0	0	*269.*	*Vittadinia triloba*	4	0	0
132.	*Goodenia* sp.	22	0	4	*270.*	**Vulpia* spp.	82	44	74
133.	**Hedypnois rhagadioloides* subsp. *Cretica*	6	0	0	*271.*	*Wahlenbergia* spp.	38	18	20
134.	**Heliotrope europaeum*	0	42	18	*272.*	*Walwhalleya subxerophila*	0	0	2
135.	*Hibiscus sturtii* var. *sturtii*	4	0	0	*273.*	*Wurmbea dioica*	4	0	0
136.	**Holcus lanatus*	0	4	0	*274.*	**Xanthium spinosum*	4	16	12
137.	**Hordeum distichon*	0	8	0	*275.*	*Xerochrysum bracteatum*	26	4	14
138.	**Hordeum leporinum*	6	34	50	*276.*	*Xerochrysum viscosum*	2	0	0

Table A3. Partial Canonical correspondence analysis (CCA) (controlled by habitat) results for composition of (a) all beetles, (b) detritivores, (c) herbivores, and (d) predators, constrained by habitat, plant species richness and vegetation structure (litter cover, total herbaceous cover, vegetation height). Percentage variation explained and significance values for each model are shown, along with marginal significance for each variable (P<0.05 in bold).

(a) Overall beetles	**% variation explained**	**F**	**Pr(>F)**	**(c) Herbivores**	**% variation explained**	**F**	**Pr(>F)**
Partial CCA Spring				**Partial CCA Spring**			
Plant variables; Condition(Habitat)	*2.67*	*1.62*	***0.001***	*Plant variables; Condition(Habitat)*	*3.97*	*0.09*	*0.091*
Plant.richness		1.55	**0.002**	Plant.richness		1.10	0.347
Litter.cover		1.91	**0.001**	Litter.cover		1.31	0.079
Vegetation height		1.45	**0.004**	Vegetation height		1.18	0.173
Total herbaceous cover		1.56	**0.001**	Total herbaceous cover		1.03	0.528
Partial CCA Summer				**Partial CCA Summer**			
Plant variables; Condition(Habitat)	*2.70*	*1.58*	***0.001***	*Plant variables; Condition(Habitat)*	*3.64*	*1.14*	***0.480***
Plant.richness		1.95	**0.001**	Plant.richness		1.43	**0.016**
Litter.cover		1.34	**0.049**	Litter.cover		1.17	0.19
Vegetation height		1.27	0.137	Vegetation height		0.78	0.809
Total herbaceous cover		1.76	**0.001**	Total herbaceous cover		1.19	0.143
(b) Detritivores	**% variation explained**	**F**	**Pr(>F)**	**(d) Predators**	**% variation explained**	**F**	**Pr(>F)**
Partial CCA Spring				**Partial CCA Spring**			
Plant variables; Condition(Habitat)	*2.79*	*0.90*	*0.086*	*Plant variables; Condition(Habitat)*	*3.15*	*1.31*	***0.019***
Plant.richness		0.91	0.213	Plant.richness		1.46	**0.044**
Litter.cover		0.54	0.899	Litter.cover		1.00	0.447
Vegetation height		0.87	0.297	Vegetation height		1.22	0.17
Total herbaceous cover		1.28	**0.007**	Total herbaceous cover		1.57	**0.014**
Partial CCA Summer				**Partial CCA Summer**			
Plant variables; Condition(Habitat)	*2.40*	*0.83*	*0.487*	*Plant variables; Condition(Habitat)*	*3.30*	*1.18*	*0.505*
Plant.richness		0.49	0.907	Plant.richness		1.04	0.641
Litter.cover		0.85	0.327	Litter.cover		1.42	0.115

Vegetation height	0.71	0.556	Vegetation height	1.42	0.095
Total herbaceous cover	1.26	0.062	Total herbaceous cover	0.86	0.877

Detailed description of results for Table A3: For beetle assemblage, the first two axes of our CCA analyses respectively explained 38.6% and 26.0% of the variation in plant richness and vegetation structure during spring, and 37.4% and 28.0% during summer. Partial CCA analyses for beetle assemblages showed that the variation explained purely by plant species richness and vegetation structure, after partialling out habitat effects, were 2.67% and 2.70% respectively during spring and summer (Table A5). Our CCA analyses showed that habitat type had a significant effect on composition of overall beetles ($P = 0.001$ during spring and summer), herbivores and detritivores (both with weaker effects during summer $P = 0.02$ than spring $P < 0.003$), and predators during spring ($P = 0.001$) (Table not shown).

Table A4. Summary of top-ranked generalized linear mixed-effect models testing responses of overall beetle species richness and abundance to the effects of plant species richness, vegetation structure (litter cover, total herbaceous cover, vegetation height), and interaction with habitat, if applicable. Direction and significance of responses are shown (+/- ‘0.05’; ++/-- ‘0.01’; +++/--- ‘0.001’; n.s. omitted). Habitats are p = patch, f = farmland and e = edge. Significant terms (P < 0.05) in bold.

	Spring					Summer				
Response	Model terms	Direction	Chisq	Df	Pr(Chisq)	Model terms	Direction	Chisq	Df	Pr(Chisq)
Species richness	*Best model: Habitat*					*Best model: Habitat + Total herbaceous cover*				
	(No vegetation effect)					Total herbaceous cover	++	7.39	1	**0.007**
Total abundance	*Best model: Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*					*Best model: Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*				
	Litter cover	---	15.05	1	**<0.001**	Litter cover	-	5.78	1	**0.016**
	Habitat*Plant richness	f(+++)	20.12	2	**<0.001**	Habitat*Plant richness	p(---); f(+++)	69.14	2	**<0.001**
	Habitat*Vegetation height	f(+++)	14.86	2	**0.001**	Habitat*Vegetation height	p(--); f(--)	14.01	2	**0.001**
	Habitat*Total herbaceous cover	p(+); e(-)	5.45	2	0.066	Habitat*Total herbaceous cover	p(+++); f(+++)	28.1	2	**<0.001**

Table A5 Summary of top-ranked generalized linear mixed-effects models testing responses of beetle species richness and abundance to the effects of plant species richness, vegetation structure (litter, total herbaceous cover, vegetation height), and habitat. Terms separated by colon indicate interactive terms. df = degrees of freedom, logLik = log likelihood, AICc = Akaike Information Criterion for small samples, ΔAICc = change in AICc, (Int) = model intercept, + = factor included in model. hab = habitat, ltr = litter, prh = plant richness, thrb = total herbaceous cover, vht = vegetation height.

			No habitat interaction					With habitat interaction								
Response	Season	Int	hab	ltr	prh	thrb	vht	ltr:hab	prh:hab	thrb:hab	vht:hab	df	logLik	AICc	delta	weight
(a)																
Beetle richness	Spring	2.39	+									5	-382.45	775.4	0	0.19
	Summer	2.25	+			0.003						6	-361.98	736.6	0	0.28
Beetle abundance	Spring	3.43	+	-0.005	0.008	-0.003	-0.004		+	+	+	15	-731.52	1497.2	0	
	Summer	3.22	+	-0.003	-0.003	0.001	0.004		+	+	+	15	-798.00	1630.1	0	
(b)																
Detritivores richness	Spring	n/a										3	-206.55	419.3	0	0.72
	Summer	1.10	+	0.016	0.043	0.016	-0.038	+	+	+	+	17	-617.63	1274.6	0	1.00
Detritivore abundance	Spring	1.72	+	0.004	0.041	-0.008	0.017		+	+	+	15	-693.63	1421.4	0	0.45
	Summer	1.10	+	0.016	0.043	0.016	-0.038	+	+	+	+	17	-617.63	1274.6	0	1.00
Herbivore richness	Spring	n/a										3	-173.79	353.8	0	0.32
	Summer	n/a										3	-164.84	335.9	0	0.41
Herbivore abundance	Spring	1.38	+	-0.020	0.020	-0.014	0.026	+		+	+	15	-380.50	795.1	0	0.67
	Summer	-0.48	+	0.018	0.114		-0.037	+	+		+	14	-325.05	681.7	0	0.68
Predator richness	Spring	n/a										3	-218.98	444.1	0	0.25
	Summer	n/a										3	-198.48	403.1	0	0.16

Predator abundance	Spring	0.58	+	-0.013	0.120	-0.011	0.018	+	+	+		15	-516.71	1067.6	0	1.00
	Summer	0.03	+	0.026	-0.023	0.023	0.002	+	+	+	+	17	-520.96	1081.3	0	1.00

Table A6. Detailed summary of generalized linear mixed models for beetle species richness and abundance response as predicted by vegetation structure or plant richness. Significant terms via Wald tests (P < 0.05) in bold.

	Spring						Summer					
Response	Model terms	Direction	Estimate	SE	F	P	Model terms	Direction	Estimate	SE	F	P
(a)												
Species richness	*Habitat*						*Habitat + Total herbaceous cover*					
	(Intercept)		2.39	0.07	35.22	**<0.001**	(Intercept)		2.25	0.10	21.53	**<0.001**
	Habitat(Farm)	-	-0.03	0.06	-0.45	0.653	Habitat(Farm)	-	-0.28	0.07	-3.96	**<0.001**
	Habitat(Patch)	-	-0.50	0.07	-6.88	**<0.001**	Habitat(Patch)	-	-0.85	0.08	-10.43	**<0.001**
							Total herbaceous cover	+	0.00	0.00	2.72	**0.007**
Total abundance	*Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*						*Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*					
	(Intercept)		3.43	0.19	17.73	**<0.001**	(Intercept)		3.22	0.19	16.64	**<0.001**
	Habitat(Farm)	-	-0.73	0.26	-2.82	**0.005**	Habitat(Farm)	-	-0.58	0.14	-4.05	**<0.001**
	Habitat(Patch)	-	-1.28	0.25	-5.20	**<0.001**	Habitat(Patch)	-	-0.74	0.21	-3.61	**<0.001**
	Plant richness	+	0.01	0.01	0.97	0.330	Plant richness	-	0.00	0.01	-0.42	0.677
	Litter cover	-	-0.01	0.00	-3.88	**<0.001**	Litter cover	-	0.00	0.00	-2.41	**0.016**
	Vegetation height	-	0.00	0.00	-0.80	0.426	Vegetation height	+	0.00	0.00	1.11	0.266
	Total herbaceous cover	-	0.00	0.00	-2.30	**0.022**	Total herbaceous cover	+	0.00	0.00	0.37	0.713
	Habitat(Farm)*Plant richness	+	0.05	0.01	3.78	**<0.001**	Habitat(Farm)*Plant richness	+	0.05	0.01	4.22	**<0.001**
	Habitat(Patch)*Plant richness	-	-0.01	0.01	-1.00	0.318	Habitat(Patch)*Plant richness	-	-0.06	0.01	-4.91	**<0.001**

	Habitat(Farm)*Vegetation height	+	0.02	0.00	3.39	**0.001**	Habitat(Farm)*Vegetation height	-	-0.02	0.01	-3.20	**0.001**
	Habitat(Patch)*Vegetation height	+	0.01	0.01	1.03	0.305	Habitat(Patch)*Vegetation height	-	-0.01	0.00	-3.02	**0.003**
	Habitat(Farm)*Total herbaceous cover	+	0.00	0.00	0.23	0.819	Habitat(Farm)*Total herbaceous cover	+	0.01	0.00	4.27	**<0.001**
	Habitat(Patch)*Total herbaceous cover	+	0.00	0.00	2.26	**0.024**	Habitat(Patch)*Total herbaceous cover	+	0.01	0.00	4.51	**<0.001**
(b)												
Detritivore richness	*None*						*Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*					
							(Intercept)		1.15	0.48	2.40	**0.017**
							Habitat(Farm)	-	-1.17	0.63	-1.85	0.064
							Habitat(Patch)	-	-0.22	0.78	-0.28	0.777
							Plant richness	-	0.00	0.02	-0.19	0.846
							Litter cover	+	0.00	0.01	0.61	0.542
							Vegetation height	-	-0.03	0.02	-2.21	**0.027**
							Total herbaceous cover	+	0.00	0.00	0.46	0.644
							Habitat(Farm)*Plant richness	+	0.03	0.03	0.86	0.391
							Habitat(Patch)*Plant richness	-	-0.04	0.04	-1.09	0.277
							Habitat(Farm)*Litter cover	-	0.00	0.01	-0.36	0.720
							Habitat(Patch)*Litter cover	-	0.00	0.01	-0.30	0.767

							Habitat(Farm)*Vegetation height	+	0.03	0.02	1.38	0.169
							Habitat(Patch)*Vegetation height	+	0.02	0.02	1.43	0.153
							Habitat(Farm)*Total herbaceous cover	-	0.00	0.01	-0.02	0.984
							Habitat(Patch)*Total herbaceous cover	-	0.00	0.01	-0.18	0.855
Detritivore abundance	_Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height_						_Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height_					
	(Intercept)		1.72	0.32	5.41	**<0.001**	(Intercept)		1.10	0.30	3.73	**<0.001**
	Habitat(Farm)	-	-2.16	0.38	-5.76	**<0.001**	Habitat(Farm)	+	0.35	0.31	1.13	0.261
	Habitat(Patch)	+	1.49	0.31	4.84	**<0.001**	Habitat(Patch)	+	0.04	0.40	0.11	0.911
	Plant richness	+	0.04	0.01	4.27	**<0.001**	Plant richness	+	0.04	0.01	2.98	**0.003**
	Litter cover	+	0.00	0.00	2.28	**0.022**	Litter cover	+	0.02	0.00	5.03	**<0.001**
	Vegetation height	+	0.02	0.01	2.64	**0.008**	Vegetation height	-	-0.04	0.01	-4.66	**<0.001**
	Total herbaceous cover	-	-0.01	0.00	-3.22	**0.001**	Total herbaceous cover	+	0.02	0.00	5.61	**<0.001**
	Habitat(Farm)*Plant richness	+	0.04	0.02	2.60	**0.009**	Habitat(Farm)*Plant richness	+	0.01	0.02	0.35	0.723
	Habitat(Patch)*Plant richness	-	-0.10	0.01	-7.61	**<0.001**	Habitat(Patch)*Plant richness	-	-0.06	0.02	-3.71	**<0.001**
	Habitat(Farm)*Vegetation height	-	0.00	0.01	-0.60	0.547	Habitat(Farm)*Litter cover	-	-0.04	0.00	-9.42	**<0.001**
	Habitat(Patch)*Vegetation	-	-0.02	0.01	-2.23	**0.026**	Habitat(Patch)*Litter cover	-	0.00	0.00	-0.38	0.706

	height											
	Habitat(Farm)*Total herbaceous cover	+	0.02	0.00	6.53	**<0.001**	Habitat(Farm)*Vegetation height	+	0.07	0.01	6.01	**<0.001**
	Habitat(Patch)*Total herbaceous cover	+	0.00	0.00	1.15	0.249	Habitat(Patch)*Vegetation height	+	0.04	0.01	4.64	**<0.001**
							Habitat(Farm)*Total herbaceous cover	-	-0.01	0.00	-3.87	**<0.001**
							Habitat(Patch)*Total herbaceous cover	-	-0.01	0.00	-3.90	**<0.001**
Herbivore richness	*None*						*None*					
Herbivore abundance	*Habitat * Litter + Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*						*Habitat * Litter + Habitat * Plant richness + Habitat * Vegetation height*					
	(Intercept)		1.38	0.44	3.12	**0.002**	(Intercept)		-0.48	0.39	-1.24	0.216
	Plant richness	+	0.02	0.01	2.03	**0.043**	Habitat(Farm)	+	1.26	0.45	2.80	**0.005**
	Habitat(Farm)	-	-1.12	0.57	-1.97	**0.049**	Habitat(Patch)	+	2.56	0.49	5.18	**<0.001**
	Habitat(Patch)	-	-2.03	0.44	-4.63	**<0.001**	Plant richness	+	0.11	0.02	5.41	**<0.001**
	Litter cover	-	-0.02	0.01	-2.51	**0.012**	Litter cover	+	0.02	0.01	3.44	**0.001**
	Vegetation height	+	0.03	0.01	2.57	**0.010**	Vegetation height	-	-0.04	0.01	-3.07	**0.002**
	Total herbaceous cover	-	-0.01	0.00	-3.39	**0.001**	Habitat(Farm)*Plant richness	-	-0.09	0.03	-3.21	**0.001**
	Habitat(Farm)*Litter cover	+	0.02	0.01	2.31	**0.021**	Habitat(Patch)*Plant richness	-	-0.16	0.03	-5.90	**<0.001**

	Habitat(Patch)*Litter cover	+	0.05	0.01	5.77	**<0.001**	Habitat(Farm)*Litter cover	-	-0.03	0.01	-4.49	**<0.001**
	Habitat(Farm)*Vegetation height	-	-0.03	0.01	-3.06	**0.002**	Habitat(Patch)*Litter cover	-	-0.02	0.01	-2.69	**0.007**
	Habitat(Patch)*Vegetation height	+	0.00	0.01	0.09	0.931	Habitat(Farm)*Vegetation height	+	0.06	0.02	3.43	**0.001**
	Habitat(Farm)*Total herbaceous cover	+	0.03	0.01	4.70	**<0.001**	Habitat(Patch)*Vegetation height	+	0.02	0.01	1.17	0.241
	Habitat(Patch)*Total herbaceous cover	+	0.01	0.00	2.62	**0.009**						
Predator richness	*None*						*None*					
Predator abundance	*Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Vegetation height*						*Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height*					
	(Intercept)		0.58	0.37	1.58	0.114	(Intercept)		0.03	0.34	0.08	0.939
	Habitat(Farm)	-	-2.68	0.52	-5.11	**<0.001**	Habitat(Farm)	+	0.17	0.36	0.49	0.628
	Habitat(Patch)	-	-0.06	0.42	-0.15	0.880	Habitat(Patch)	+	2.28	0.44	5.15	**<0.001**
	Plant richness	+	0.12	0.02	7.58	**<0.001**	Plant richness	-	-0.02	0.01	-1.62	0.105
	Litter cover	-	-0.01	0.01	-2.65	**0.008**	Litter cover	+	0.03	0.00	6.40	**<0.001**
	Vegetation height	+	0.02	0.00	5.72	**<0.001**	Vegetation height	+	0.00	0.01	0.27	0.790
	Total herbaceous cover	-	-0.01	0.00	-4.24	**<0.001**	Total herbaceous cover	+	0.02	0.00	7.27	**<0.001**
	Habitat(Farm)*Plant richness	-	-0.05	0.02	-2.11	**0.034**	Habitat(Farm)*Plant richness	+	0.11	0.02	6.10	**<0.001**
	Habitat(Patch)*Plant richness	-	-0.11	0.02	-5.96	**<0.001**	Habitat(Patch)*Plant richness	-	-0.03	0.02	-1.57	0.117
	Habitat(Farm)*Litter cover	+	0.01	0.01	0.65	0.518	Habitat(Farm)*Litter cover	-	-0.04	0.01	-6.93	**<0.001**

Habitat(Patch)*Litter cover	+	0.02	0.01	4.18	**<0.001**	Habitat(Patch)*Litter cover	-	-0.03	0.01	-4.86	**<0.001**
Habitat(Farm)*Total herbaceous cover	+	0.04	0.00	7.81	**<0.001**	Habitat(Farm)*Vegetation height	+	0.01	0.01	1.13	0.260
Habitat(Patch)*Total herbaceous cover	+	0.02	0.00	5.08	**<0.001**	Habitat(Patch)*Vegetation height	-	-0.03	0.01	-2.86	**0.004**
						Habitat(Farm)*Total herbaceous cover	-	-0.02	0.00	-4.24	**<0.001**
						Habitat(Patch)*Total herbaceous cover	-	-0.01	0.00	-2.74	**0.006**

Paper IV: Supplementary materials

Table S1. Vegetation variables recorded in a 20 m by 10 m plot at each pitfall trap location. Raw cover scores were based on the middle percentage values of the following six categories: 0–1%; 1–5%; 5–25%; 25–50%; 50–75%; and 75–100%.

Vegetation variable	Unit	Description	Habitat type:	Crop	Edge	Patch	Planting	Fallow	Woody debris
Bare ground cover	Cover score	Area of bare soil	Min	10	10	10	10	10	10
			Max	127.5	105	127.5	140	187.5	117.5
			Mean	73.3	57.8	50.3	64.9	77.9	62.9
Total herbaceous cover	Cover score	Sum of cover scores for native forb, native grass, exotic perennial grasses and exotic annual forbs and grasses	Min	1	0	1	7	4	5
			Max	85	65	75	45	55	80
			Mean	37.6	20.4	23.1	25.3	17.7	39.8
Litter cover	Cover score	Detached leaf and grass litter	Min	2.5	2.5	2.5	2.5	2.5	2.5
			Max	85	62.5	85	85	62.5	85
			Mean	19.6	22.3	40.1	30.1	9.8	27.4
Ground-layer vegetation height	Centimetre	Average height of dominant grasses, forbs, shrubs and other vegetation < 1 m high	Min	2.5	2.5	2.5	2.5	2.5	2.5
			Max	85	85	62.5	37.5	62.5	62.5
			Mean	20.2	19.6	8.7	8.5	10.2	17.7

Table S2. Summary of ground beetles (Carabidae) sampled in our study (2014–2015).

			Farmland				**Edge**				**Woodland**
ID	**Subfamily**	**Genus/species**	**Crop**	**Woody debris**	**Fallow**	**Planting**	**Crop–woodland edge**	**Woody debris–woodland edge**	**Fallow–woodland edge**	**Planting–woodland edge**	**Woodland**
C009	Harpalinae	*Gnathaphanus melbournensis*	11	12	12	5	5	5	7	1	11
C020	Scaritinae	*Laccopterum foveigerum*	4	1	0	1	1	1	1	2	10
C032	Scaritinae	*Clivina* sp.	5	2	1	2	0	0	2	0	0
C034	Pterostichinae	*Pterostichinae* sp.	1	0	0	0	0	0	0	0	0
C036	Pentagonicinae	*Scopodes boops*	2	1	4	2	3	2	1	0	5
C039	Pterostichinae	*Simodontus* sp.	4	2	0	0	1	0	0	0	1
C042	Psydrinae	*Mecyclothorax punctipennis*	4	1	2	0	0	0	0	1	3
C043	Pterostichinae	*Sarticus coradgeri*	4	3	3	3	0	0	0	2	3
C055	Pterostichinae	*Rhytisternus liopleurus*	0	0	1	0	0	0	0	0	0
C061	Harpalinae	*Harpalinae* sp.	5	0	2	3	0	0	0	0	5
C069	Carabinae	*Calosoma schayeri*	1	0	0	0	0	0	0	0	1
C086	Harpalinae	*Egadroma* sp.	5	2	1	1	1	3	1	2	2
C114	Harpalinae	*Hypharpax* sp.	1	3	7	6	3	1	0	0	4

C120	Harpalinae	*Harpalinae* sp.	2	1	1	2	0	0	0	0	1
C122	Harpalinae	*Harpalinae* sp.	1	0	2	2	0	0	0	0	0
C127	Pterostichinae	*Pterostichinae* sp.	0	0	0	0	0	0	0	0	1
C137	Harpalinae	*Hypharpax* sp.	1	0	5	3	3	2	4	0	2
C142	Harpalinae	*Harpalinae* sp.	0	1	5	2	0	0	1	0	3
C143	Harpalinae	*Gnathaphanus multipunctatus*	4	4	17	7	3	8	8	5	4
C164	Bembidiinae	*Pericompsus* sp.	3	3	1	3	1	1	0	1	1
C206	Harpalinae	*Hypharpax ranula?*	0	0	0	1	0	0	0	1	0
C216	Pentagonicinae	*Homothes elegans?*	1	2	1	1	0	0	0	0	1
C251	Psydrinae	*Neonomius laticollis?*	4	4	5	5	4	3	0	2	8
C252	Amblystominae	*Amblystomus* sp.	0	2	4	0	2	4	2	2	22
C270	Harpalinae	*Harpalinae sp?*	0	0	0	1	0	1	0	0	0
C280	Scaritinae	*Scaritinae* sp.	1	1	0	1	0	0	0	0	0
C292	Pterostichinae	*Sarticus cyaneocinctus*	2	2	2	0	0	0	2	1	1
C293	Harpalinae	*Notiobia* sp.	5	2	9	1	2	2	3	6	7
C303	Harpalinae	*Hypharpax* sp.	0	0	1	0	0	0	0	0	0
C310	Pseudomorphinae	*Pseudomorphinae* sp.	1	1	0	0	0	0	0	1	0
C311	Agoninae	*Laemostenus* sp.*?*	1	0	0	0	0	0	0	0	1
C315	Cicindelinae	*Cicindelinae* sp.	0	0	0	0	0	0	0	0	1
C347	Scaritinae	*Scaritinae* sp.	3	0	0	1	0	1	0	0	0
C353	Paussinae	*Arthropterus* sp.	0	0	0	0	0	1	2	0	2

C355	Scaritinae	*Scaraphites lenaeus*	0	0	0	0	0	0	0	0	1
C359	Lebiinae	*Speotarus* sp.*?*	0	0	0	0	0	0	0	0	1
C389	Pseudomorphinae	*Adelotopus* sp.*?*	0	0	1	1	0	0	0	0	0
C405	Psydrinae	*Mecyclothorax* sp.*?*	1	0	1	0	0	0	0	0	0
C434	Harpalinae	*Harpalinae* sp.	0	0	1	1	0	0	0	0	0
C439	Pseudomorphinae	*Cainogenion* sp.	0	0	0	1	0	0	0	0	0
C456	Harpalinae	*Diaphoromerus* sp.*?*	0	0	0	0	0	0	0	0	1
C477	Harpalinae	*Notiobia germari*	4	2	2	7	0	0	1	4	2
C487	Lebiinae	*Anomotarus* sp.*?*	1	0	1	0	0	0	0	0	1
C488	Harpalinae	*Gnathaphanus* sp.	1	0	3	2	0	0	0	3	1
C493	Broscinae	*Promecoderus* sp.	2	0	0	0	1	1	0	0	0
C495	Harpalinae	*Harpalinae* sp.	0	0	1	0	0	0	0	0	0
C505	Broscinae	*Pramecoderus gracilis*	4	2	3	1	0	0	0	0	1
C529	Harpalinae	*Harplaner* sp.*?*	0	0	0	1	0	0	0	0	0
C536	Harpalinae	*Hypharpax* sp.	1	0	2	6	0	2	3	3	2
C573	Pseudomorphinae	*Sphallomorpha* sp.	0	0	0	0	0	0	0	0	1
C590	Lebiinae	*Microlestodes* sp.*?*	1	0	0	0	0	0	0	0	0
C603	Harpalinae	*Harpalinae* sp	0	0	1	2	0	0	0	0	0
C616	Helluoninae	*Gigadema bostocki?*	0	0	0	0	0	0	1	0	0
C633	Harpalinae	*Harpalinae* sp.	0	0	0	0	0	0	1	0	0
C663	Harpalinae	*Cenogmus* sp.	2	1	0	2	0	0	0	0	0
C672	Chlaeniinae	*Chlaenius australis*	0	0	1	0	0	0	0	0	0

C673	Harpalinae	*Hypharpax* sp.	0	0	1	0	0	0	0	0	0
C674	Scaritinae	*Geoscaptus laevissimus*	3	1	0	0	0	0	0	0	0
C681	Amblystominae	*Amblystominae* sp.	1	1	5	0	1	2	1	3	1
C702	Harpalinae	*Harpalinae* sp.	0	0	0	0	1	0	0	0	0
C677	Scaritinae	*Philoscaphus tuberculatus*	0	0	0	0	0	0	0	0	2
C707	Scaritinae	*Carenum* sp.	0	0	0	0	0	0	0	0	1
C710	Agoninae	*Agoninae* sp.	1	0	0	0	0	0	0	0	0

Table S3. Summary of morphological traits and allometric regressions with body length (pooled from all habitats) (*). Allometric equation: $\log(Y) = a + b \log(\text{body length})$.

	Trait statistics (um)					**Allometry**				
Trait (Y)	**Min**	**Max**	**Mean**	**SE**	**R2**	**adjusted R2**	**a**	**SE of a**	**b**	**SE of b**
Eye diameter	99.6	1784.8	573.8	41.7	0.82	0.82	-0.29	0.18	0.77	0.05
Head width	9.0	203.0	113.4	7.2	0.08	0.06	0.70	0.56	0.33	0.14
Head length	203.9	7000.0	1351.2	161.4	0.89	0.89	-1.29	0.19	1.11	0.05
Pronotum width	438.2	39853.3	3379.5	642.2	0.91	0.91	-0.81	0.17	1.08	0.04
Pronotum length	5.0	208.0	112.5	7.6	0.05	0.04	0.78	0.65	0.30	0.17
Pronotum depth	245.7	13500.0	1577.9	228.2	0.85	0.85	-0.99	0.22	1.05	0.06
Elytra width	4.8	208.0	109.1	8.0	0.23	0.22	-0.55	0.58	0.64	0.15
Elytra length	925.9	16105.7	5500.2	455.7	0.98	0.98	0.05	0.06	0.93	0.02
Rear femur length	341.4	7000.0	2020.4	170.1	0.88	0.88	-0.27	0.16	0.90	0.04
Metratrochanter length	173.4	3400.0	965.5	75.6	0.82	0.82	-0.28	0.19	0.83	0.05
Eye protrusion	69.3	270628.1	4946.8	4355.7	0.34	0.33	-0.89	0.65	0.94	0.17
Mandible protrusion	1.0	2809.4	482.1	76.8	0.38	0.37	-3.10	0.91	1.42	0.24
Body length	1428.8	40500.0	9184.0	876.7	N/A	N/A	N/A	N/A	N/A	N/A

(*) Details on analysis method and results:

We examined the allometric trends for each trait to understand how changes in body shape-related traits relate to changes in body size (Barton et al. 2011a; Ribera et al. 1999; Shingleton 2010). This was determined by calculating the residuals from linear regressions of $\log_{10}$(trait) against $\log_{10}$(body length) for each trait outside of body length (Barton et al. 2011a; Shingleton 2010).

Majority of log(traits) showed positive allometry with log(body length), except for head width, pronotum length, elytra width, mandible protrusion, and eye diameter showing slopes (b-value) that diverge from unity (Table S3). In contrast to the size-grain hypothesis (Kaspari and Weiser 1999), we did not find differences in allometry of leg length with body length of ground beetles occurring in woodlands (b = 0.88) and farmlands (b = 0.90) (data not shown).

Table S4. Multivariate analyses results showing significance of habitat (farmland use, distance) and vegetation structure on ground beetle composition and occurrence. $P < 0.05$ shown in bold. Morphospecies "C" codes shown. Interactions of farmland use (crop, woody debris, fallow, planting) and distance (1 = 200m in farmland, 2 = 20m in farmland, 3 = 0m edge, 4 = 20m in woodland, 5 = 200m in woodland) shown. See also details in related result Figure S4.

Predictor variables		**Deviance**	**p-value**	**Positively associated species**	**Negatively associated species**
Habitat	Farmland use	214.6	0.030	N/A[a]	N/A[a]
	Distance	390.3	0.001	N/A[a]	N/A[a]
	Region	525.5	0.001	N/A[a]	N/A[a]
	Farmland use:Distance	321.9	0.002	C032 (crop.2); C042 (crop.2); C477 (planting.2); C536 (planting.2), C114 (fallow.2); C143 (fallow.1, fallow.2, fallow.3, woodydebris.3); C039 (woodydebris.1); C252 (woodydebris.4)	None
Vegetation structure	Vegetation height	137.7	0.001	C009; C020; C032; C039; C042; C086; C164	C114; C143; C293
	Litter cover	130.3	0.001	None	C009; C086; C143; C293
	Total herbaceous cover	190.2	0.001	C477	C252
	Bare ground cover	75.6	0.052	C137; C143; C293	None
	Region	458.7	0.001	N/A[a]	N/A[a]

[a] Species details not provided because effects of region, and non-interactive effects of farmland use and distance, were not the focus of this study

Table S5. Summary of final generalized linear mixed models for vegetation structural variables of vegetation height, litter cover, bare ground cover and total herbaceous cover. $P < 0.05$ shown in bold.

Response variable	Model terms	Chisq	Df	Pr(>Chisq)
Vegetation height	Transect	38.6	3	**< 0.001**
	Distance	311.0	4	**< 0.001**
	Region	0.9	2	0.641
	Transect:Distance	264.7	12	**< 0.001**
Litter cover	Transect	1.6	3	0.664
	Distance	1003.6	4	**< 0.001**
	Region	3.2	2	0.198
	Tansect:Distance	644.4	12	**< 0.001**
Bare ground cover	Transect	8.0	3	0.047
	Distance	512.9	4	**< 0.001**
	Region	16.1	2	**0.000**
	Transect:Distance	329.3	12	**< 0.001**
Total herbaceous cover	Transect	0.6	3	0.904
	Distance	628.4	4	**< 0.001**
	Region	13.5	2	**0.001**
	Transect:Distance	169.3	12	**< 0.001**

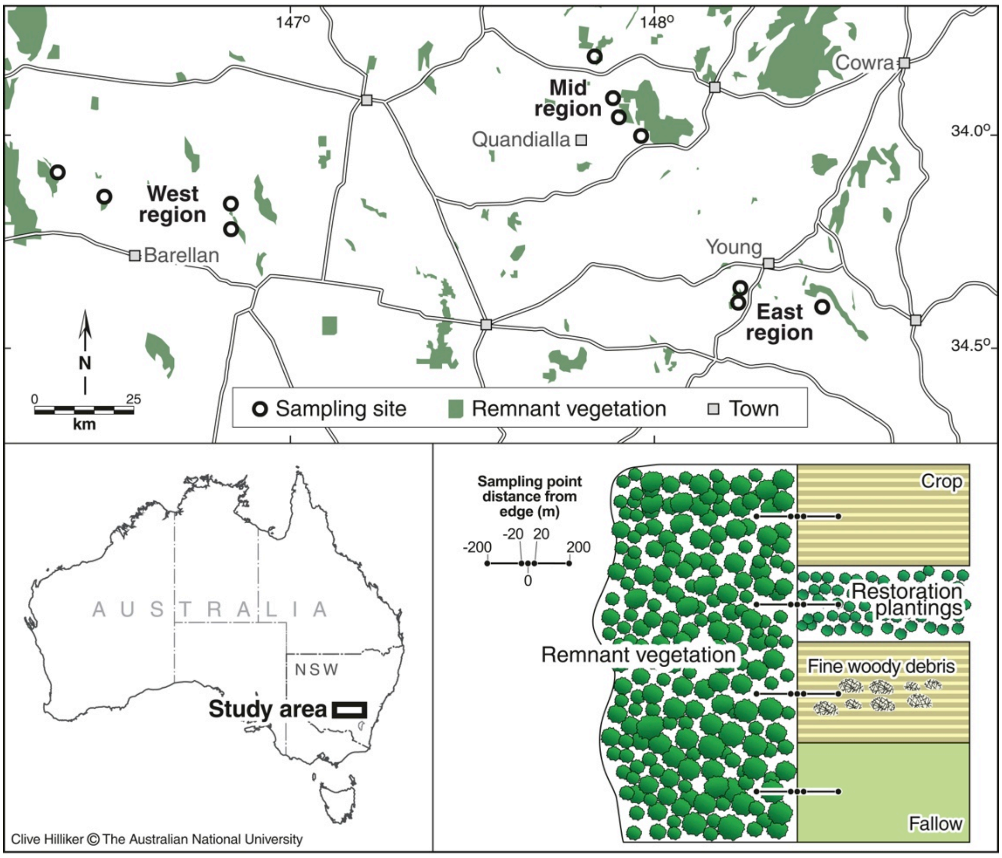


Figure S1. Map showing study sites in New South Wales, south-eastern Australia. Inset shows stylized image of experimental design and pitfall traps placement along four 400 m transects between remnant woodland patch and four adjoining farmland uses.

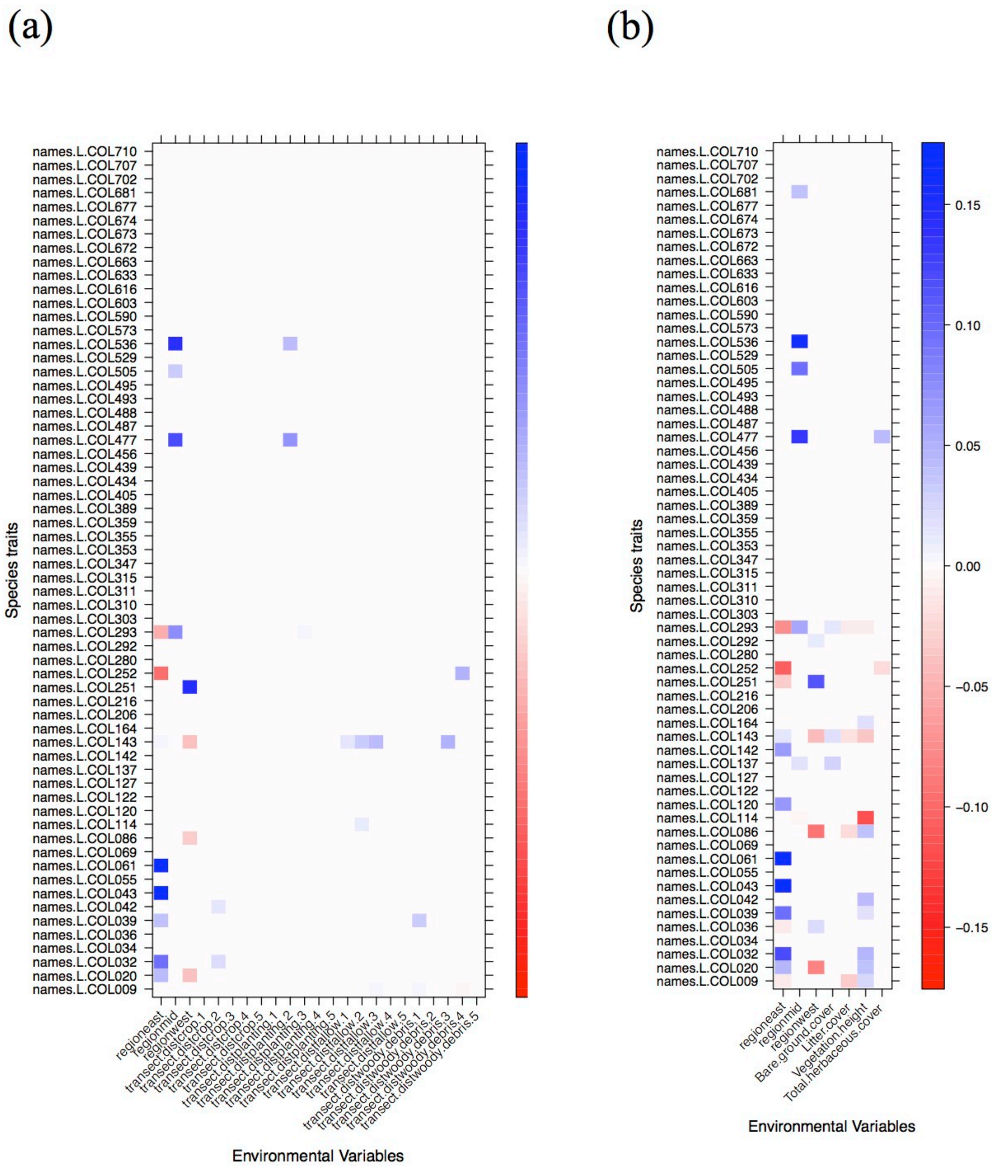


Figure S2. Multispecies model results showing individual species responses to habitat type (farmland use, distance) (a), and vegetation structure (b). Distance variables: 1 = 200m in farmland, 2 = 20m in farmland, 3 = 0m edge, 4 = 20m in woodland, 5 = 200m in woodland (*).

(*) Detailed results for descriptive analyses of beetle species composition

We identified significant interactive effects of ‘farmland use’ and ‘distance’ on species composition (P = 0.002) (Table S4; Figure S2a). Vegetation height, litter cover and total herbaceous cover were also significant vegetation variables affecting species composition (P = 0.001), while bare ground cover had marginal effects (P = 0.052). Seven species responded positively to vegetation height, and three species responded negatively. Four species responded negatively to increasing litter cover. Total herbaceous cover was positively associated with *Notiobia germari* and negatively with *Amblystomus* sp. C252 (Table S4; Figure S2b).

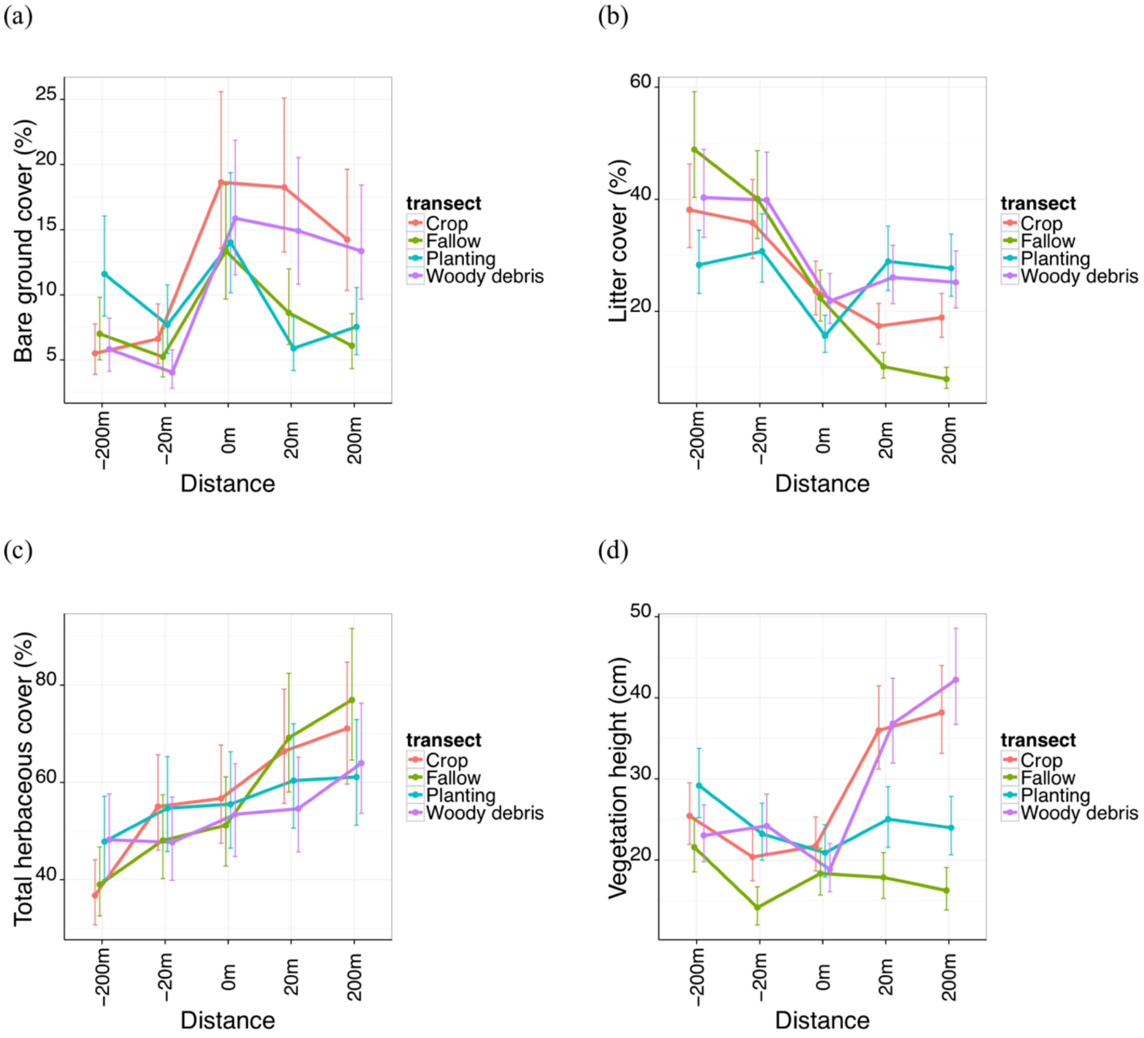
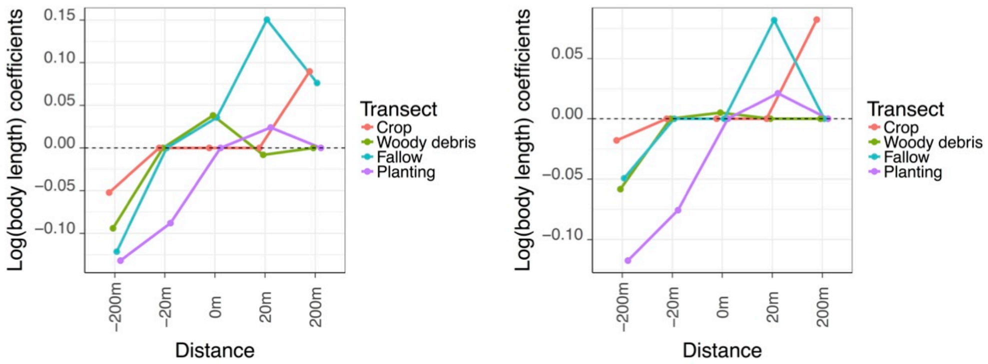


Figure S3. Effect of habitat type and distance (all farmland use:distance responses: $P < 0.001$) from edges on predicted: bare ground cover (a), litter cover (b), total herbaceous cover (c), and vegetation height (d). Distance -200m and -20m refers to the patch, 0m the edge, and 200m and 20m the farmland adjoining the patch. ±95% confidence intervals shown; lines as a visual aid to show general trends.

(a) Model: Farmland use × distance × log(body length) + vegetation height × log(body length)

(b) Model: Farmland use × distance × log(body length) + litter cover × log(body length)



(c) Model: Farmland use × distance × log(body length) + bare ground cover × log(body length)

(d) Model: Farmland use × distance × log(body length) + total herbaceous cover × log(body length)

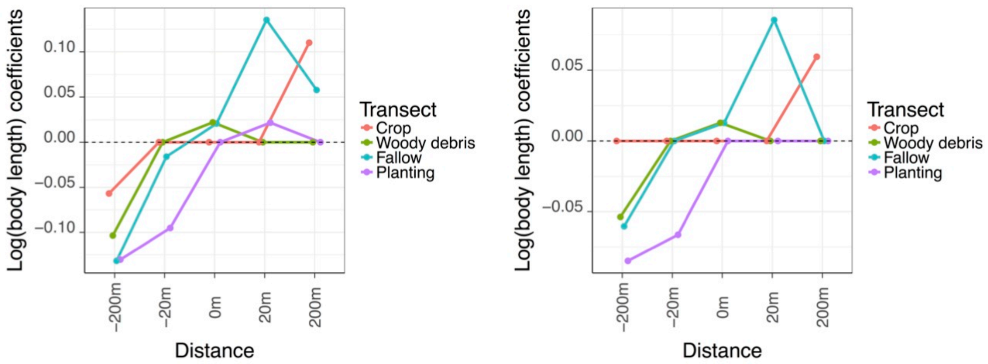


Figure S4. Coefficients of fourth-corner interaction showing relationships between log(body size) and the interaction between farmland use and distance (*). Significant relationships are non-zero values, with direction of relationships shown as positive or negative values. Distance -200m and -20m refers to the patch, 0m the edge, and 200m and 20m the farmland adjoining the patch. Lines show general trends only, and cannot be used to infer magnitude of differences between treatments. Fitted models as follows: accounting for vegetation height only (a), accounting for litter cover only (b), accounting for bare ground only (c), accounting for total herbaceous cover only (d).

(*) Details on analysis method and results:

For body size, we also fitted four more models with each of the four vegetation variables (vegetation height, bare ground cover, litter cover, total herbaceous cover) added *separately* to model (I) to examine the relative contribution of *individual* vegetation variables (details in main manuscript).

It was difficult to clearly isolate effects of individual vegetation variables on body size in relation to 'farmland use' and 'distance' (cf. Figure 2a, Figure S4a-d). However, low litter cover may explain some of the occurrence of larger beetles 200m and 0m in fallows, and high litter cover may explain the occurrence of smaller beetles in -20m in patches adjoining fallows (cf. Figure 2a, Figure S4b, Figure S3b). Low vegetation height also likely explained some of the occurrence of smaller beetles in -20m in patches adjoining fallows (cf. Figure 2a, Figure S4a, Figure S3d).