

Biodiversity and Conservation

Dynamic effects of ground-layer plant communities on beetles in a fragmented farming landscape --Manuscript Draft--

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Abstract:	<p>Vegetation effects on arthropods are well recognized, but it is unclear how different vegetation attributes might influence arthropod assemblages across mixed-agricultural landscapes. Understanding how plant communities influence arthropods under different habitat and seasonal contexts can identify vegetation management options for arthropod biodiversity. We examined relationships between vegetation structure, plant species richness and plant species composition, and the diversity and composition of beetles in 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, activity-density 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-harvest in summer. Plant composition better predicted beetle composition than vegetation structure. Both plant richness and vegetation structure significantly and positively affected beetle activity-density. 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 maximize 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 ground cover in all habitats may improve activity-density of all beetle trophic groups. The impacts of existing weed control strategies in Australian crop margins on arthropod</p>	

biodiversity require further study.

Response to Reviewers:

*** IMPORTANT: SEE ATTACHED WORD VERSION OF "RESPONSE TO REVIEWERS COMMENTS" TO VIEW FIGURES ***

Response to reviewers' comments

REVIEWER #1 COMMENT:

Reviewer #1: The paper entitled "Dynamic effects of ground-layer plant communities on beetles in a fragmented farming landscape" is very interesting and worth publishing. It is very interesting as the authors considered the relationships between plant composition and beetles and as they focus on different seasons. The hypotheses are well presented particularly thanks to the Fig. 1 (except for one arrow - see specific comment for line 626) and the analyses are sound. However, I have some issues with the material and methods which need to be clearer. I recommend publication from the moment the suggested revisions have been made.

RESPONSE TO REVIEWER #1 COMMENT:

We thank Reviewer #1 for commending our work. We have addressed all the general and specific comments from the reviewer (as detailed below) to help guide a thorough set of revisions for the manuscript.

GENERAL COMMENT (1):

- The idea of considering several seasons (spring and summer) is very interesting. Nevertheless, I would have appreciated that you considered a whole year of survey. Indeed, it is commonly acknowledged that beetles have a peak of species richness in autumn and you can also sample some very interesting species in winter. I obviously guess that it's too late but I would recommend you to discuss a little about this idea in the discussion section when you wrote about the temporally dynamic vegetation effects on beetles.

RESPONSE TO GENERAL COMMENT (1):

We agree that it would have been very interesting to sample a complete annual cycle. Limited project resources meant that we could sample only a limited time period and have thus selected spring and summer. These are two distinct periods of the cropping cycle (peak crop growth, and post-crop harvest), which we expected to have substantially different seasonal activity of beetles and peak species richness during the year. To address this comment, we have added the following text to acknowledge this limitation in Lines 496-499: "However, more species-level data and data from other seasons (e.g. winter and autumn) are needed to determine how different species use vegetation resources across the landscape at different times of the year..., this information is severely lacking for most beetle species (outside of Europe)".

GENERAL COMMENT (2):

- I have several issues with the material and methods. Please, see the specific comments for modifications.

RESPONSE TO GENERAL COMMENT (2):

We have addressed issues relevant to the material and methods section in Response to specific comments (7) to (14).

GENERAL COMMENT (3):

- To go further and as you considered two different habitats and the edges between them, I would recommend you to discuss a little on the questions of movements of the beetle species. Indeed, you have shown that species in remnant patches may be dispersal limited. But are the species of the farmland colonizing the others habitats; are the habitats suitable enough for it?

RESPONSE TO GENERAL COMMENT (3):

We thank the reviewer for raising this important point. We have recently published a paper on the movement patterns of beetle assemblages across the different habitats in this study landscape (Ng et al. 2018 Landscape Ecology). Findings in this paper include identified movement of detritivorous beetles from farmlands towards woodlands

during spring, and movement of predatory beetles towards edges from farmlands during summer.

To address this comment, we have stated the role of movement more clearly in the "Discussion" paragraph Lines 352-362, and referred to our movement paper (which addresses movement patterns in this landscape in further detail). Relevant text in the revised paragraph include: "... beetles in remnant patches may be dispersal-limited woodland specialists ...", "beetle assemblages may be more dissimilar with increasing distance between sites due to limited species movement ...", and "spatio-temporal turnover in beetle assemblages ... likely linked to fluctuations in connectivity of habitat resources [...] and cross-habitat movement ... Seasonal movement patterns of beetles between different farmland-woodland edges in this study landscape are detailed in Ng et al. (2017)".

SPECIFIC COMMENT (1):

- Line 23; 53 and study site: In the abstract, you are speaking about "dynamically changing agricultural landscapes". I would recommend giving us some information about the history of the different habitats (i.e. since how many years it is a woodland or a farmland; were there some modifications of habitat type in the time...) and inform us to what extent they are indeed dynamically changing.

RESPONSE TO SPECIFIC COMMENT (1):

We have removed reference to the term "dynamic", and instead refer to mixed-farming landscapes directly: Line 53: "... across human-modified landscapes, such as mixed-farming landscapes that include crop-pasture rotation (Bell and Moore 2012)". We have also revised Line 23 to "mixed-agricultural landscapes", and Line 136 in the "Study site and sampling design" section to state how many years of farming has established in the landscape: "Widespread clearing for agriculture over 100 years ago has restricted native Eucalyptus woodland remnants to infertile, steeper areas. Many remnants also have been modified by livestock grazing (mainly cattle and sheep), invasion of exotic weeds, and altered fire regimes (e.g. reduced fire frequency) ...". It is difficult to obtain historical information on the specific land use changes in our study region and similar agricultural regions in Australia (such information being completely lacking or available only through unverifiable and sometimes unreliable anecdotes), although the cited article Norris and Thomas (1991) and references therein provides detail on land use trends in the broader central New South Wales region that our study region is in.

SPECIFIC COMMENT (2):

- Line 37: There is a space lacking between "ground" and "cover".

RESPONSE TO SPECIFIC COMMENT (2):

Fixed.

SPECIFIC COMMENT (3):

- Line 58: The reference « Haddad et al 2001 » (introduction, line 58) is lacking in the reference section. Furthermore, a space is lacking between "et" and "al" in the text line 58.

RESPONSE TO SPECIFIC COMMENT (3):

These two issues have been fixed.

SPECIFIC COMMENT (4):

- Line 68: I would recommend you to define immediately what you mean using the expression "vegetation structure". Indeed, different parameters can be considered for this purpose from one paper to another (height; cover; density...). So please, move your definition you chose from lines 88-89 to line 68.

RESPONSE TO SPECIFIC COMMENT (4):

To address this comment, we have reordered this section by describing "vegetation structure" first, followed by plant species richness and plant species composition. As suggested by the reviewer, we have moved the definition of vegetation structure immediately after its introduction.

SPECIFIC COMMENT (5):

- Lines 83-84: As you say that there are many studies that have found positive relationships between plant diversity and the diversity of consumer assemblages, I would expect that you mentioned several references. Please provide some ones.

RESPONSE TO SPECIFIC COMMENT (5):

References have been added to support this statement (i.e. Agrawal et al. 2006; Perner et al. 2005; Siemann 1998; and Siemann et al. 1999).

SPECIFIC COMMENT (6):

- Line 109: It doesn't seem that you have really tested the difference between the seasons with your data analysis. It seems that you have analysed the seasons independently as in your models in Table 3, you have not included the season as an explanatory variable. You bring the information for the two seasons but you do not test the variation between the two of them. I recommend to reformulate your aim of study or to change your analysis.

RESPONSE TO SPECIFIC COMMENT (6):

We thank the reviewer for highlighting the point that we have indeed not explicitly tested for seasonal (and habitat) effects in some analyses (e.g. MRM analysis). Rather, we have generally explored how vegetation and beetle assemblage patterns varied between the different habitats, as well as how changes within these habitats might vary between the two seasons. To address this comment, we have made a subtle change in our research question (2) to be more descriptive rather than predictive, i.e. from "Do these plant-beetle relationships vary between habitats or seasons?" to "How do plant-beetle relationships vary between the different habitats (woodland patch, farmland, and their edges) over two seasons (spring and summer)?". This change was also applied in the Abstract.

SPECIFIC COMMENT (7):

- Line 131: Could you please develop a little on your sampling site? Why is it interesting to consider in ecology?

RESPONSE TO SPECIFIC COMMENT (7):

We have added the following text in Lines 139-144 (in the same paragraph) to explain why our site is interesting to consider in ecology: "Our study area is characteristic of highly cleared farming landscapes in southern Australia, where remnant native vegetation is at risk from additional clearing and further agricultural intensification. These kinds of fragmented landscapes occur in other parts of world such as South America, eastern Europe, and Asia (Uchida et al. 2016). However, the impact of land-use changes on biodiversity is less understood in these regions compared to Northern America, and Northern and Western Europe (Sutcliffe et al. 2015; Uchida et al. 2016)".

SPECIFIC COMMENT (8):

- Line 135: You provide a reference of 1991 for the description of your study site. But with weed invasions issues and changes of land use and practices, there must be some differences with today. Therefore, could you precise i) which species are used for grazing, ii) which main weeds invaded the site (are they the same species as the exotic annual grasses and forbs you cited for farmland description?); iii) which are the recent fire regimes?

RESPONSE TO SPECIFIC COMMENT (8):

We have expanded this line to clarify more precisely the livestock animals of interest (cattle and sheep), relevant weeds (exotic species), and main changed fire regime pattern of concern (reduced fire frequency).

The Line now reads as follows: "Many remnants also have been modified by livestock grazing (mainly cattle and sheep), invasion of exotic weeds, and altered fire regimes (e.g. reduced fire frequency) (Norris and Thomas 1991)".

SPECIFIC COMMENT (9):

- Line 136: I would appreciate a map of your study site which would notably localize the different patches and the distances between them.

RESPONSE TO SPECIFIC COMMENT (9):

A map of the study location, which includes latitude/longitude information and a scale, has been added in the Supplementary Information. This map is now referred to in Line 135 as "Online resource, Fig. A1".

SPECIFIC COMMENT (10):

- Line 139: If I'm correct, you considered as the same "farmland", different situations like "winter wheat crops", "fallow fields", "fine woody debris applied over harvested wheat crops", "restoration plantings". Could you please develop how you could consider all these types as a single 'farmland' habitat type? And especially considering the "restoration plantings" which seems to be quite different from the others as you find for this type Eucalyptus which characterizes your other habitat type: "patches"? If you have an analysis that proves that there are no differences between all those different situations, I would highly recommend you to add it in supplementary material.

RESPONSE TO SPECIFIC COMMENT (10):

We confirm that we have pooled wheat crop, fallow fields, fine woody debris treatment and recent restoration plantings (<7 years old) into a single farmland habitat type in this paper. Most of the structural and species compositional differences among landscape elements in our study region are represented by habitat contrasts between the remnant woodland patches and farmlands, rather than by differences among the subtypes of farmlands. In particular, mature woodland trees and shrubs, and a higher diversity of native ground cover species occur in woodland patches, while these have been cleared in farmlands (recent plantings were <7 years old within previously cultivated farmlands and did not contribute to the mid-storey and tree canopy layer). Nonetheless, habitat (or spatial) treatment and vegetation effects were controlled for separately in the statistical analyses (e.g. the use of both fixed and random effects in GLMM).

We confirm that major differences between woodland patches and farmlands are supported by pairwise comparisons of compositional dissimilarity (Bray-Curtis) of beetle communities between different land-uses, based on permutational multivariate analysis of variance (PERMANOVA) (examined in Ng et al 2017, Ecosphere), where we have found, for example, that overall beetle species composition was always significantly different between remnant patches and all farmland matrix types during spring (although patterns are more complex during summer and could be linked to seasonal movement; Ng et al. 2018 Landscape Ecology – note that the issue of movement is discussed in our Response to general comment (3)). In addition to the PERMANOVA tests, detailed CCA ordination plots also show distinct clustering of beetle assemblages between remnant patches and the different farmland types (and edges) – this plot is shown further below and is also now in Fig. A2 of the supplementary material.

To state the differences between woodland patches and farmlands more clearly, we have revised Lines 150-151 to the following: "Farmland and patches differed strongly structurally and floristically, and showed significantly different composition of beetle species (Ng et al. 2017; see also Fig. A2). 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*). Patches have higher plant species richness and higher proportion of native species (particularly *Acacia*, *Austrostipa*, *Sida* and *Calotis*) (Table 1; Table A2)." and Line 156 of our manuscript: "... trees were always present in patches and mostly absent from farmland"). Summary of plant data is available in the Supplementary Material (Table A2), and raw data (showing distinct plant and beetle species between the main habitats) will be attached in the CSIRO Data Portal (excel spreadsheet attached in revised submission).

Note that this paper intends to focus on the seasonal differences in plant-beetle relationships between uncropped (natural) and cropped (disturbed) habitats, where our experimental design allowed us to examine more interesting level of heterogeneity in vegetation attributes across a realistic mixed-farming system. For example, woody debris treatment contributes to litter component, restoration planting contributes to shrub component, while crops and fallow contributes to variability in vegetation composition and structure.

Fig. A2. Canonical Correspondence Analysis (CCA) ordination showing beetle composition during both seasons, with respect to the detailed habitat types:

[in doc attachment]

SPECIFIC COMMENT (11):

- Line 170: As you assigned the trophic group at the species level, why are you saying that it was based at the family and subfamily levels? Didn't you consider first the species level? Indeed, it can be difficult for some beetle families to assess and generalize a predominant feeding behaviour as it depends on which species you have captured in your particular study. For instance, Carabidae can be considered as mainly predators but perhaps you got only granivorous species... Maybe you can suppress the second part of the sentence.

RESPONSE TO SPECIFIC COMMENT (11):

We clarify that we have assigned trophic groups by family or subfamily, and not necessarily at the species level. This is because species-level information does not exist in most cases and family level inference is the best way around this knowledge gap. Coarse family and subfamily-level phylogeny assignment of trophic levels has been shown to be useful for examining highly diverse beetle assemblages (Hunt et al 2007 Science, Tscharntke et al 2005 Ecol Letters), and has been effectively used in many studies on Australian beetle fauna (e.g. Evans et al 2016 Landscape Ecol; Barton et al 2011 J App Ecol; Barton et al. 2010 J of Biogeography; Cunningham & Murray 2007 Oecologia).

Note that we have classified all carabids as predators given the prevalence of predatory carabids in Australia. This clarification has been added in the "Beetle sampling" section: "We assigned all carabids as predators because purely phytophagous species are considered uncommon in Australia (Gibb et al. 2017)".

SPECIFIC COMMENT (12):

- Line 231: Change "sites" for "pairs of traps".

RESPONSE TO SPECIFIC COMMENT (12):

Done.

SPECIFIC COMMENT (13):

- Lines 246-247: I'm not familiar with the MRM models but why are you saying that vegetation structural dissimilarity was a weak predictor in patches during summer? Isn't it a significant result highlighting that vegetation structure is important for predator species?

RESPONSE TO SPECIFIC COMMENT (13):

We had intended to say "weakly significant predictor", rather than "weak predictor". To clarify this, we have updated this line to say "vegetation structure was significantly (albeit weakly) correlated with ...".

SPECIFIC COMMENT (14):

- Line 255: Again, as you decided that your results were significant at the threshold of 0.05, the effects of litter cover are significant (must be in bold in Table A3). I recommend suppressing "effects of litter cover (P=0.049)".

RESPONSE TO SPECIFIC COMMENT (14):

We have updated this sentence to improve its accuracy. This Line now reads as follows: "During summer, effects of litter cover on overall beetle composition were weakly significant (P = 0.049) ..."

SPECIFIC COMMENT (15):

- Line 261: Add "species" between "plant" and "richness".

RESPONSE TO SPECIFIC COMMENT (15):

Done.

SPECIFIC COMMENT (16):

- Line 342: Add "ground cover" as another factor.

RESPONSE TO SPECIFIC COMMENT (16):

Done.

SPECIFIC COMMENT (17):

- Line 626: On your figure 1, I don't understand what the meaning of the arrow for prediction 1 is.

RESPONSE TO SPECIFIC COMMENT (17):

To address this comment, we have modified Fig. 1's arrow for prediction 1 to point from the plant composition to the arthropod community box.

SPECIFIC COMMENT (18):

-Supplementary materials, Table A1: I would appreciate to have also the detail between spring and summer data. I would like to see the list of beetle species and not only the family list.

-

RESPONSE TO SPECIFIC COMMENT (18):

To address this comment we intend to publish the raw data for this manuscript in the CSIRO Data Portal – this raw data are attached in Excel format for the reviewer. We believe that such detailed species-level information is more suitable if it is placed in the data portal rather than in the supplementary material.

We have added a data availability statement in Line 675: "The datasets generated during and/or analysed in this study will be made available from the CSIRO Data Access Portal upon acceptance of this manuscript (<https://data.csiro.au/>)".

REVIEWER #2 COMMENT:

Reviewer #2:

This paper presents interesting results of a study investigating the effect of some vegetation attributes (structure, species richness, species composition) on the diversity and composition of beetles communities in three habitat types (remnant woodland patches, farmland and their edges) and during two seasons.

Whilst the paper is generally well-written and clearly falls within the remit of Biodiversity and conservation, there are some points relating to structure but also important at a fundamental level and that have to be clarified or fixed when preparing any other version.

My comments are as follow.

RESPONSE TO REVIEWER #2 COMMENT:

We thank Reviewer 2 for acknowledging the suitability of our study for Biodiversity and Conservation, and for raising many points for improvement. We have addressed all of the reviewer's recommendations above in the following comments.

SPECIFIC COMMENT (19):

First, using the term landscape in your title seems unjustified since you do not consider the effect of the landscape in your study. Actually, the objectives of your study were to examine the relationships between vegetation structure and the diversity and composition of beetles communities, and the variation of these relationships in three habitat types (remnant woodland patches, farmland and their edges) and during two seasons. It's not to detract from the study but just be clear about what you are actually testing. You should be accurate and concise about the objectives of your study.

RESPONSE TO SPECIFIC COMMENT (19):

We agree with the reviewer that our study does not explicitly examine landscape level effects in its analyses. Our title was intended to simply states the context of the study, i.e. conducted within a farming landscape that has a history of fragmentation and agricultural intensification in its land use change. To clarify this, we have added new text to explain the nature of the landscape in our study area i.e. in Lines 139-144 of the

“Study site” paragraph: “ ... Our study area is characteristic of highly cleared farming landscapes in southern Australia, where remnant native vegetation is at risk from additional clearing and further agricultural intensification. These kinds of fragmented landscapes occur in other parts of world such as South America, eastern Europe, and Asia (Uchida et al. 2016). However, the impact of land-use changes on biodiversity is less understood in these regions compared to Northern America, and Northern and Western Europe (Sutcliffe et al. 2015; Uchida et al. 2016) ...”.

We have not altered the title of the manuscript (“Dynamic effects of ground-layer plant communities on beetles in a fragmented farming landscape”), because we think that having a reference to the study location provides a more contextual title on first glance (compared to perhaps “Dynamic effects of ground-layer plant communities on beetles”). However, we would be more than happy to reconsider the title of the paper if the Editor believed that a change is warranted.

SPECIFIC COMMENT (20):

The data of beetles are taken to be abundances, but it is well-known that pitfalls do not trap species equally efficiently and are affected by vegetation and the movement of species over the soil surface. The data are in fact activity-densities, not abundances. The effects of the vegetation structure and the trappability cannot be properly disentangled. So, the analysis of the vegetation effects on the activity density in each habitat should be interpreted with much caution, and arguments have to be put forward to justify the conclusion.

RESPONSE TO SPECIFIC COMMENT (20):

We agree with the reviewer on the known limitations of pitfall trap data. We have added the following text in the “Beetle sampling” section to mention this caveat: “We recognize that data from pitfall traps represent a compound measure of abundance, surface activity and species trappability, which may be habitat-dependent (Greenslade 1964; Woodcock 2007). For example, under-sampling of flight-dispersing individuals or specialist feeders restricted to host plants may influence findings for some groups. Nonetheless, pitfall traps provide a consistent and efficient sampling method of studying assemblage differences when results are interpreted carefully (Greenslade 1964; Woodcock 2007). The objective of our study was not to sample all species, but to compare assemblages between treatments for relatively common species. Using drift fences and leaving traps open for two weeks in our study was employed to increase the efficiency of captures (Duelli 1997; Weibull et al. 2003)”.

We have also revised our text to use the term “activity-density” instead of “abundance” throughout the manuscript.

In addition, we have added caveats on data interpretation in relevant parts of the discussion i.e. Lines 393-395: “It should be noted that these results are affected by limitations of pitfall traps and may, for example, reflect seasonal turnover or movement of beetle species, or reduced species trappability in patches”.

SPECIFIC COMMENT (21):

Furthermore, the number of individuals collected with pitfalls can influence the species richness analysis. To ensure that the difference in species richness detected, or not, is not due to the difference in the number of individuals captured, a rarefaction analysis should be performed.

RESPONSE TO SPECIFIC COMMENT (21):

To address this comment, we have conducted an exploratory rarefaction analysis for our pitfall data across the three habitat types. This provides some information about assemblage richness and heterogeneity among the different habitats in our study. The rarefaction curves as now provided in the Supplementary material (i.e. Fig. A3). The rarefaction curves show that the number of species does not converge to an asymptote for all habitats, which is not surprising and probably unavoidable in this landscape (where we expect a high number of rare species in respective habitats e.g. high proportion of edge specialists).

Note that we have not included rarefaction in our actual analysis because further modeling of species richness to adjust for detection rates (e.g. using Chao1 and other

diversity measures) did not change our results substantially, and is actually problematic to apply in situations where there are a high proportion of rare species. Rather, the spatial structure of our study design (paired farmland & woodland across their edge) allows us to compare differences in the beetle assemblage between the habitat types, where using standardized sampling effort via pitfall traps is appropriate for our research aims.

Fig. A3. Sample-based rarefaction curves comparing beetle species richness between the remnant patch, farmland and their edges. Sample-based rarefaction curves were computed to preserve the data's spatial structure (Gotelli & Colwell, 2011).

[in doc attachment]

SPECIFIC COMMENT (22):

I've a concern about the non-consideration of the variation intra-farmlands (i.e. your mixed farm fields) in your analysis. Indeed, this variation within the farmlands could certainly result in varying environmental conditions within the same plots and therefore in the composition of different beetle communities.

RESPONSE TO SPECIFIC COMMENT (22):

Note that this issue was also raised by Reviewer #1, and is addressed in detail in our Response to specific comment (10). We confirm that most of the habitat structural and species compositional differences (for plant and beetles) among landscape elements (i.e. different land-uses) in our study region are indeed represented by habitat contrasts between the remnant woodland patches and farmlands, rather than by differences among the subtypes of farmlands. In particular, mature woodland trees and shrubs and a higher diversity of native ground cover species occur in woodland patches, while these have been cleared in farmlands.

The strong differences in between woodland patches and farmlands are now more clearly mentioned in our manuscript in Lines 149-152 ("Farmland and patches differed strongly structurally and floristically, and showed significantly different composition of beetle species (Ng et al. 2017; see also Fig. A2). ...". Significant differences between woodland patches and farmlands are supported by pairwise comparisons of beetle compositional dissimilarity (Bray-Curtis) between different land-uses, based on permutational multivariate analysis of variance (PERMANOVA) (examined in Ng et al 2017, Ecosphere). See also Response to comment (10), which provides more detail on these differences.

SPECIFIC COMMENT (23):

The relationships between the species composition of beetle communities and some vegetation attributes have been examined. The effect of some attributes has proven more significant than others. However, it is unclear how the effect of this or that variable occurs at the level of beetle communities (as an example, you mention in line 241 that "Trophic groups showed mixed responses to plant composition and vegetation structure", but you don't explain how these vegetation components affect these beetles composition). Something that could be driven from the design by analysing the autecological information on the species (or by group/ family of species) the dataset contains. So, I'm really wondering about the accuracy and usefulness of your approach. I would suggest removing it and concentrating on the autecological information on the species (by group/ family).

RESPONSE TO SPECIFIC COMMENT (23):

To address this comment, we have improved the focus of the results by emphasizing the vegetation effects on the different autoecological (trophic group) information for beetle species composition more clearly (this intent was not apparent in how this text was initially written) in this paragraph. We have also focused on significant effects of vegetation in this paragraph to simplify the "Results" section. So Line 259+ (previously Line 241+) now reads as follows: "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 ... More similar plant species composition was significantly correlated with more similar herbivore species composition in edges ...".

On a related issue, we have improved the presentation of the “Results” section by simplifying and reordering text, as well as improving emphasis on the results for trophic groups in most cases; this is described in detail in our Response to specific comments (43) and (44).

SPECIFIC COMMENT (24):

Abstract

L25 replace "quantified" by "examined"

L27 "from" by "in"

RESPONSE TO SPECIFIC COMMENT (24):

Both suggestions above have been applied.

SPECIFIC COMMENT (25):

L32 change "significantly affected beetle abundance" by "significantly and positively affected beetle activity-density"

RESPONSE TO SPECIFIC COMMENT (25):

Done.

SPECIFIC COMMENT (26):

L36-38 the question here is : should we develop strategies with the global objective of biodiversity conservation, or to conserve some beetle groups for the services they provided (eg. Predators for pest biological control, or detritivores for nutrient cycling)? And are the biodiversity conservation strategy and that targeting the conservation of this or that species group for the service they provide, are compatible goals?

RESPONSE TO SPECIFIC COMMENT (26):

We thank the reviewer for raising this very interesting point. In this paper, we have intended to assess the beetle community and diversity for the overall group and for each trophic groups in an objective manner, without necessarily recommending the conservation of one group over the other. This is because land managers may have different priorities depending on their specific conservation goals. Indeed, there are often asymmetries between management for biodiversity and ecosystem services, although synergies exist between the two (Macfadyen et al. 2012 Journal of Applied Ecology). In areas such as farmlands where there is also the need to improve productivity, increased diversity of herbivorous insects, for example, may be deemed as unacceptable if it leads to increased herbivory of cultivated crops. More fieldwork is also needed to infer actual impact on ecosystem services of activity-density and species richness differences in our study landscape (e.g. whether increased natural enemies have a discernible impact in suppressing crop pests; e.g. Zalucki et al 2014 Insect Science; Macfadyen et al 2014 Insect Science).

Given that the issue of compatibility of conservation goals for different arthropod groups is outside of the scope of this paper, we have not altered the Abstract Lines 36-38, which currently reads as follows: "...management that promotes plant richness at edges, and promotes herbaceous cover during summer, can support beetle diversity. Conserving ground cover in all habitats may improve activity-density of all beetle trophic groups. ...".

SPECIFIC COMMENT (27):

L51 replace "for arthropod biodiversity" by "for conserving arthropod biodiversity"

L61 change "distinct associations between vegetation and arthropod communities" by "distinct plant-arthropod relationships"

L66 delete "which might otherwise be masked at broader scales"

L98 "across a fragmented mixed-farming landscape" by "within a fragmented mixed-farming landscape"

L106 "and that of trophic groups" for "and trophic groups"

RESPONSE TO SPECIFIC COMMENT (27):

These five suggested changes have been applied.

SPECIFIC COMMENT (28):

L110-118 there is some redundancy and also a contradiction in your first and second predictions since you firstly expected a strong effect of plant species composition on overall beetle assemblages and just below you expect predators to be generally more influenced by vegetation structure than plant species richness and composition. More precision is need here. I suggest removing the first prediction that is, in my opinion, generalist. Actually, it is wiser to look at things in detail, namely for each group distinguishing predators and herbivores. In addition, you should precise the direction of the effects you expect, are they positive or negative? How you expect the plant compositions change beetle assemblages?

RESPONSE TO SPECIFIC COMMENT (28):

To address this comment, we have modified the ordering of the predictions (focusing on trophic groups more broadly first, then by habitat, then by time), and altered the text to remove the contradictory statement. Where it is supported by the literature, we have added the direction of effects (positive/negative) as suggested by the reviewer.

Note that we have not focused solely on the trophic groups throughout the “predictions” text because we expect complex interactive effects of habitat and season. In many cases, trophic-level specific predictions are either not known or contradictory (having both positive and negative effects) in the literature. The first part of the predictions paragraphs has now been modified to the following:

“In general, we expected predators to be more positively influenced by vegetation structure than plant species richness and composition, while herbivores would be more positively influenced by plant species richness or composition than vegetation structure (Prediction I; Fig. 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 effect of biodiversity (Perner et al. 2005; Schaffers et al. 2008; Siemann 1998).

In certain habitats, however, we expected stronger effects of plant species composition on beetle assemblages compared to other vegetation attributes (Prediction II; Fig. 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). ... ”

SPECIFIC COMMENT (29):

L118 "bottom-up effect of biodiversity" for "bottom-up approach of biodiversity"

L123 : replace « In contrast » by « however » ; you give the impression of an opposite understanding of the « resource concentration hypothesis »

RESPONSE TO SPECIFIC COMMENT (29):

These two suggested changes have been applied.

SPECIFIC COMMENT (30):

Materials and methods

L131 "highly fragmented and mixed cropping-grazing landscape" for "highly fragmented mixed cropping-grazing landscape"

RESPONSE TO SPECIFIC COMMENT (30):

Done.

SPECIFIC COMMENT (31):

L149- 157 I think this paragraph may be better in the "beetle sampling" sub-heading.

RESPONSE TO SPECIFIC COMMENT (31):

We have moved this paragraph to the “beetle sampling” section as suggested.

SPECIFIC COMMENT (32):

L167-168 can you give more details?

RESPONSE TO SPECIFIC COMMENT (32):

Exampled provided. The Line now reads as follows: “Where specimens could not be identified to species, measures of activity-density and richness corresponded to

morphospecies (e.g. Carabidae sp. 1, Carabidae sp. 2, etc.; sensu Oliver and Beattie 1996)”

SPECIFIC COMMENT (33):

L174 delete "and"

RESPONSE TO SPECIFIC COMMENT (33):

Done.

SPECIFIC COMMENT (34):

L172-177 "Plant surveys" section deserve to be more detailed

In table 1, cover percentage and the height were presented in cumuli for the total herbaceous and not by species groups as announced? In addition, it is mentioned that plant composition was recorded using five quadrats. What about the other variables? Why the "bare soil" was not taken into account in your work? Several authors have emphasized the importance of this variable on the ground beetle communities (eg. Brose,2003 and Rouabah et al. 2015 you cited).

RESPONSE TO SPECIFIC COMMENT (34):

To address this comment, we have updated Table 1 with the underlying vegetation data that contributes towards total herbaceous cover (this was previously missing and thus causing confusion). We clarify that the other structural variables were measured “within a 20 × 10 m plot centred around the sampling location” (now in Line 192, previously Line 175).

In our study we have actually sampled a number of vegetation structural variables, including bare soil. We will be making raw data available, including details on all vegetation variables for the study, via the CSIRO Data Portal upon acceptance of the manuscript (attached in Excel format in this response for the reviewer). During preliminary analyses, we have included bare soil and a number of other structural variables that are expected to be ecologically meaningful, but found that in our study landscape there was no significant influence of bare soil on the assemblage of overall beetles and their trophic groups. To ensure enough statistical power in the data during the final analysis, we have simplified the models by fitting a parsimoniously small number (<4) of explanatory variables, and omitted variables with non-significant effects.

SPECIFIC COMMENT (35):

Statistical analyses

There are some redundancies in the statistic analysis section, especially between the introductory paragraph and the sub parts, which introduces confusions. This part should be simplified by well explaining what was done, and justifying the choice of analysis and variables introduced in each of these analysis.

RESPONSE TO SPECIFIC COMMENT (35):

We have included additional background text at the start of the “Statistical analyses” section to explain the reasoning behind the use of the three different analytical methods. This includes explaining differences between multivariate and univariate data types in our study that are supported in some methods but not others. This is why the text appears repetitious in the statistical analyses and its subheadings.

To address this comment, we have reduced the length of overall text after locating a couple of avoidable repetitions (i.e. repeating analyses over spring and summer data could be summarized at the start in Line 201, rather than within each subheading; and by simplifying and reducing the length of the introductory text even further).

SPECIFIC COMMENT (36):

L180 replace "respectively" by "to the vegetation attributes"

L181 delete "For all approaches"

L183 replace "approaches" by "analysis"

RESPONSE TO SPECIFIC COMMENT (36):

These three suggestions have been applied.

SPECIFIC COMMENT (37):

L184 how this geographic proximity was obtained? Why does it only appear now?

RESPONSE TO SPECIFIC COMMENT (37):

Geographic distance between samples was calculated using Euclidean distances between sites. This point is detailed in Line 217: "geographic distances were based on Euclidean distances between sites", where this is possible because latitude/longitude information for each site was recorded using a GPS (mentioned in Line 212). To avoid confusion, we have removed mention of "geographic proximity" too early in the "Statistical analyses" section.

Geographic distance is a commonly used site-level predictor for MRM analysis, and is used here to control for (smaller scale) spatial effects, comparable to the use of habitat type in the CCA and GLMM analyses. Unfortunately, it is not technically possible to use habitat type as a predictor in the MRM analysis. This is due to inherent differences in the data type used in our study. To clarify this limitation, we have amended text in Lines 201-204: "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 treatment, and (2) plant species richness and plant species composition are intrinsically correlated (and is thus not typically examined concurrently) ..."; Lines 210-212: "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 (geographic distance is used instead of habitat type because the latter is not a suitable data type for MRM)"; Lines 220: "Controlling for geographic distance allowed us to compare vegetation effects after having accounted for spatial autocorrelation".

SPECIFIC COMMENT (38):

L190-191 why not transform (in $\log/\log(x+1)$) your beetles data?

RESPONSE TO SPECIFIC COMMENT (38):

Unfortunately, we could not successfully fit our multivariate models using beetle activity-density/abundance data, this issue was also the case for log transformed activity-density/abundance data.

SPECIFIC COMMENT (39):

L196-197 again, why not value data of vegetation by plant species group?

RESPONSE TO SPECIFIC COMMENT (39):

We have used total herbaceous cover, rather than the component vegetation groups because total herbaceous cover is a useful measure of total vegetation's productive biomass and groundlayer structural complexity (rather than considering the influence native vs exotic grasses, native vs exotic forbs separately, for example). To make this point clearer, we have updated Line 213 (previously Line 196) to the following: "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, which are collectively a useful measure of structural complexity; Table 1) ...".

SPECIFIC COMMENT (40):

L219 It is well-known that pitfalls do not trap species equally efficiently and are affected by vegetation and the movement of species over the soil surface. Beetles data should than taken to be activity-densities, not abundances. This is valid for the rest of the manuscript

RESPONSE TO SPECIFIC COMMENT (40):

We are aware that all sampling methods have their biases, including pitfall trapping of insects. In this revision, we have now acknowledged the caveats of the pitfall trapping method (this is addressed in detail in Response to specific comment (20)), and have revised text to use the term "activity-density" instead of "abundance" throughout the manuscript.

SPECIFIC COMMENT (41):

Results

I find your results interesting, but deserve to be better exploited, both in terms of

statistical analysis and presentation. Indeed, and just as an example of the effect of the plant composition and vegetation structure on beetle composition, you mention that vegetation structure, and geographic distance were generally able to predict overall beetle composition, but you do not tell us how? The same shall apply to the effects of plant richness and vegetation structure on beetle composition.

Unlike the effects on the species richness and the activity-density of beetles, where you presented where the effects of vegetation attributes were positive or negative, in no case you tell us how these attributes affect the composition of beetle assemblages. You're just telling us that such or such vegetation attributes better predicts this beetle composition (which is insufficient to understand the effects of vegetation on beetle communities), but we do not know how the effect of these vegetation attributes was reflected on the species composition of beetle communities? I urge you to well examine these relationships.

RESPONSE TO SPECIFIC COMMENT (41):

To address this comment, we have modified the "Results" section to provide the specific nature of the relationships. We have added more detail for the MRM-based results: i.e. Line 255 "... i.e. more similar plant communities displayed more similar beetle communities than contrasted vegetation structure"; Lines 260 "In particular, more similar plant species composition was significantly correlated with more similar detritivore species composition in edges during spring and summer ...", Line 269 "Overall beetle species composition became more dissimilar as geographic distance between samples increased in edges ...", and others.

For the GLMM results, we have added the direction of responses where they were missing i.e. Lines 301-303 "... litter cover had significant positive effects on detritivore activity-density in edges, but effects were negative in farmland ($P < 0.001$). During summer, vegetation height had significant negative effects on predator activity-density in patches ($P = 0.004$)".

SPECIFIC COMMENT (42):

In addition, a rarefaction analysis should be performed to ensure that the difference in species richness obtained is not due to the difference in the number of individuals captured

RESPONSE TO SPECIFIC COMMENT (42):

We have provided a rarefaction analysis also requested by the Reviewer in Comment (21). The rarefaction curves are now in the Supplementary material (i.e. Fig. A3) and provide some information about richness and variability in assemblages sampled from the different habitats in our study, which could be used when interpreting our results. We have also provided more detail on this issue in Response to specific comment (21).

SPECIFIC COMMENT (43):

In terms of presentation, it is important to follow the same pattern so that the reader can better follow. Since your objective is to show the variation of beetle responses (in general and by species group) to the effects of vegetation between the three habitats and during the two seasons sampled, I suggest to present the results of beetles in general then by trophic group showing each time the variations obtained between habitats and that between seasons for the different variables tested.

RESPONSE TO SPECIFIC COMMENT (43):

To address this comment, we have reviewed and modified text in the "Results" section to ensure that the flow of results start with the overall beetles followed by trophic groups. Results for different categories (e.g. by season) were presented together where possible. We have also amended the ordering of the CCA and Partial CCA results to improve readability ("Effects of plant richness and vegetation structure on beetle species composition" section). Lastly, we have reduced text substantially by focusing on significant results and omitting non-significant and low priority results that were not related to the study's focus.

SPECIFIC COMMENT (44):

It was hard to follow your way of presenting the results, I really struggled with this section.

Your tables are too long and not clear (particularly table3), you have to make choices. I

am not sure that everything must be presented.

RESPONSE TO SPECIFIC COMMENT (44):

This comment has been addressed by revisions applied as part of our Response to specific comment (43) (where we have made substantial changes in the “Results” section to improve its readability) and Response to specific comment (41) (where we have described the specific nature of the relationships more clearly). We believe that these changes have helped make the “Results” section much easier to follow and link back to the main result tables. To improve the readability and typesetting for the manuscript, we have already simplified Table 3 to omit results for total species richness and total abundance (also mentioned in Response to specific comment (66)). Additional results relating to Table 3 are available in the Supplementary material (Tables A4, A5, A6). We are, however, hesitant in showing only a subset of results for certain trophic groups in our key tables. This is because this study aims to examine the diversity and composition of each trophic groups in an objective manner, without necessarily recommending the conservation of one group over the other (this point is discussed in our Response to specific comment (26)).

SPECIFIC COMMENT (45):

L232 which online resources?

RESPONSE TO SPECIFIC COMMENT (45):

Online resources refer to the Supplementary Material, and will be linked in the final manuscript. The term “online resource/s” follows the journal’s preferred format, for example “Online resource: Table A2”.

SPECIFIC COMMENT (46):

L248 "We found significant positive correlations between geographic distance and overall beetle composition dissimilarity." What does this mean? In addition, I still not understand how the geographic distance was obtained?

RESPONSE TO SPECIFIC COMMENT (46):

We have modified this line to describe the results more directly. This Line is now as follows (now Line 269): “Overall beetle species composition became more dissimilar as geographic distance between samples increased in edges, ...”.

Our Response to specific comment (37) describes in detail the improvements we have made to explain the method and reasoning behind the use of geographic distance. In particular, geographic proximity among sites was obtained using ordinary Euclidean trigonometry (detailed in Line 217: “geographic distances were based on Euclidean distances between sites”), where this is possible because latitude/longitude information for each site was recorded using a GPS (mentioned in Line 212). This point, and other related background information on geographic distance are detailed in our Response to specific comment (37).

SPECIFIC COMMENT (47):

L252 effects of plant richness and vegetation structure on beetle composition: how these effects were reflected on the species composition of beetle communities? You most certainly examined these effects on group/ family of species!

RESPONSE TO SPECIFIC COMMENT (47):

We confirm that the intent of this results section (heading titled “Effects of plant richness and vegetation structure on beetle composition”) is indeed to reflect the effect of plant species richness and vegetation structure on beetle species composition (based on univariate-multivariate CCA analyses described in the corresponding methods section “Effects of plant richness and vegetation structure (univariate) on beetle composition (multivariate)”.

To make it clearer that the initially used term “beetle composition” refers to the species composition of beetles, we have amended relevant lines to clearly state this, i.e. Lines 252: “MRM models incorporating plant compositional dissimilarity, vegetation structure, and geographic distance were generally able to predict the species composition of the overall beetle community”, and Lines 259-260: “The species composition of beetle trophic groups showed mixed responses to plant species composition and vegetation

structure ... ". To reduce ambiguity, we have also modified the manuscript to refer to "species composition" throughout the manuscript rather than just "composition".

SPECIFIC COMMENT (48):

Don't forget to specify in the title of the fig.2 that "+" is for edges, "o" is for patches, and "▲" is for farmlands.

RESPONSE TO SPECIFIC COMMENT (48):

We have edited the caption of fig. 2 (Line 688) to add this following text: "(habitat types are: o = patch, + = farmland, = ▲edge)".

SPECIFIC COMMENT (49):

L253 you mean between (and not among) habitat types?

RESPONSE TO SPECIFIC COMMENT (49):

We have updated the text to use "between" (now Line 274).

SPECIFIC COMMENT (50):

L256 delete ' :'

RESPONSE TO SPECIFIC COMMENT (50):

Done.

SPECIFIC COMMENT (51):

272-274 revise sentence (too long and incomprehensible). In addition, it contradicts what you announced in the sentence before.

RESPONSE TO SPECIFIC COMMENT (51):

We have revised this sentence so that it is clearer. The revised text now reads: "During summer, litter cover had significant positive effects on detritivore activity-density in edges, but effects were negative in farmland ($P < 0.001$). During summer, vegetation height had significant negative effects on predator activity-density in patches ($P = 0.004$) (Table 3)".

SPECIFIC COMMENT (52):

Discussion

I found the discussion difficult to read in places. Some paragraphs are not clear, with some contradictions, and should be revised and clarified. I would strongly encourage the authors to examine this closely and perhaps get assistance from colleague(s).

RESPONSE TO SPECIFIC COMMENT (52):

We have carefully revised all text in the "Discussion" where sentences were unclear. These include most of the paragraph Lines 376-395, and we have simplified and reduced the length of sentences in several parts of the two sections: "Stronger influence of plant composition on beetle composition than vegetation structure" and "Spatially and temporally dynamic vegetation effects on beetles". We have also added a section subheading "Effects of geographic distance on beetle species composition" to improve the structure of the Discussion.

SPECIFIC COMMENT (53):

L312 delete 'selection'

RESPONSE TO SPECIFIC COMMENT (53):

Done.

SPECIFIC COMMENT (54):

L314 I prefer "cropped and non cropped habitats" to "managed and natural habitats"

RESPONSE TO SPECIFIC COMMENT (54):

We have revised the text to use uncropped (i.e. natural) and cropped habitats.

SPECIFIC COMMENT (55):

L338-340 this sentence seems incomplete and doesn't make sense. Please formulate differently

RESPONSE TO SPECIFIC COMMENT (55):

We have revised this sentence to now read: “The effects of plant diversity and vegetation structure on arthropod abundance may, however, be auto-correlated (Lassau et al. 2005; Perner et al. 2005).”

SPECIFIC COMMENT (56):

L349-363 it is difficult to follow you, Can you clarify? Make short sentences

RESPONSE TO SPECIFIC COMMENT (56):

We have modified these lines and it now reads as follows (Lines 376-395): “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 patterns that are consistent with the “natural enemies” hypothesis in farmland during summer, i.e. greater predator activity-density in more species-rich vegetation and greater herbivore activity-density in species-poor vegetation. The “resource concentration” hypothesis also appeared to be supported but only in patches of native vegetation, where higher herbivore activity-density occurred in more species-poor sites and there were no effects of plant richness on predator diversity (Table 3). These contradictory findings highlight dependence of plant-arthropod relationships on habitat context, particularly the influence of more complex associations in mature forest or woodland ecosystems (Zou et al. 2013). The first pattern of increasing predator activity-density with increasing plant richness in farmland suggests that productive farmland can provide seasonal refuge from predation (enemy-free space hypothesis; Brose 2003) as well as provide stable prey resources for predatory beetles. Such positive effects of plant richness on predator activity-density are typically associated with top-down control processes in agricultural ecosystems (Zou et al. 2013), which are also linked to negative effects on herbivore activity-density (Joern and Laws 2013; Koricheva et al. 2000; Tews et al. 2004). The second pattern of decreasing herbivore activity-density with increasing plant richness in remnant patches may be due to it being more challenging for woodland specialist beetles to locate host plants (Agrawal et al. 2006; Root 1973), and/or increased predation risks on beetles (hunting efficiency hypothesis; Brose 2003) by patch-associated predators (e.g. birds). It should be noted that these results are affected by limitations of pitfall traps and may, for example, reflect seasonal turnover or movement of beetle species, or reduced species trappability in patches”.

SPECIFIC COMMENT (57):

L370-372 can you give examples of these changes in host plant use by beetles of different lifecycle stages? I would add the effect of the temporal evolution in the composition of communities (as species arrive and others leave these communities), an effect that you can explore using your results.

RESPONSE TO SPECIFIC COMMENT (57):

We have revised the text to now read (now Lines 402-404): “Pronounced seasonal and habitat effects on beetle-plant relationships can be explained by a combination of changes in plant host use at different stages of beetle lifecycles (e.g. different specialised diets between the larvae and adult form), ...”.

We have added text in the same paragraph to mention temporal turnover, Lines 410-412: “These dynamic patterns are also expected to be influenced by seasonal turnover of beetle species composition across the different habitats, which may be associated with plant species turnover across the seasons (Ng et al. 2017b)”. Here, we have referred to a previous paper (Ng et al 2017 Ecosphere), which found strong turnover of beetle communities over time and between habitats in the same study landscape.

Unfortunately, we do not have adequate data (i.e. no larvae data and inadequate species-level data for robust statistical analyses) to identify specific host plant use at different lifecycle stages.

SPECIFIC COMMENT (58):

L375-377 are you speaking about plants in edge (or patches) in comparing with the farmland?

RESPONSE TO SPECIFIC COMMENT (58):

We meant comparing between spring and summer in the first part, and then comparing between edges and interior of farmlands/woodlands in the second part. We have updated the relevant sentences in this paragraph to improve clarity (now Lines 407-414): “We suggest that some 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 (compared to spring when vegetation is at peak growth and prior to crop harvest). ... Field edges may provide temporally stable foraging and nesting sites for many beetles due to low disturbance and cross-habitat mixing of woodland and agrestal plants ...”

SPECIFIC COMMENT (59):

L380 which geographic factors?

RESPONSE TO SPECIFIC COMMENT (59):

We had corrected this text to say “vegetation variables” rather than “geographic factors”.

SPECIFIC COMMENT (60):

L392-398 it is difficult to follow you, Can you clarify? You speak about significant effects of the plant composition on the composition of the herbivorous in the edge (an effect that you do not tell us how it was reflected on the composition of beetle communities), then you try to explain these effects by the positive relationship between plant species richness and the abundance of these herbivores!

RESPONSE TO SPECIFIC COMMENT (60):

We have simplified this text by removing the previous interpretation, and instead, suggested simply the possible relationship between edge-dependent species of plants and herbivorous beetles in explaining the significant association between herbivore species composition and plant species composition at edges. This Line (now Line 427-430) has been modified to the following: “...significant correlations between plant species composition and herbivore species composition in edges suggest that a high proportion of herbivorous beetles may be attracted to plant species that are largely limited to habitat edges (e.g. *Erodium crinitum*, *Salsola australis*, and *Sisymbrium* sp.)”.

Note that the specific nature of species composition relationships are described in our Response to specific comment (41) i.e. “more similar plant species composition was significantly correlated with more similar herbivore species composition”).

SPECIFIC COMMENT (61):

L407 change "Like plant composition, vegetation structure and plant richness on beetle" by "Like plant composition, effects of vegetation structure and plant richness on beetle"

RESPONSE TO SPECIFIC COMMENT (61):

Done.

SPECIFIC COMMENT (62):

L410-413: I fully agree, but how? Given your results, what you suggest as conservation strategies to enhance predator diversity and/or abundance considering that this is what could improve pest biological control in farmlands?

RESPONSE TO SPECIFIC COMMENT (62):

We have added a text in this paragraph to be better linked to subsequent three paragraphs in this section (“Plant species richness and vegetation structure”). The three following paragraphs were intended to provide specific examples of conservation strategies, specific to the different taxonomic groups, spatial and temporal levels mentioned. The relevant text in the paragraph now reads as follows: “Our findings suggest that manipulating vegetation structure for beetle conservation needs 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. Here, we discussed relationships between plant species richness or vegetation structure and different beetle trophic groups shown in our data, while a

summary of management recommendations are provided in the following section”.

We have decided to apply the guiding text above, rather than repeating similar text in different sections of the manuscript.

SPECIFIC COMMENT (63):

L422-427 there is a contradiction in what you are saying here about the fact that vegetation height could impede species movements in summer but not in spring. And here I would like to remind you that pitfall do not trap species equally efficiently and are affected by vegetation and the movement of species (we are measuring activity-density and not abundance). Thus the interpretations need to be reviewed throughout the manuscript.

RESPONSE TO SPECIFIC COMMENT (63):

We agree with the reviewer on the known limitations of pitfall trap data. We have modified the text to remove the contradiction, so the text now reads as follows in Lines 460-464: “... However, we found negative effects of vegetation height on predator activity-density in remnant patches during summer (Table 3). This suggests a possible influence of other environmental or biotic factors (Siemann et al. 1998; Zou et al. 2013), and/or pitfall sampling effects on predator activity-density in more complex woodland ecosystems (e.g. dormant species not sampled; Greenslade 1964; Woodcock 2007)”.

We have dealt with the limitations of pitfall sampling in our other responses to previous comments (i.e. see Response to specific comments (20)).

SPECIFIC COMMENT (64):

L457-459 I think that you can answer part of this question by making better use of the results obtained in this good work.

RESPONSE TO SPECIFIC COMMENT (64):

We had intended to say the following, also amended in revised manuscript (now Lines 496-498): “However, more species-level data ... are needed to determine how different species use vegetation resources across the landscape at different times of the year ...” because there is unfortunately not enough statistical power for most of our species-level data to determine the use of vegetation resources by beetles in our study.

SPECIFIC COMMENT (65):

Supplementary Material

I think the paragraph detailing the results of CCA analysis may be better in the "results" section

RESPONSE TO SPECIFIC COMMENT (65):

To address this comment, we have moved the detailed CCA results from the Supplementary Material to the main manuscript, and also edited the overall text to improve readability (“Effects of plant richness and vegetation structure on beetle species composition” results section).

SPECIFIC COMMENT (66):

I do not understand why you have presented results of the GLM on the total abundance and species richness (Table A4) separately from those by trophic groups (in table3).

RESPONSE TO SPECIFIC COMMENT (66):

This is to reduce the length of Table 3 to simplify its readability and typesetting for the manuscript. We have considered the reviewer’s comment again and decided that, given that total species richness and total abundance forms a secondary result for GLM, these results are more suitable kept in the Supplementary material.

[Click here to view linked References](#)

Ng et al.

Plant-beetle relationships

1 *Submission of Original Research Paper for Biodiversity and Conservation*

2 **Title:** Dynamic effects of ground-layer plant communities on beetles in a fragmented
3 farming landscape

4
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16 **Running title:** Plant-beetle relationships

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19 *legends (167, 3 tables); Figure legends (151, 3 figures)*

20

Abstract

Vegetation effects on arthropods are well recognized, but it is unclear how different vegetation attributes might influence arthropod assemblages across mixed-agricultural landscapes. Understanding how plant communities influence arthropods under different habitat and seasonal contexts can identify vegetation management options for arthropod biodiversity. We examined relationships between vegetation structure, plant species richness and plant species composition, and the diversity and composition of beetles in 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, activity-density 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-harvest in summer. Plant composition better predicted beetle composition than vegetation structure. Both plant richness and vegetation structure significantly and positively affected beetle activity-density. 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 maximize 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 ground cover in all habitats may improve activity-density 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 conserving arthropod biodiversity.

It is unclear how specific attributes of vegetation communities might influence arthropod assemblages across human-modified landscapes, such as mixed-farming landscapes that include crop-pasture rotation (Bell and Moore 2012). 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 previously been 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 characterize human-modified landscapes. Some agro-ecological studies, however, have found distinct plant-arthropod relationships 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.

67 Three attributes are often used to characterize plant communities and their effects on arthropod
68 assemblages: vegetation structure, plant species richness, and plant species composition, with the former two
69 attributes more commonly used in fauna studies (Schaffers et al. 2008). Vegetation structure – the physical
70 architecture of plant communities such as tree canopy and grass cover – directly influences the survival and
71 persistence of arthropod populations by providing microhabitats (e.g. ovipositioning or shelter sites) or
72 altering microclimatic conditions, and indirectly by modifying individual behaviour (e.g. altered movement
73 through different vegetation densities) or species interactions (e.g. hunting efficiency) (Brose 2003; Landis et
74 al. 2005; Siemann 1998). Positive correlations between vegetation-driven structural complexity and animal
75 diversity are well documented in many studies, although contradictory results have been found for some
76 taxonomic groups (Joern and Laws 2013; Tews et al. 2004), including carabid beetles (Brose 2003).

77 Plant species richness is a second commonly used vegetation attribute which represents a diversity of
78 available resources (Perner et al. 2005). Many studies have found positive relationships between plant
79 diversity and the diversity of consumer assemblages (Agrawal et al. 2006; Perner et al. 2005; Siemann 1998;
80 Siemann et al. 1999). Previous empirical studies have, however, yielded contrasting results (Agrawal et al.
81 2006; Perner et al. 2005; Siemann 1998). Inconsistencies in correlations between plant diversity and
82 arthropod activity-density have been linked to site-specific factors such as abiotic conditions, disturbance and
83 productivity (Perner et al. 2005).

84 Individual plant species or combinations of species can provide direct food or habitat resources for
85 many arthropod species (Perner et al. 2005; Schaffers et al. 2008; Siemann 1998). Yet, many studies on
86 plant-arthropod relationships have overlooked plant species composition (Joern and Laws 2013; Schaffers et
87 al. 2008). This is likely due to structural attributes being easier to observe in the field by researchers without
88 specialized botanical expertise (Schaffers et al. 2008). Often community studies can access the resources and
89 expertise to focus on only one taxonomic group in detail (i.e. plants *or* invertebrates), with plant species
90 identity considered mainly in work on host plant specialists. Relatively few studies that explicitly analysed
91 plant species composition have identified that plant species composition as a better predictor of arthropod

92 assemblages than vegetation structure and other environmental factors like habitat type (Nyafwono et al.
93 2015; Perner et al. 2005; Schaffers et al. 2008). From a theoretical perspective, this is unsurprising given that
94 plant species composition not only forms the basis of structural characteristics of vegetation communities,
95 but also incorporates other indirect biotic and abiotic influences on arthropod assemblages (Joern and Laws
96 2013; Schaffers et al. 2008).

97 Using a split-plot study design with repeated measures, we quantified relationships between three
98 vegetation attributes (vegetation structure, plant species richness, plant species composition) and the diversity
99 and species composition of beetles (including their trophic groups) among three habitat types within a
100 fragmented mixed-farming landscape. The habitat types were remnant woodland patches, adjacent farmland,
101 and their edges, which we sampled during two distinct periods of the farming cycle (spring and summer). We
102 focused on beetles because they are sensitive to small-scale environmental changes (Gibb and Cunningham
103 2010) and are functionally diverse, with different trophic groups providing distinct ecological functions such
104 as pest control (predators), nutrient cycling (detritivores), and weed control (herbivores) (Grimbacher et al.
105 2006; Landis et al. 2000). Previously, we found that the composition and diversity of beetle assemblages
106 responded strongly to habitat type (Ng et al. 2017). Here, we further examined whether responses of overall
107 beetle assemblages and that of trophic groups were mediated by within-habitat vegetation attributes. Our
108 research questions were: (1) What is the relative importance of plant species richness, vegetation structure
109 and plant species composition in explaining beetle species richness, activity-density and species
110 composition? (2) How do plant-beetle relationships vary between the different habitats (woodland patch,
111 farmland, and their edges) over two seasons (spring and summer)? In general, we expected predators to be
112 generally more positively influenced by vegetation structure than plant species richness and composition,
113 while herbivores would be more positively influenced by plant species richness or composition than
114 vegetation structure (Prediction I; Fig. 1). This is because, regardless of habitat type, many phytophagous
115 species are assumed to be more host plant-dependent than predatory species following a bottom-up effect of
116 biodiversity (Perner et al. 2005; Schaffers et al. 2008; Siemann 1998).

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

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

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

131 **Materials and methods**

132 *Study site and sampling design*

133 Our study area was a highly fragmented and mixed cropping-grazing landscape within the Lachlan River
134 Catchment, New South Wales, southeastern Australia (location of sites ranging from -34.036 S, 146.363 E; -
135 33.826 S, 147.855 E; to -34.411 S, 148.499 E; Online resource: Fig. A1). Widespread clearing for agriculture
136 over 100 years ago has restricted native *Eucalyptus* woodland remnants to infertile, steeper areas. Many
137 remnants also have been modified by livestock grazing (mainly cattle and sheep), invasion of exotic weeds,
138 and altered fire regimes (e.g. reduced fire frequency) (Norris and Thomas 1991). Our study area is
139 characteristic of highly cleared farming landscapes in southern Australia, where remnant native vegetation is
140 at risk from additional clearing and further agricultural intensification. These kinds of fragmented landscapes

141 occur in other parts of world such as South America, eastern Europe, and Asia (Uchida et al. 2016).

142 However, the impact of land-use changes on biodiversity is less understood in these regions compared to
143 Northern America, and Northern and Western Europe (Sutcliffe et al. 2015; Uchida et al. 2016).

144 We selected eleven remnant vegetation patches on the basis that they were *Eucalyptus* woodland
145 communities with high ground-, mid- and over-storey native vegetation complexity (i.e. ‘patch’ habitat type),
146 and adjoined mixed farm fields which, for the purposes of this study, were pooled as a single ‘farmland’
147 habitat type. The farmland types within the fields were: winter wheat crops, fallow fields, fine woody debris
148 applied over harvested wheat crops, and restoration plantings (*Eucalyptus* and native shrubs <7 years old).
149 Farmland and patches differed strongly structurally and floristically, and showed significantly different
150 composition of beetle species (Ng et al. 2017; see also Fig. A2). The ground layer in farmland is
151 characterized by lower plant species richness and dominated by exotic annual grasses and forbs (notably
152 *Triticum aestivum*, *Hypochaeris*, *Lolium*, and *Bromus*). Patches have higher plant species richness and higher
153 proportion of native species (particularly *Acacia*, *Austrostipa*, *Sida* and *Calotis*) (Table 1; Table A2). To test
154 if plant-beetle relationships varied between habitats, we selected vegetation attributes that had similar (and
155 therefore comparable) ranges of values within each habitat type (Table 1). This is because some vegetation
156 attributes did not vary between habitats (e.g. trees were always present in patches and mostly absent from
157 farmland).

158 ***Beetle sampling***

159 Our survey design consisted of four 400 m transects running from inside each patch out into the adjoining
160 farmland. We sampled beetles at three locations along each transect: 200 m inside the patch, 200 m inside the
161 farmland, and 0 m at the patch-farmland boundary. We chose 200 m because it represented the interior of
162 smaller farm fields. We included the edge (0 m) as a separate habitat type because edges were previously
163 found to have distinct beetle assemblages (Ng et al. 2018) and may be affected by farming activities
164 differently to the farm interior (Weibull et al. 2003). We sampled from the same trap location during two
165 distinct periods in terms of plant phenology and agronomic practices in farmland: spring when crops and

166 spring-active species were at peak growth, and summer when crops have been harvested (stubble retained;
167 fine woody debris treatment applied) and summer-active species at peak growth.

168 Each sampling location comprised a pair of pitfall traps, consisting of plastic jars (6.5 cm diameter,
169 250 ml) dug into the ground with the rim level with the soil surface, filled with 100 ml of preservative (1:3
170 glycol – water mixture, and a drop of detergent to reduce surface tension). Individual traps from each pair
171 were placed on either side of a drift fence (60 cm long x 10 cm high) to help direct arthropods into the trap.
172 We opened a total of 132 pairs of traps (11 replicate sites x 4 transects x 3 trap pairs) for 14 days during
173 spring (October–November 2014) and summer (January–February 2015).

174 We recognize that data from pitfall traps represent a compound measure of abundance, surface
175 activity and species trappability, which may be habitat-dependent (Greenslade 1964; Woodcock 2007). For
176 example, under-sampling of flight-dispersing individuals or specialist feeders restricted to host plants may
177 influence findings for some groups. Nonetheless, pitfall traps provide a consistent and efficient sampling
178 method of studying assemblage differences when results are interpreted carefully (Greenslade 1964;
179 Woodcock 2007). The objective of our study was not to sample all species, but to compare assemblages
180 between treatments for relatively common species. Using drift fences and leaving traps open for two weeks
181 in our study was employed to increase the efficiency of captures (Duelli 1997; Weibull et al. 2003).

182 Arthropods were preserved in 70% ethanol. All adult beetles were removed and sorted to family and
183 to genus or species where possible. Beetle taxonomy followed Lawrence and Britton (1994). Where
184 specimens could not be identified to species, measures of activity-density and richness corresponded to
185 morphospecies (e.g. *Carabidae* sp. 1, *Carabidae* sp. 2, etc.; *sensu* Oliver and Beattie 1996), henceforth
186 referred to as species. Each species was assigned to one of three generalized trophic groups: predators,
187 herbivores and detritivores (including fungivores), based on the predominant feeding behaviour of adults at
188 the family and subfamily level (Lawrence and Britton 1994). We assigned all carabids as predators because
189 purely phytophagous species are considered uncommon in Australia (Gibb et al. 2017).

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, 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 species 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 (MRM, CCA and partial CCA) for analysing multivariable response variables, 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 species composition and vegetation structure (multivariate) on beetle species composition (multivariate)

We ran multiple regression on distance matrices (MRM) (Lichstein 2007) to compare relative effects of plant species composition, vegetation structure, and geographic distance between sites (latitude/longitude information for each site was recorded using a GPS) on beetle species composition (geographic distance is used instead of habitat type because the latter is not a suitable data type for MRM). The vegetation structural

214 variables were: vegetation height (cm), litter cover (%) and total herbaceous cover (%) (derived from the sum
215 of the cover of forbs and grasses, which are collectively a useful measure of structural complexity; Table 1),
216 and they were not strongly correlated (< 0.5 Pearson correlation). Beetle and plant species composition
217 matrices were based on Bray-Curtis dissimilarities, while vegetation structure and geographic distances were
218 based on Euclidean distances between sites. MRM allows multiple matrices to be used as predictor variables.
219 It creates a multiple regression model for a response matrix against multiple predictor matrices, and uses a
220 permutation procedure to test for statistical significance. Controlling for geographic distance allowed us to
221 compare vegetation effects after having accounted for spatial autocorrelation. We repeated MRM tests for
222 subsets of data within each of the three habitats (patches, edges, farmland). We assessed the statistical
223 significance of each MRM model based on 999 permutations. We used the ‘ecodist’ package for the MRM
224 tests (Goslee and Urban 2007) in R 3.2.0 (R Development Core Team 2015).

225 **Effects of plant richness and vegetation structure (univariate) on beetle species composition** 226 **(multivariate)**

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

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

236 We used GLMM with Poisson errors to determine the effects of plant richness and the three vegetation
237 structural variables on beetle activity-density 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. 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 pairs of traps during spring and summer. We recorded a total of 276 plant species representing 179 genera and 58 families (Online resource: Table A1,A2).

Effects of plant species composition and vegetation structure on beetle species composition

MRM models incorporating plant species composition, vegetation structure, and geographic distance were generally able to predict the species composition of the overall beetle community ($0.029 < R^2 < 0.229$; 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

262 during spring and summer ($P = 0.002$; Table 2c), and in patches ($P = 0.001$; Table 2a) and farmland ($P =$
263 0.019 ; Table 2b) only during summer. More similar plant species composition was significantly correlated
264 with more similar herbivore species composition in edges during spring ($P = 0.002$) and summer ($P = 0.033$)
265 (Table 2c). More similar plant species composition was significantly correlated with more similar predator
266 species composition in edges during summer ($P = 0.001$; Table 2c), while more similar vegetation structure
267 was significantly (albeit weakly) correlated with more similar predator species composition in patches during
268 summer ($P = 0.043$; Table 2a).

269 Overall beetle species composition became more dissimilar as geographic distance between samples
270 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
271 > 0.116). Geographic distance effects on the species composition each beetle trophic group depended on
272 habitat and season (details in Table 2).

273 ***Effects of plant richness and vegetation structure on beetle species composition***

274 Beetle species composition showed distinct clustering between habitat types (Fig. 2). For the species
275 composition of the overall beetle assemblage, the first two axes of our CCA analyses respectively explained
276 38.6% and 26.0% of the variation in plant richness and vegetation structure during spring, and 37.4% and
277 28.0% during summer (Online resource: Table A3). Our CCA analyses also showed that habitat type had a
278 significant effect on species composition of overall beetles ($P = 0.001$ during spring and summer), herbivores
279 and detritivores (both with weaker effects during summer $P = 0.02$ than spring $P < 0.003$), and predators
280 during spring ($P = 0.001$) (KN data unpub.).

281 Partial CCA analyses for the overall beetle assemblage showed that the variation explained purely by
282 plant species richness and vegetation structure, after partialling out habitat effects, were 2.67% and 2.70%
283 respectively during spring and summer (Online resource: Table A3). Partial CCA (after accounting for
284 habitat type) showed that both plant richness and all vegetation structural variables had significant effects on
285 overall beetle species composition during spring ($P < 0.004$). During summer, effects of litter cover on
286 overall beetle species composition were weakly significant ($P = 0.049$). Partial CCA also revealed significant

287 effects of total herbaceous cover on detritivore species composition during spring ($P = 0.007$), significant
288 effects of plant species richness on herbivore species composition during summer ($P = 0.016$), and significant
289 effects of plant species richness ($P = 0.044$) and total herbaceous cover ($P = 0.014$) on predator species
290 composition during spring (Online resource: Table A3).

291 ***Effects of plant richness and vegetation structure on beetle diversity***

292 Plant richness and vegetation structure variables (litter cover, total herbaceous cover and/or vegetation
293 height) were always included in the top-ranked models for the activity-density of overall beetles, herbivores,
294 predators, and detritivores (Table 3; Online resource: Table A4; model details in Tables A5,A6).

295 Species richness of overall beetles had a significant positive association with total herbaceous cover
296 during summer, regardless of habitat type ($P = 0.007$) (Online resource: Table A4).

297 In farmland during summer, herbivore activity-density significantly decreased with plant richness (P
298 < 0.001), while predator activity-density significantly increased with plant richness. However, in patches
299 during summer, herbivore activity-density significantly decreased with plant richness ($P < 0.001$), and there
300 were no effects of plant richness on the activity-density and richness of predators (Table 3).

301 During summer, litter cover had significant positive effects on detritivore activity-density in edges,
302 but effects were negative in farmland ($P < 0.001$). During summer, vegetation height had significant negative
303 effects on predator activity-density in patches ($P = 0.004$) (Table 3).

304 During spring, regardless of habitat type, litter cover had a significant positive effect on detritivore
305 activity-density ($P = 0.022$), while vegetation height had a significant positive effect on predator activity-
306 density ($P < 0.001$).

307 Vegetation structure variables often had interactive effects with habitat for beetle activity-density,
308 where the direction or strength of effects within a habitat often changed between spring and summer. For
309 example, total herbaceous cover had a significant positive effect during spring and negative effect during
310 summer on predator activity-density in patches and farmland. In contrast, total herbaceous cover had a

311 significant negative effect on predator activity-density at edges during spring ($P < 0.001$), and a significant
312 positive effect during summer ($P < 0.001$) (Table 3).

313 Habitat edges were characterized by mostly significant positive associations between plant richness
314 and activity-density of all trophic groups (Online resource: Table A6).

315 **Discussion**

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

329 ***Effects of plant species composition and vegetation structure on beetle species composition***

330 We identified plant species composition to be a stronger predictor of beetle species composition than
331 vegetation structure in all habitats during both seasons. This is generally consistent with our Prediction II of
332 stronger effects of plant species composition compared to other vegetation attributes in some habitats. Our
333 prediction of beetles in farmlands being predominantly habitat generalists and therefore less affected by plant
334 species composition (compared to remnant patches and edges) was not supported (Table 2). Our findings are

335 consistent with studies that explicitly compared the effects of plant species composition and other vegetation
336 attributes on arthropod species composition (Koricheva et al. 2000; Müller et al. 2011; Perner et al. 2005;
337 Schaffers et al. 2008). Schaffers et al. (2008) used a predictive co-correspondence approach to demonstrate
338 that plant species composition best predicted the species composition of several arthropod groups, including
339 beetles, compared to vegetation structure and environmental condition. Similar studies concluded that the
340 identity or combination of plant species was more important than other vegetation attributes in determining
341 the abundance (or activity-density) of most arthropods (Koricheva et al. 2000; Perner et al. 2005). This is
342 because plant species composition directly mediates vegetation structure, microclimate and environmental
343 factors (Joern and Laws 2013; Koricheva et al. 2000; Müller et al. 2011; Perner et al. 2005; Schaffers et al.
344 2008), and potentially influence microhabitat preferences of individual beetle species (Buse 1988; Niemelä
345 and Spence 1994). Importantly, our findings provide evidence of the overriding effects of plant species
346 composition on arthropod composition both in uncropped (i.e. natural) and cropped habitats occurring in
347 modified landscapes. These effects are likely masked in zoological studies relying on coarser measurements
348 of vegetation structure, because environmental influences at smaller spatio-temporal scales are not
349 adequately characterized.

350 ***Effects of geographic distance on beetle species composition***

351 We identified higher species dissimilarity with increasing geographic distance for overall beetle species
352 composition in farmland and edges, but not in remnant patches. This suggests that beetles in remnant patches
353 may be dispersal-limited woodland specialists (Driscoll et al. 2010). In farmland and edges, beetle
354 assemblages may be more dissimilar with increasing distance between sites due to limited species movement
355 or high environmental heterogeneity in mixed-farmland contributing to niched-based species sorting
356 (Soininen et al. 2007; Tews et al. 2004). We also found differences in geographic distance effects on beetle
357 trophic groups between habitats and seasons. This indicates spatio-temporal turnover in beetle assemblages
358 (Driscoll et al. 2010; Tews et al. 2004), likely linked to fluctuations in connectivity of habitat resources (e.g.
359 summer aggregation of detritivorous *Latridius* sp. 437 in edges and *Ommatophorus* sp. 98 in patches; KN

360 data unpub.) (Duflot et al. 2016) and cross-habitat movement (Ng et al. 2018). Seasonal movement patterns
361 of beetles between different farmland-woodland edges in this study landscape are detailed in Ng et al. (2018).

362 ***Beetle responses to plant species richness and vegetation structure***

363 Both plant species richness and vegetation structure significantly influenced the activity-density of all beetle
364 trophic groups to some extent (Table 3). These results do not support Prediction I of predators showing
365 stronger associations with vegetation structure, and herbivores with plant species richness. Instead, our
366 findings are consistent with studies showing that multiple vegetation characteristics contribute to species
367 habitat preferences and structuring of different trophic group (Lassau et al. 2005; Nyafwono et al. 2015;
368 Tews et al. 2004). Plant species richness is commonly linked to the diversity of available resources for
369 arthropods (Perner et al. 2005), while vegetation structure is typically linked to biophysical resources such as
370 food, shelter and ovipositioning sites (Landis et al. 2005). The effects of plant diversity and vegetation
371 structure on arthropod abundance may, however, be auto-correlated (Lassau et al. 2005; Perner et al. 2005).
372 Further manipulative experiments would be useful in disentangling effects of these two vegetation attributes
373 and other confounding factors, such as species interactions, plant productivity, ground cover, soil
374 characteristics, or microclimate (Niemelä and Spence 1994; Perner et al. 2003; Siemann et al. 1999).

375 Our data did not support the “enemies hypothesis” in remnant patches, and “resource concentration
376 hypothesis” in farmland (Prediction III; Root 1973). Conversely, we found plant-beetle relationship patterns
377 that are consistent with the “natural enemies” hypothesis in farmland during summer, i.e. greater predator
378 activity-density in more species-rich vegetation and greater herbivore activity-density in species-poor
379 vegetation. The “resource concentration” hypothesis also appeared to be supported but only in remnant
380 patches, where higher herbivore activity-density occurred in more species-poor sites and there were no
381 effects of plant richness on predator diversity (Table 3). These contradictory findings highlight dependence
382 of plant-arthropod relationships on habitat context, particularly the influence of more complex associations in
383 mature forest or woodland ecosystems (Zou et al. 2013). The first pattern of increasing predator activity-
384 density with increasing plant richness in farmland suggests that productive farmland can provide seasonal

385 refuge from predation (enemy-free space hypothesis; Brose 2003) as well as provide stable prey resources for
386 predatory beetles. Such positive effects of plant richness on predator activity-density are typically associated
387 with top-down control processes in agricultural ecosystems (Zou et al. 2013), which are also linked to
388 negative effects on herbivore activity-density (Joern and Laws 2013; Koricheva et al. 2000; Tews et al.
389 2004). The second pattern of decreasing herbivore activity-density with increasing plant richness in remnant
390 patches may be due to it being more challenging for woodland specialist beetles to locate host plants
391 (Agrawal et al. 2006; Root 1973), and/or increased predation risks on beetles (hunting efficiency hypothesis;
392 Brose 2003) by patch-associated predators (e.g. birds). It should be noted that these results are affected by
393 limitations of pitfall traps and may, for example, reflect seasonal turnover or movement of beetle species, or
394 reduced species trappability in patches.

395 *Spatially and temporally dynamic vegetation effects on beetles*

396 *Plant species composition*

397 We found that the influence of vegetation composition on the beetle community was stronger in summer than
398 in spring, and stronger at edges followed by farmland and patches (Table 2). Differences in the effects of
399 plant species composition on beetles across different habitats and time supports our Prediction III (varying
400 plant-beetle relationships in different habitats), and Prediction IV (differences in plant-beetle relationships
401 over time). Pronounced seasonal and habitat effects on beetle-plant relationships can be explained by some or
402 all of the following: plant host use at different stages of beetle lifecycles (e.g. different specialized diets
403 between the larvae and adult form); changes in plant phenology and succession (e.g. growth, flowering or
404 senescence of annual vegetation) (Landis et al. 2005; Lassau et al. 2005; Parry et al. 2015; Rouabah et al.
405 2015); and varying environmental conditions (e.g. seasonal fluctuations in temperature and humidity)
406 (Landis et al. 2000; Niemelä and Spence 1994). We suggest that some plant species might be particularly
407 important in providing food or habitat resources for beetles during hot and dry summer conditions when plant
408 resources are likely in short supply (compared to spring when vegetation is at peak growth, and prior to crop
409 harvest). These dynamic patterns are also expected to be influenced by seasonal turnover of beetle species

410 composition across the different habitats, which may be associated with plant species turnover across the
411 seasons (Ng et al. 2017). Field edges may provide temporally stable foraging and nesting sites for many
412 beetles due to low disturbance and cross-habitat mixing of woodland and agrestal plants (Holland et al. 2005;
413 Rouabah et al. 2015).

414 Beetle trophic groups were differently affected by vegetation variables between different habitats and
415 time periods. This result is consistent with studies showing varying responses of trophic groups to vegetation
416 resources depending on spatial and temporal differences (Lassau et al. 2005; Niemelä and Spence 1994;
417 Tews et al. 2004; Woodcock and Pywell 2010). Herbivores are often assumed to be more sensitive to plant
418 species composition than predators (Buse 1988; Siemann 1998; Siemann et al. 1998; Woodcock and Pywell
419 2010) but we did not find this to be the case. Nor did we find predators to be more influenced by vegetation
420 structure and herbivores by plant species composition (Prediction I). Rather, we found correlations between
421 plant and beetle composition for all trophic levels in certain habitats and seasons. We found that herbivore
422 species composition (represented by a large proportion of Curculionidae in our data) was significantly
423 affected by plant species composition only at edges, while during summer, predator species composition was
424 significantly affected by plant species composition at edges and by vegetation structure in patches (Table 2).

425 Plausible explanations for the mixed responses of herbivores and predators to plant species
426 composition or vegetation structure include the following. First, significant correlations between plant
427 species composition and herbivore species composition in edges suggest that a high proportion of
428 herbivorous beetles may be attracted to plant species that are largely limited to habitat edges (e.g. *Erodium*
429 *crinitum*, *Salsola australis*, and *Sisymbrium* sp.). Second, associations between predator species composition
430 and the species composition or structure of plants appears consistent with literature suggesting that many
431 predatory arthropods use floral food resources directly in field edges (e.g. nectar, pollen; Landis et al. 2005;
432 Ramsden et al. 2015; Woodcock et al. 2016), as well as use plant-mediated resources indirectly (e.g.
433 increased plant-associated prey, and correlations with productivity or structural complexity; Joern and Laws
434 2013; Koricheva et al. 2000; Tews et al. 2004). Our data identified that remnant patches might specifically

435 provide structural refuge (e.g. ovipositioning or aestivation sites; Landis et al. 2000) for predatory beetles
436 during the austral summer (e.g. *Diaphoromerus* sp. 456; KN data unpub.).

437 *Plant species richness and vegetation structure*

438 Like plant species composition, effects of vegetation structure and plant richness on beetle trophic groups
439 often varied with habitat type, and the strength or direction of effects was seasonally variable. This was
440 exemplified by changes between spring and summer in the direction of the relationship between total
441 herbaceous cover and predator activity-density in all habitats (Table 3). Our findings suggest that
442 manipulating vegetation structure for beetle conservation needs to be targeted at appropriate taxonomic,
443 spatial and temporal levels, because a structural change which benefits a trophic group in one habitat type
444 during spring may have adverse consequences for different trophic groups or habitats, or when applied
445 during different seasons. Here, we discussed relationships between plant species richness or vegetation
446 structure and different beetle trophic groups shown in our data, while a summary of management
447 recommendations are provided in the following section.

448 During spring, litter and vegetation height appeared to positively influence the activity-density of
449 both detritivores and predators, regardless of habitat type, but the effects were habitat-specific during
450 summer (Table 3). Positive effects of litter on detritivore activity-density during spring are consistent with
451 studies showing the benefits of coarse woody debris for many species of saproxylic beetles (Barton et al.
452 2009; Gibb et al. 2006). We found contrasting effects of litter on detritivore activity-density in different
453 habitat types during summer (positive effects in edges, negative in farmland; Table 3). This may be linked to
454 differences in the quality of litter over time (e.g. litter from more diverse vegetation at edges may provide
455 preferred food sources compared to litter dominated by annual grasses in farmland) (Woodcock and Pywell
456 2010). Positive effects of vegetation height on predator activity-density during spring may be explained by
457 increased structural refugia from predation, prey resources and soil moisture availability associated with
458 higher vertical habitat complexity (Dennis et al. 1998; Lassau et al. 2005; Rouabah et al. 2015). However, we
459 found negative effects of vegetation height on predator activity-density in remnant patches during summer

(Table 3). This suggests a possible influence of other environmental or biotic factors (Siemann et al. 1998; Zou et al. 2013), and/or pitfall sampling effects on predator activity-density in more complex woodland ecosystems (e.g. dormant species not sampled; Greenslade 1964; Woodcock 2007).

During summer, beetle species richness was positively affected by total herbaceous cover (Online resource: Table A4). 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 effects (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. They had greater activity-density of all trophic groups where vegetation was more species-rich. This is consistent with other studies of field edges, which were found to support higher arthropod populations than adjoining habitats (particularly farmland) (Landis et al. 2005; Magura 2002; Ramsden et al. 2015; Rouabah et al. 2015; Woodcock et al. 2016). These authors attributed these finding to the blending of elements from habitats adjoining the edge, which lead to increased structural refuges and diversity of plant or prey foraging resources. Similarly, we previously found that habitat edges not only supported several potential edge-specialists, but were also permeable to cross-habitat movement for all trophic groups depending on the degree of (vegetation-mediated) contrast between the adjoining habitats (Ng et al. 2018).

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 (Fig. 1): plant-beetle relationships can be better understood by deconstructing their associations at a fine spatial and temporal scale (e.g.

485 between growing season, within farm fields, field margins or patches), and considering multiple vegetation
486 attributes – particularly plant species composition. We suggest that more collaboration between plant and
487 insect ecologists is needed to enable collection of high quality species-level data in community-based studies
488 on plant-arthropod relationships.

489 Conservation and management strategies based on altering vegetation structure or plant species
490 richness need careful consideration, because changes focused on improving the habitat for a given trophic
491 group (e.g. natural enemies) may negatively impact the activity-density of other trophic groups providing
492 important ecosystem services, or have adverse effects at other time periods. Our findings indicate that
493 managing plant species composition at edges (compared to remnant patches and farmland), and during
494 summer (compared to spring), are effective ways of altering the species composition of beetle trophic groups
495 (Fig. 3). However, more species-level data and data from other seasons (e.g. winter and autumn) are needed
496 to determine how different species use vegetation resources across the landscape at different times of the year
497 (Joern and Laws 2013; Souza et al. 2016; Woodcock and Pywell 2010) – this information is severely lacking
498 for most beetle species (outside of Europe).

499 Our study has several general findings that could contribute to beetle conservation (Fig. 3). First, in
500 all habitats in spring, management that leads to increased vegetation height supports predators, increased
501 litter cover supports detritivores, and higher plant richness supports herbivores. Second, enhanced total
502 herbaceous cover during summer (e.g. through fallowing, revegetation or reducing grazing), can increase
503 overall beetle species richness. Third, promoting plant richness at the edge between woodland and farmland
504 can improve overall beetle activity-density (Fig. 3). Arthropod conservation is currently focused on
505 protecting extant native vegetation in Australia (Parry et al. 2015), but our study showed that management of
506 vegetation along edges and field margins could be altered to support beetles in the wider agricultural
507 landscape. Approaches employed in well-established European agri-environment schemes to manage floral
508 resources in field edges for arthropod diversity (Rouabah et al. 2015; Woodcock et al. 2016) could be
509 relevant to Australian agroecosystems. In Australian croplands, current weed control practices at edges focus

510 on the use of broad-spectrum herbicides or soil tillage (Preston 2010; Preston et al. 2017). More research is
511 needed to determine whether the timing and tactics of existing weed control strategies have off-target
512 negative impacts on beetle biodiversity particularly through the loss of plant diversity at edges, which
513 provide habitat resources for beetles.

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671

672

673 **Data availability**

674 The datasets generated during and/or analysed in this study will be made available from the CSIRO Data

675 Access Portal upon acceptance of this manuscript (<https://data.csiro.au/>).

676

677 **Figure captions**

678

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

686

687 **Fig. 2.** Canonical correspondence analysis (CCA) ordination showing beetle composition for spring (a) and
688 summer (b) with respect to habitat (habitat types are: ○ = patch, + = farmland, = ▲ edge). Ellipses indicate
689 one standard deviation from the centroid of each habitat group.

690

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

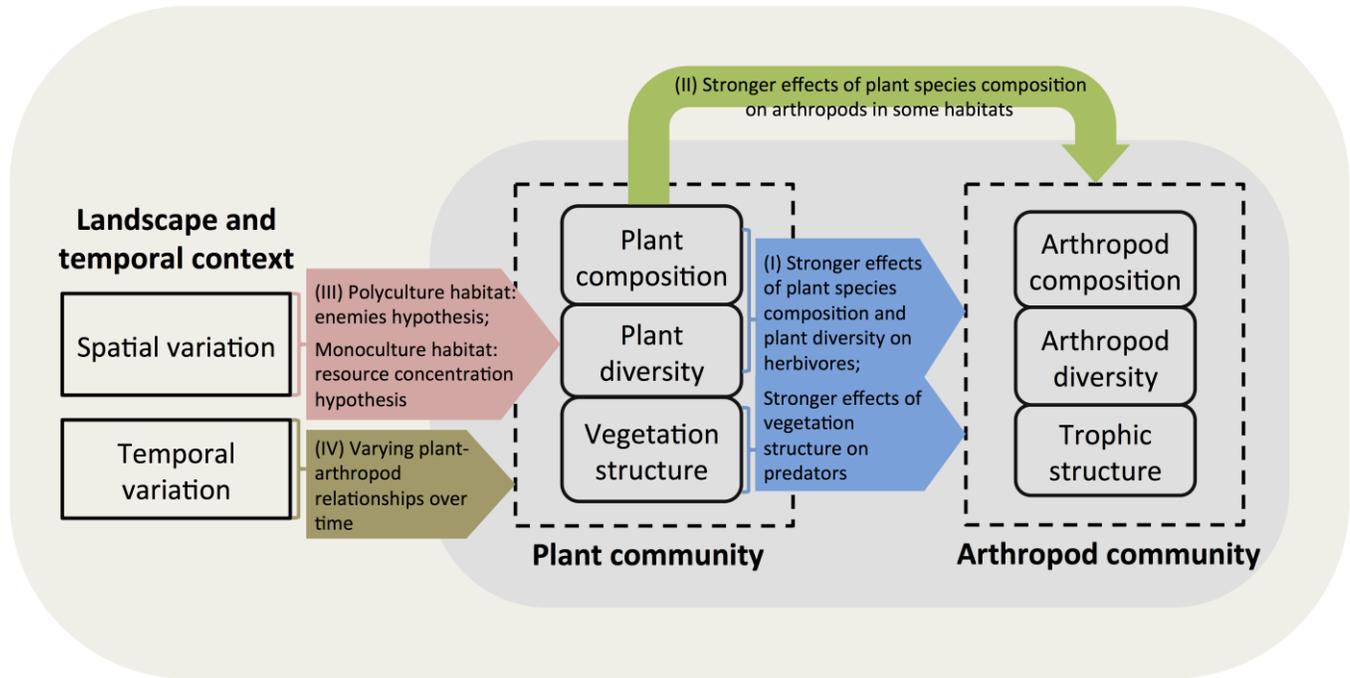
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694

695 **Figures**

696

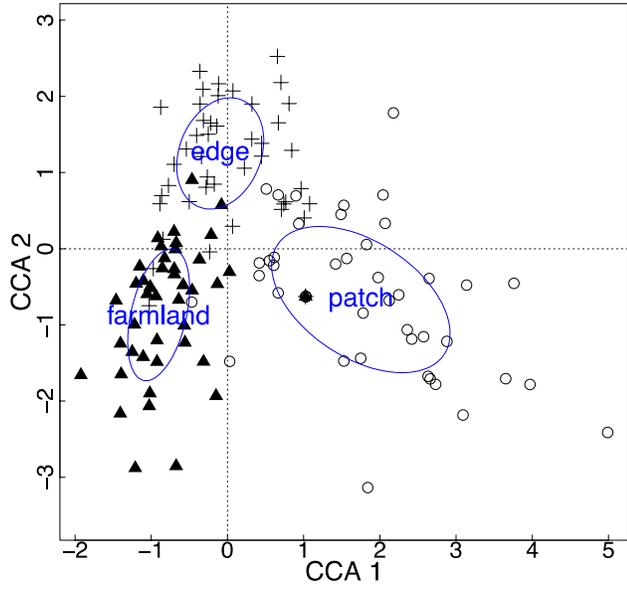
697 Fig. 1



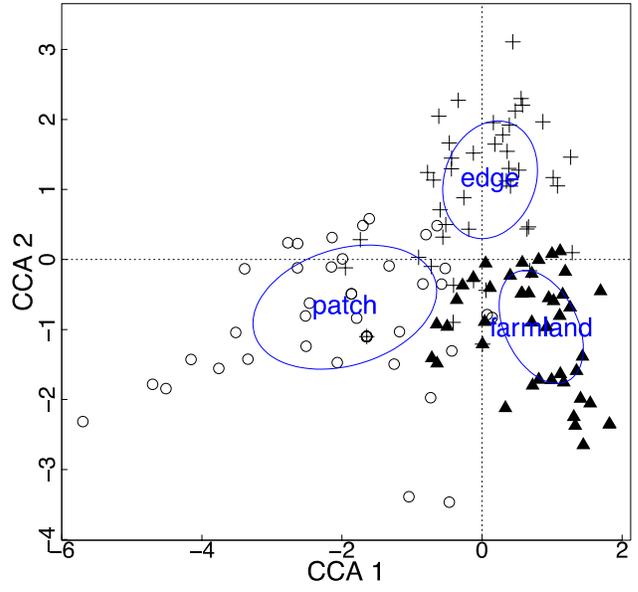
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(a)

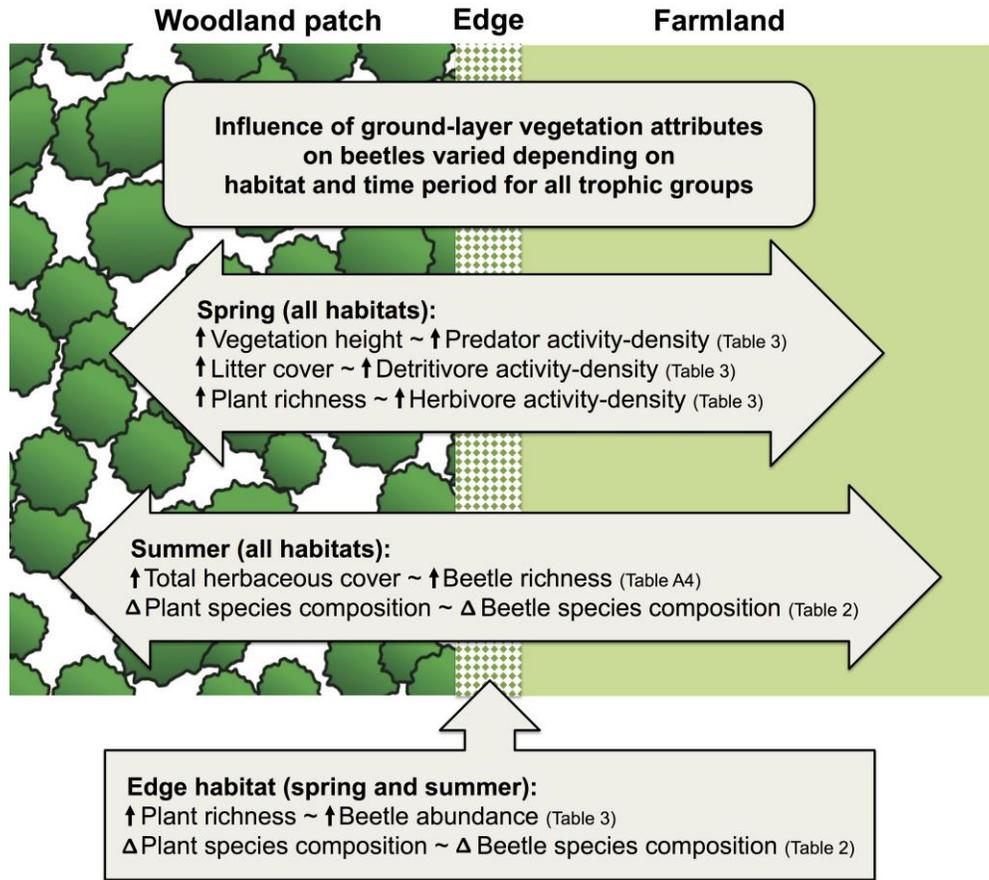


(b)



701

702



705 **Tables**

706

707 **Table 1.** Vegetation variables recorded in a 20 m by 10 m plot at each pitfall trap location, collected during

708 spring and summer. Raw cover scores were based on the middle percentage values of the following six

709 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)
Native forb cover	Cover score	Canopy cover of native forbs	Spring: 2.5 to 62.5 (10.4) Summer: 2.5 to 62.5 (9.1)	Spring: 2.5 to 15 (3.6) Summer: 2.5 to 37.5 (9.0)	Spring: 2.5 to 15 (3.1) Summer: 2.5 to 37.5 (9.4)
Native grass cover	Cover score	Canopy cover of native grasses	Spring: 2.5 to 85 (17.1) Summer: 2.5 to 85 (24.4)	Spring: 2.5 to 62.5 (10.2) Summer: 2.5 to 62.5 (27.3)	Spring: 2.5 to 36.5 (4.4) Summer: 2.5 to 85 (12.8)
Exotic perennial grass cover	Cover score	Canopy cover of exotic perennial grasses	Spring: 2.5 to 2.5 (2.5) Summer: 2.5 to 15 (2.8)	Spring: 2.5 to 2.5 (2.5) Summer: 2.5 to 37.5 (4.1)	Spring: 2.5 to 37.5 (4.1) Summer: 2.5 to 85 (9.0)
Exotic annual forb and grass cover	Cover score	Canopy cover of exotic annual forbs and grasses	Spring: 2.5 to 85 (21.1) Summer: 2.5 to 15 (3.1)	Spring: 2.5 to 85 (51.9) Summer: 2.5 to 37.5 (6.9)	Spring: 2.5 to 97.5 (71.7) Summer: 2.5 to 85 (32.0)
Total	Cover	Sum of cover scores	Spring: 10 to 127.5	Spring: 10 to 105	Spring: 22.5 to 125.5

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herbaceous	score	for native forb, native	(51.1)	(68.2)	(83.3)
cover		grass, exotic perennial	Summer: 10 to 105	Summer: 10 to 105	Summer: 10 to 130
		grasses and exotic	(39.4)	(47.5)	(63.3)
		annual forbs and			
		grasses			
Litter cover	Cover	Detached leaf and	Spring: 2.5 to 85	Spring: 2.5 to 62.5	Spring: 2.5 to 85
	score	grass litter	(34.9)	(14.6)	(11.0)
			Summer: 15 to 85	Summer: 2.5 to 62.5	Summer: 2.5 to 85
			(47.7)	(30.1)	(31.7)
Groundstorey	Centi	Average height of	Spring: 5 to 60 (25.4)	Spring: 0 to 60 (22.5)	Spring: 7 to 85 (45.7)
vegetation	metre	dominant grasses,	Summer: 1 to 75	Summer: 1 to 65	Summer: 1 to 35
height		forbs, shrubs and	(25.3)	(18.3)	(15.7)
		other vegetation < 1			
		m high			

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

Model ~ Predictor variables	Model	Coefficients		Coefficients		
	R ²	Intercept	P	Model R ²	Intercept	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

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Plant composition dissimilarity		0.417	0.002	0.298	0.002
Vegetation structure		0.006	0.732	<0.001	0.991 715
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

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

Response	Spring					Summer					
	Model terms	Directi on	Chisq	D f	Pr(Chis q)	Model terms	Directi on	Chisq	D f	Pr(Chis q)	
Detritivore richness	<i>Best model: None</i>	<i>Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height</i>									
		Habitat*Vegetation height	e(-)	3.4	1	0.067					
Detritivore activity- density	<i>Best model: Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height</i>	<i>Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height</i>									
		Litter cover	+	5.2	1	0.022	Habitat*Plant richness	p(---); e(++)	19.1	2	<0.001
		Habitat*Plant richness	p(---); e(+++); f(++)	91.2	2	<0.001	Habitat*Litter cover	e(+++); f(---)	104.1	2	<0.001
		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

721

richness *Best model: None* *Best model: None*

Herbivore

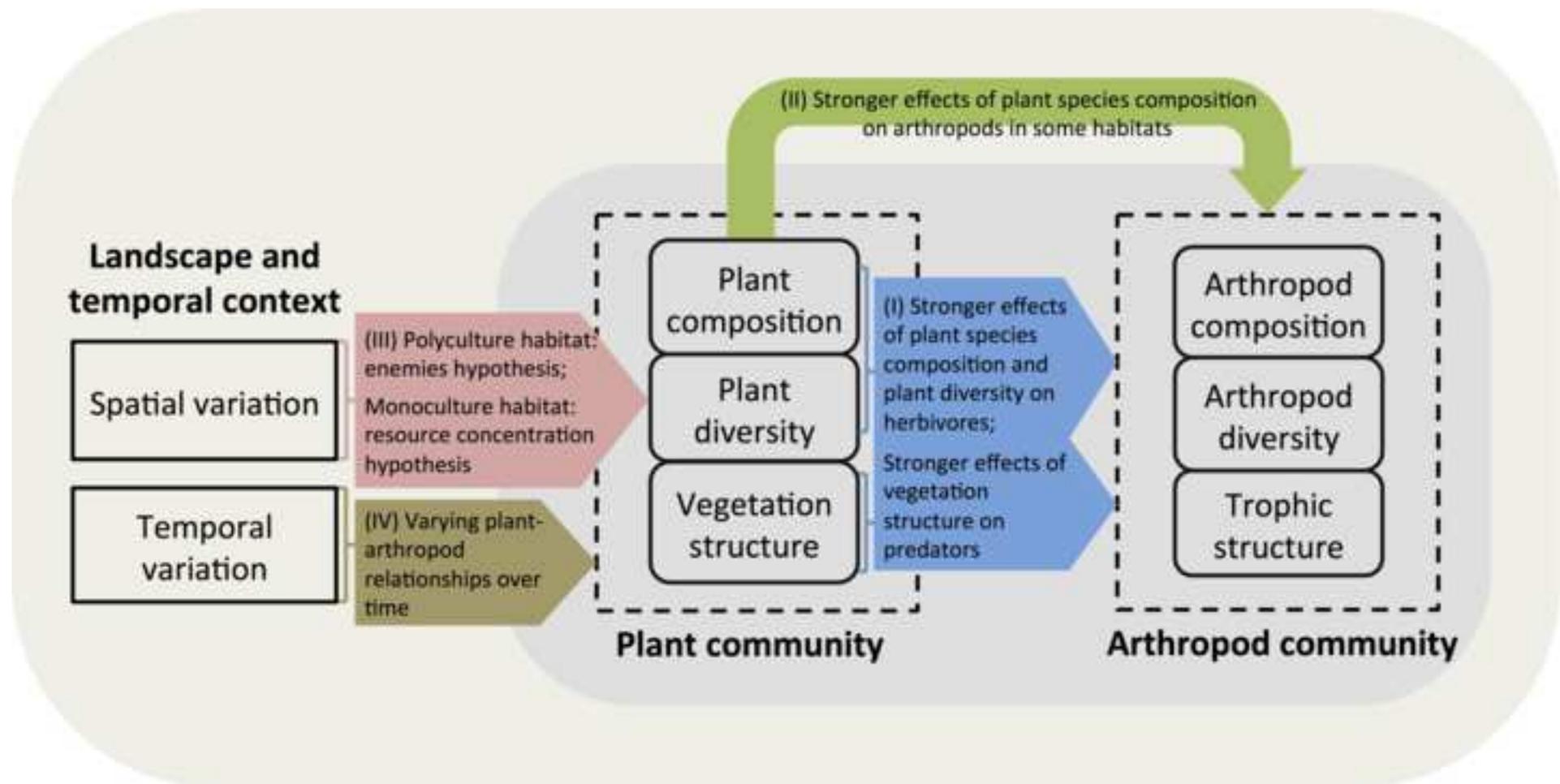
activity- density	<i>Best model: Habitat * Litter + Plant richness + Habitat * Total herbaceous cover + Habitat * Vegetation height</i>				<i>Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Vegetation height</i>			
Plant richness	+				Habitat*Plant richness	p(---); e(+++);		
		4.1	1	0.043		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

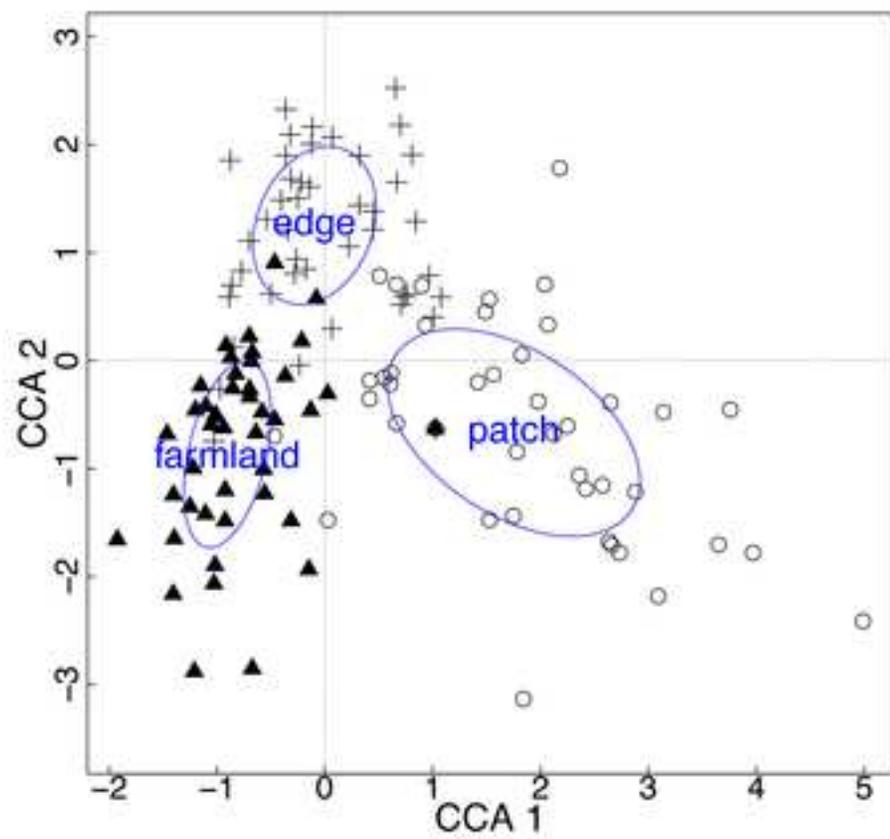
richness *Best model: None* *Best model: None*

Predator

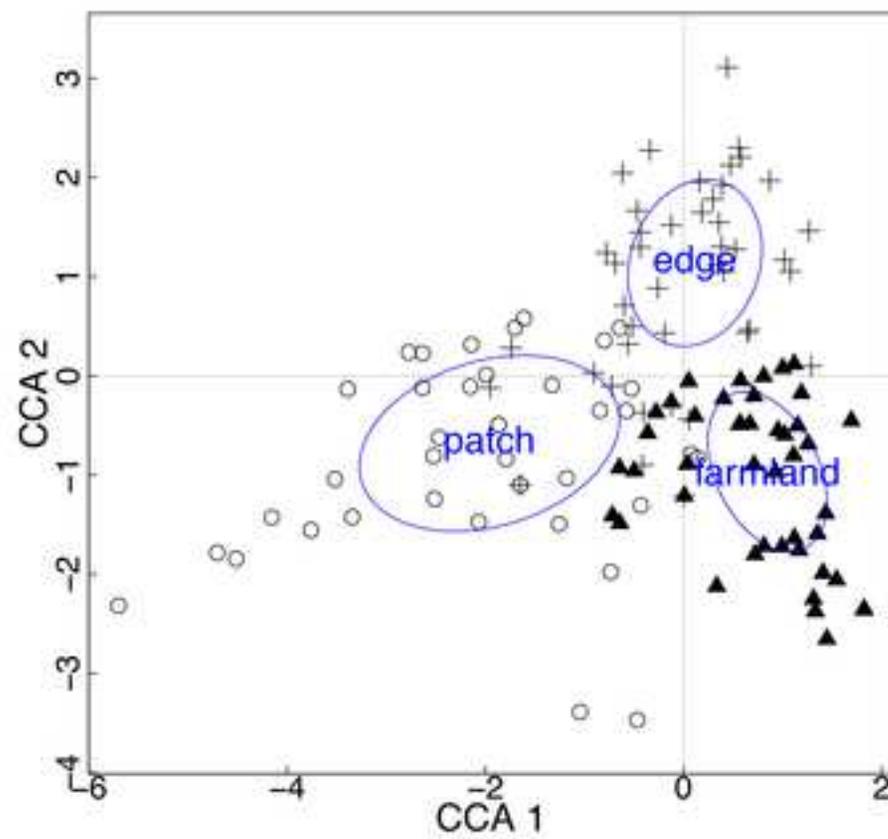
activity- density	<i>Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Total herbaceous cover + Vegetation height</i>				<i>Best model: Habitat * Litter + Habitat * Plant richness + Habitat * Vegetation height</i>			
Vegetation height	+++	32.8	1	<0.001	Habitat*Plant richness	f(+++)	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(---);	70.7	2	<0.001	Habitat*Total herbaceous cover	p(--); e(+++);	18.5	2 <0.001

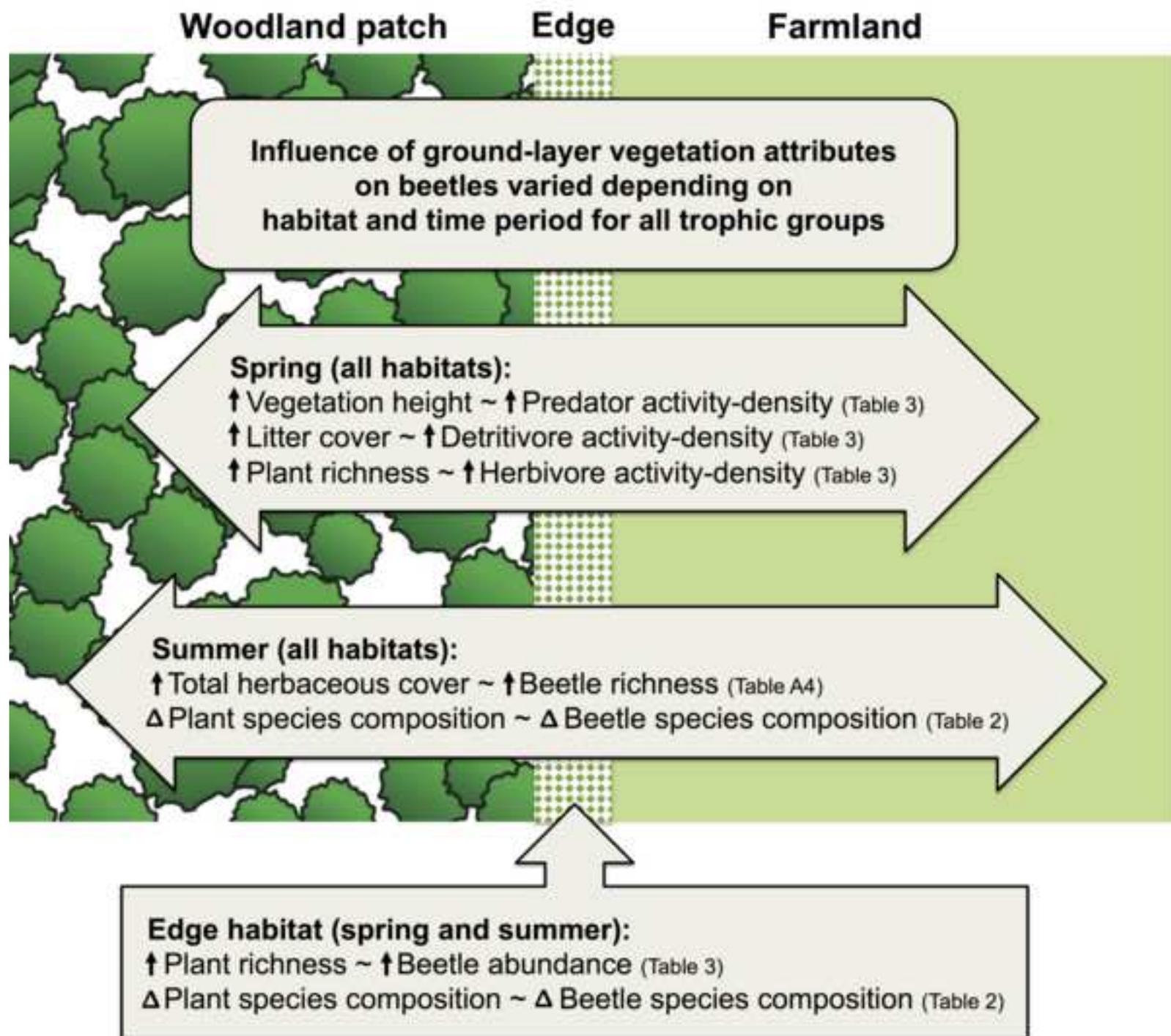


(a)



(b)







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