



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

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Abstract

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

Keywords Fourth-corner analysis · Fragmented landscape · Size–grain hypothesis · Soft traits · Textural-discontinuity hypothesis

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This study deserves to be honoured as a highlighted student paper because it uncovers the ecological mechanisms underpinning fauna responses to land-use change. Our study is the first to quantify how changes in farmland use and vegetation structure both influence a universally important trait, body size, across the landscape. The novelty of our study lies in the use of traits-based approaches in a robust landscape-level experimental design. In contrast to the perception that farmlands are biodiversity poor, our findings highlight that a diversity of species were represented by a range of traits which enable their persistence in these dynamic farming landscapes.

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Introduction

Trait-based approaches are useful in generalizing predictions of arthropod community responses (Gibb et al. 2015; McGill et al. 2006). Information gained from traits can provide additional insights into the mechanisms influencing arthropod responses to environmental change (Barton et al. 2011; Gerisch 2011; Magura et al. 2017; Yates et al. 2014), and determine which species might be particularly sensitive to anthropogenic environmental changes (Gibb and Parr 2013; Gibb et al. 2017; Ribera et al. 2001; Seibold et al. 2015). Moreover, information based on traits that are relatively simple to consistently measure may help us to identify strategies for managing arthropod biodiversity beyond individual species. For example, it may be possible to identify how indicator traits with known ecological function might positively or negatively respond to changes in land use and

management (Gibb and Parr 2013; Gibb et al. 2017; Ribera et al. 2001).

Morphological traits, such as dispersal ability, foraging efficiency, feeding and sensorial capacity, strongly influence how organisms interact with their environment (Barton et al. 2011; Moretti et al. 2017; Weiser and Kaspari 2006; Wood et al. 2015). Morphological traits are particularly useful for studying arthropod assemblages such as beetles, where detailed biological information on diet, life history, and physiology (Moretti et al. 2017) for each species are not always known. Environmental changes can influence species differently depending on their morphological traits (Davies et al. 2000; Duflot et al. 2014; Gibb and Parr 2010; Tscharnkte et al. 2012). For example, larger species are generally more prone to extinction from agricultural intensification (Davies et al. 2000; Kotze and O'Hara 2003; Seibold et al. 2015), with habitats experiencing high disturbance selecting for smaller species with higher dispersal ability, while less disturbed habitats are more suitable for larger species with lower dispersal ability (Gerisch 2011; Lovei and Sunderland 1996; Ribera et al. 2001). Yet, studies have found mixed responses of body size to habitat disturbance, including negative (Ribera et al. 2001; Winqvist et al. 2014), positive (Gibb and Parr 2013; Kaspari 1993; Rouabah et al. 2015), and neutral (Gibb and Parr 2013; Wiescher et al. 2012) relationships. These contradictory effects on body size might be due to some larger species having greater longevity (Davies et al. 2000) or dispersal abilities, while some larger species have lower population densities with increased disturbance (Tscharnkte et al. 2012).

There are large knowledge gaps on how species traits might differ across contrasting land uses, as well as across the edges between them (Evans et al. 2016; Öckinger et al. 2010). Most trait-based studies focus on single habitat types (e.g., woodlands, grasslands, or specific crop fields) and do not explicitly consider the spatial heterogeneity that typically characterize human-modified landscapes (Allen et al. 2006; Gibb et al. 2015; Wood et al. 2015). Intensively farmed areas, in particular, are often assumed to be homogenous habitats (Driscoll et al. 2013), but from the perspective of arthropods, there are subtle variations within each field type that may strongly influence their assemblage patterns. These include variations in vegetation structure (Rouabah et al. 2015), seasonal management regimes (Ribera et al. 2001) and edge-mediated changes in microhabitat conditions (Evans et al. 2016). All of these can affect habitat suitability for different species and, therefore, combinations of traits (Rouabah et al. 2015). While considerable research has been done on the effects of edges on the taxonomic diversity and composition of arthropod assemblages (e.g., Magura 2017; Ries et al. 2004), the use of trait-based approaches in edge-effects studies remains scant but promising (but see Barnes et al. 2014; Evans et al. 2016). Disentangling the

various effects of land-use changes, edge effects and vegetation structure on the traits of species making up each assemblage could help reveal specific mechanisms shaping assemblages responses to landscape modification (Evans et al. 2016; McGill et al. 2006).

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

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

As for traits relating to dispersal and body shape, species with weaker dispersal ability (e.g., wingless or with shorter legs) may be favoured in woodland habitats. Species with greater dispersal ability, on the other hand, may be favoured in farmland monoculture habitats due to higher predation risks on weaker dispersers, where vegetation is less structurally complex (Chown and Gaston 2010). Beetles with feeding traits adapted for larger prey (i.e., increased head

width) have been associated with more productive farmland habitats than with less productive remnant habitats (Laparie et al. 2010). Open farmland habitats might also contain more visual hunters with larger eye protrusion and surface area than more complex woodland habitats (Fountain-Jones et al. 2015; Talarico et al. 2011).

Materials and methods

Study sites

Our study was conducted in a fragmented cropping-grazing landscape within the Lachlan River Catchment, New South Wales, southeastern Australia. Widespread clearing for agriculture has restricted native Eucalyptus woodlands to infertile steeper areas. Many remnants have also been modified by livestock grazing, weed invasion, and altered fire regimes (Norris and Thomas 1991). The study sites were clustered in three regions (east, mid, and west), which spanned approximately 250 km along a decreasing elevation and rainfall gradient (Online Resource 1: Fig. S1).

Experimental design

We selected 11 woodland patches as our study sites on the basis that they were Eucalyptus woodland communities (at the same mid-successional stage) with high ground-, mid- and over-storey native vegetation complexity, and adjoined four farmland uses: (1) winter wheat crop; (2) fallow (rested from crop rotation or sown-pasture rotation); (3) plantings of native trees and shrubs (<7 years old); and (4) winter wheat crop over which eucalypt-based fine woody debris was applied (a treatment to promote ground cover resources for ground-dwelling arthropods). Our experimental design consisted of four 400 m transects running from inside each woodland patch out into each adjoining farmland. To quantify potential edge effects on beetle species traits, we sampled beetles at five locations along each transect: 200 and 20 m inside woodlands, 200 and 20 m inside farmlands, and at the woodland–farmland edge (0 m) (Online Resource 1: Fig. S1). These distances reflected average movement rates of carabids (e.g., 11 m a day; Brouwers and Newton 2009), and the 200 m distance represented the habitat interior which we expect to be less influenced by edge effects.

Beetle sampling

Each sampling location comprised a pair of pitfall traps, consisting of plastic jars (6.5 cm diameter, 250 ml) dug into the ground with the rim level with the soil surface, filled with 100 ml of preservative (1:3 glycol—water mixture, and a drop of detergent to reduce surface tension).

Individual traps from each pair were placed directly next to each other, but they were separated by a drift fence (60 cm long x 10 cm high) to help direct arthropods into traps. We opened a total of 220 pairs of traps for 14 days during spring (Oct–Nov 2014), and repeated sampling during summer (January–February 2015). Arthropods were preserved in 70% ethanol. All adult carabids (Carabidae) were separated and identified to genus and to species where possible. Beetle taxonomy followed Lawrence and Britton (1994) and Lawrence et al. (2000). Where specimens could not be identified to genus or lower, measures of abundance, and richness corresponded to morphospecies (sensu Oliver and Beattie 1996), henceforth referred to as species. Beetle samples from each pitfall trap pair, and across the two time periods, were pooled to provide one sample per sampling location.

Morphological trait measurements

We measured 12 morphological traits from all 62 carabid species caught in our study (Table 1), focusing on traits that reflected differences in species' size, shape, and other life-history attributes among species in the carabid assemblage. We chose these traits based on their likely functional role as described in the literature (Table 1). We measured up to six individuals per species, using individuals from different regions and of differing sex where possible, to account for geographical variability and sexual dimorphism. We took photographs of individuals using a digital camera mounted on a stereomicroscope, and measured traits using the "ImageJ" software (Rasband 2007). Total body length, a useful approximation of body size (Ribera et al. 2001), was calculated by summing the lengths of the head, pronotum, and elytra (which were unaffected by preservatives).

Vegetation surveys

The same observer (KN) recorded seven ground-layer vegetation structural variables within a 20 × 10 m plot centred around each pitfall location during beetle sampling. The variables were: vegetation height, and cover of litter, bare ground, native forb, native grass, exotic perennial grasses, and exotic annual forbs and grasses. We calculated total herbaceous cover (%) from the sum of forb and grass cover (Online Resource 1: Table S1). We selected these vegetation variables, because they had similar (and, therefore, comparable) ranges of values within each habitat type. Other vegetation variables did not vary between habitats (e.g., trees were always present in woodlands and mostly absent from farmland).

Table 1 Morphological traits of ground beetles measured in this study

Morphological trait	Type	Description	Functional role
Wing occurrence	Nominal: Macropterous or brachypterous (including apterous)	Having fully developed wings (macropterous), or having reduced or no wings (brachypterous/apterous)	Dispersal ability (Driscoll and Weir 2005; Kotze and O'Hara 2003)
Head width	Continuous (μm)	Maximum dorsal head width, including eyes	Feeding and foraging ability, e.g., preferred prey size (Kaspari and Weiser 1999)
Head length	Continuous (μm)	Maximum dorsal head length, excluding mandibles	Robustness, microhabitat choice (Barton et al. 2011; Ribera et al. 1999), dispersal, visual ability (narrow shape allows greater elytra spread and rear visual field; Forsythe 1987)
Pronotum width	Continuous (μm)	Maximum dorsal pronotum width	Robustness (Ribera et al. 1999)
Pronotum length	Continuous (μm)	Maximum dorsal pronotum length	
Pronotum depth	Continuous (μm)	Maximum pronotum depth	
Elytra width	Continuous (μm)	Maximum dorsal elytra width	
Elytra length	Continuous (μm)	Maximum dorsal elytra length	
Rear femur length	Continuous (μm)	Maximum length of rear femur	
Metatrochanter length	Continuous (μm)	Maximum length of metatrochanter	
Eye protrusion	Continuous (μm)	Difference between maximum head width with eyes, and maximum head width without eyes	Dispersal ability and foraging range (Kaspari and Weiser 1999; Ribera et al. 1999)
Mandible protrusion	Continuous (μm)	Difference between maximum head length with mandibles, and maximum head length without mandibles	Running or pushing ability (Forsythe 1987)
Body length	Continuous (μm)	Sum of head length, pronotum length and elytra length as a measure of body size	Activity period, hunting and dispersal behaviour (Forsythe 1987; Gibb and Parr 2013; Weiser and Kaspari 2006)
			Diet preferences (Gibb et al. 2015)
			Disturbance tolerance (Ribera et al. 2001), reproduction (Kotze and O'Hara 2003), and feeding rate (Rusch et al. 2015)

Data analyses

We used the average trait values across all individuals for each species and log-transformed trait values prior to analysis. In addition to running a model-based fourth-corner analysis for our main research questions, we also ran several secondary analyses for additional information (e.g., patterns of species composition and vegetation structure) to help with interpretation of the main results (details in Table 2 and Online Resource: Table S2).

Fourth-corner modelling

We used fourth-corner analyses (Brown et al. 2014; Warton et al. 2015) to quantify relationships between morphological traits and environmental variables of farmland use (Question 1) and vegetation structure (Question 2). Fourth-corner approaches provide a powerful, standardized way

of analyzing relationships between a species trait matrix (Q) and an environmental variable matrix (R) by way of a species abundance/occurrence matrix (L) (Legendre et al. 1997). We used the ‘traitglm’ function in the ‘mvabund’ R package (Wang et al. 2016). This function fits a fourth-corner model to predict abundance/occurrence across multiple taxa (L) as a function of environmental variables (R) and traits (Q). R–Q interactions represent the fourth corner, and the coefficients quantify how environmental responses across taxa vary with traits (Brown et al. 2014; Wang et al. 2016).

We fitted multivariate generalized linear fourth-corner models (with a binomial distribution) for species occurrence (absence/presence) as a function of the species traits matrix, environmental variable matrix, and their interactions. We used absence–presence data to reduce the influence of very rare or abundant species (Ribera et al. 2001). We fitted models for each species trait separately: $\log_{10}(\text{body length})$ and

Table 2 Summary of statistical approaches used in this study

Analysis	Description	Methods and results location
Principal components analysis (PCA)	PCA conducted over twelve trait variables (Table 1), identified traits that varied independently of each other. It reduces data dimensionality by creating new, simplified compound axes of variation that contain meaningful functional and allometric information (Ribera et al. 1999; Weiser and Kaspari 2006). The four compound PCA dimensions were used as predictor variables in the fourth-corner models	<i>Methods:</i> Online Resource 1: Table S2. <i>Results:</i> Online Resource 1: Tables S2, S7; Fig. S2
Fourth-corner modelling	Predictive analysis used to answer research questions: (1) “How do traits differ between woodlands and different adjoining farmland uses, and do effects depend on increasing distances from the farmland–woodland edge?” and (2) “Does vegetation structure explain observed effects of adjoining farmland use and edge effects on these traits?”. Fourth-corner models allow standardized analyses of trait–environment relationships in community ecology by directly linking actual abundance/occurrence data (Legendre et al. 1997)	<i>Methods:</i> In manuscript. <i>Results:</i> Figs. 1, 2; Online Resource 1: Fig. S4
Generalized linear mixed-effect modelling	Secondary analyses to examine effects of habitat type and distance from edges on vegetation structure. Information on the spatial variation of vegetation structure in our study landscape can provide additional context on observed beetle trait responses to vegetation structure, in relation with habitat type and distance from edges	<i>Methods:</i> Online Resource 1: Table S2. <i>Results:</i> Online Resource 1: Tables S2, S6; Fig. S3
Multivariate generalized linear modelling	Secondary analyses to examine whether beetle species composition differed depending on habitat type and distance from edges, or vegetation structure. These results can provide background information on whether certain species identities might be underpinning trait–environment relationships observed in the fourth-corner analyses	<i>Methods:</i> Online Resource 1: Table S2. <i>Results:</i> Online Resource 1: Tables S2, S5; Fig. S5

three PCA component variables representing body shape (Dim.2, Dim.3, and Dim.4; PCA analyses detailed in Table 2 and Online Resource: Table S2). We used body length as a direct measure of body size instead of the first component of our PCA (Dim.1) that also represented body size to enable higher repeatability and comparison with other studies (Barton et al. 2011; Ribera et al. 2001).

We fitted two models per trait variable in relation with Questions (1) and (2), respectively.

For Question 1, we fitted fourth-corner models using our design's experimental treatments as predictor variables. The model structure was (I): farmland use:distance:trait + region:trait. Farmland use comprised four categorical levels (planting, fallow, crop, woody debris), each with five nested distances (− 200, − 20, 0, 20, 20 m).

For Question 2, we fitted models of beetle occurrence against the vegetation structural variables (bare.ground.cover, litter.cover, total.herbaceous.cover, and vegetation.height). The model structure was (II): bare.ground.cover:trait + litter.cover:trait + total.herbaceous.cover:trait + vegetation.height:trait + region:trait. Vegetation variables were continuous, and rescaled to have a mean of zero and standard deviation of 1. We included region (west, mid, east) as an additive term in all models to account for possible effects of regional variation (region:trait). To determine how much vegetation structure might be correlated with and, therefore, account for trait responses to farmland use and distance, we ran another model structure (III) that additively combined terms from the first two models (I) and (II) above. If only vegetation variables were present in the final model (III), where there were also edge and treatment effects in model (I) (i.e., experimental variables were penalised), then we considered the edge and treatment effects shown in Question (1) to be explained by these vegetation variables. That is, the edge effects are driven by those changes in vegetation. Body size exhibited significant terms for both the edge/treatment and vegetation parts of the fitted combined model (III) (while the other response variables—Dim.2, Dim.3, and Dim.4—were only significantly influenced by vegetation variables across the three models). Therefore, for body size, we also compared coefficients of the combined model (III) with model (I) to further determine the extent by which vegetation structure contributes to some of the variation in body size across farmland use and/or distance.

For all the models above, we ran model selection by applying a LASSO penalty (i.e., method = 'glm1path' that uses cross validation to choose the amount of smoothing, λ) which penalises coefficients that do not reduce BIC to zero (Tibshirani 1996). We conducted inferences on the direction of associations based on the fitted model's coefficients. Note that this method does not allow comparison of the magnitude of differences between treatments, because determining

reliable standard errors from LASSO is mathematically non-trivial (Lockhart et al. 2014). We inspected diagnostic plots to check that model assumptions were met.

Results

We collected 1566 individual carabid beetles, which comprised 62 morphospecies (47 with wings, 15 wingless or with reduced wings) (Online Resource 1: Table S3). Body sizes across all species ranged from 1.43 to 40.5 mm long (Online Resource 1: Table S4), with Scaritinae, Carabinae, and Helluoninae representing the largest three subfamilies and Pseudomorphinae, Bembidiinae, and Amblystominae representing the smallest three.

PCA results identified four main dimensions in which the morphological traits of carabid beetles varied: Dim.1 (decreasing body size), Dim.2 (measure of diet), Dim.3 (increasing robustness), and Dim.4 (increasing visual ability) (details in Online Resource 1: Table S2).

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

Fourth-corner analyses showed associations between interactions of 'farmland use' and 'distance' with body size (β values in Fig. 1a), but not for other body-shape-related morphological traits (represented by PCA component variables Dim.2, Dim.3, and Dim.4) and wing presence (i.e., farmland use' \times 'distance' effects: $\beta = 0$). Winged beetles were negatively associated with − 200 m in the woodland interior ('distance' effect only: $\beta = -0.30$).

When not accounting for vegetation structure [model (I)], there was a general pattern of higher occurrence of smaller species in woodlands and higher occurrence of larger species in crop and fallow farmland uses (Fig. 1a). Smaller sized beetle species were associated with interior (− 200 m) of woodlands for all adjoining farmland types ($-0.13 < \beta < -0.06$), and near edges (− 20 m) of woodlands adjoining plantings ($\beta = 0.096$) and fallows ($\beta = -0.017$). Larger sized beetles were associated with interior (200 m) of fallows ($\beta = 0.057$) and crops ($\beta = 0.11$), and near edges (20 m) of fallows ($\beta = 0.14$) and plantings ($\beta = 0.021$). Larger body sizes also were associated with edges (0 m) of woodland–fallow ($\beta = 0.057$) and woodland–woody debris ($\beta = 0.022$) habitats (Fig. 1a).

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

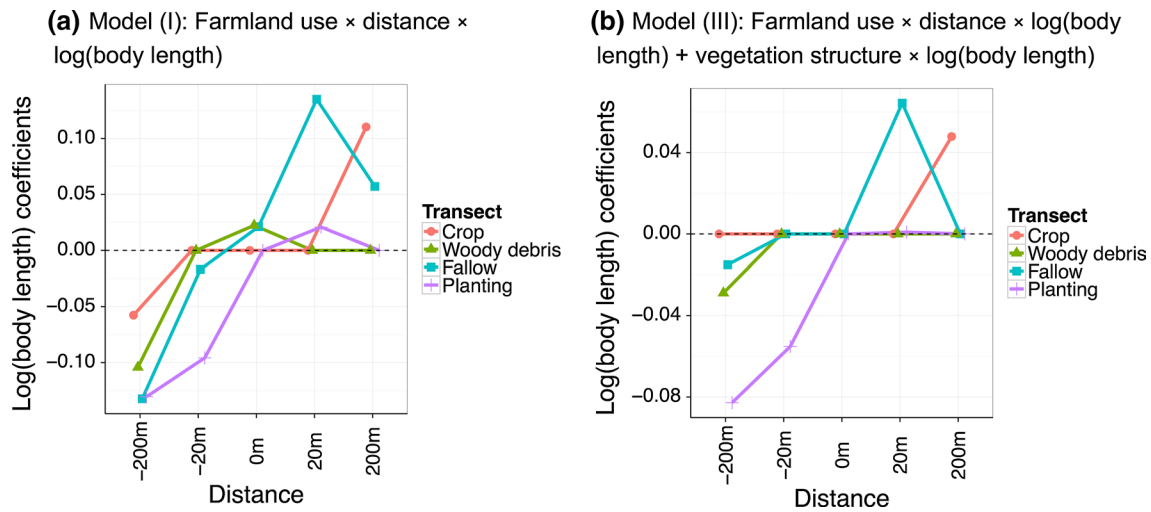


Fig. 1 Coefficients of fourth-corner interaction showing relationships between log (body length) and the interaction between farmland use and distance. Significant relationships are non-zero values, with direction of relationships shown as positive or negative values. Distance - 200 and - 20 m refers to the woodland, 0 m the edge, and 200 and 20 m the farmland adjoining the woodland. Adjoining farm-

land types are crop (circle), woody debris (triangle), fallow (square), and planting (cross). Lines show general trends only, and cannot be used to infer magnitude of differences between treatments. Fitted models as follows: **a** excluding vegetation structural variables, **b** accounting for vegetation structural variables

Vegetation structure accounted for some of the interactive effects of ‘farmland use’ and ‘distance’ on body size [combined model (III); cf. Fig. 1a, b]. After accounting for all four vegetation variables (vegetation height, litter cover, bare ground cover, and total herbaceous cover), larger sized beetles were found near edges (20 m) of fallows ($\beta = 0.06$) and in the interior (200 m) of crops ($\beta = 0.05$). Smaller sized beetles were still associated with areas near edges (- 20 m) ($\beta = - 0.05$) of woodlands adjoining plantings, and the interior (- 200 m) of woodlands adjoining fallow, woody debris and plantings, but not crops (Fig. 1b).

Regardless of farmland use [model (II)], body size was negatively related to litter cover ($\beta = - 0.05$), and positively related to bare ground cover ($\beta = 0.02$) and total herbaceous cover ($\beta = 0.06$) (Fig. 2a).

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

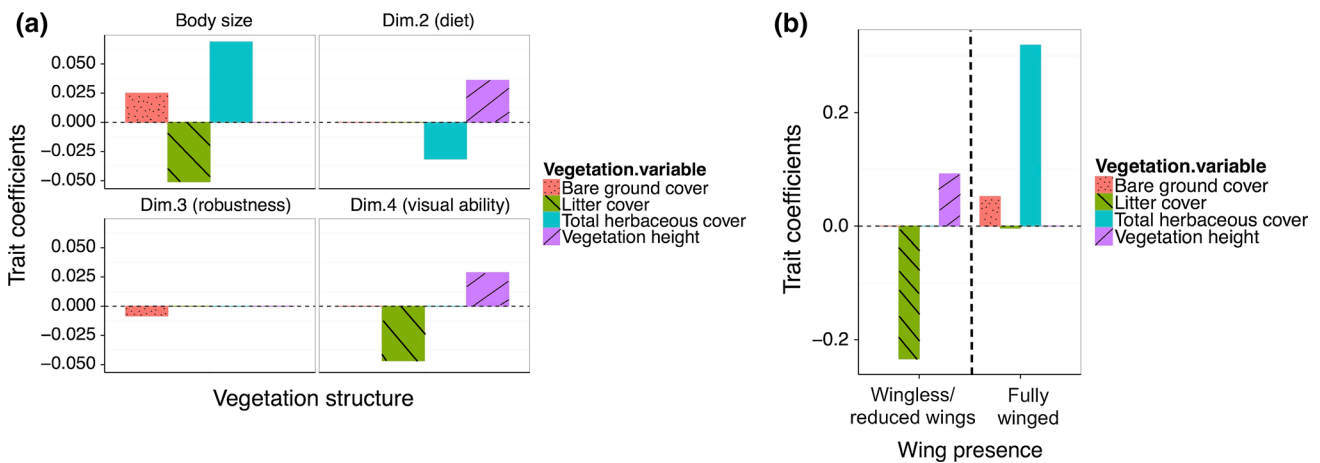


Fig. 2 Coefficients of fourth-corner interaction showing associations between vegetation structure and ground beetle traits of: body length and PCA dimensions Dim.2 (diet), Dim.3 (robustness) and Dim.4

(visual ability) summarising **a** traits, and **b** wing presence. Bars for four vegetation variables shown in the following order: bare ground cover, litter cover, total herbaceous cover and vegetation height

($\beta = -0.05$) and positively associated with vegetation height ($\beta = 0.03$) (Fig. 2a).

Wingless beetles (and those with reduced wings) were associated with increased vegetation height ($\beta = 0.09$) and decreased litter cover ($\beta = -0.23$). Winged beetles were associated with increased bare ground cover ($\beta = 0.05$), increased total herbaceous cover ($\beta = 0.32$), and decreased litter cover ($\beta = -0.003$) (Fig. 2b).

Discussion

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

Differences in body size and flying ability between woodlands and adjoining farmlands

We found higher occurrence of smaller beetles in the interior of woodlands, regardless of adjoining farmland type, and larger beetles in crop and fallow fields (Fig. 1a). This result is consistent with the textural-discontinuity hypothesis, which predicts that animal body size would exhibit discontinuous distribution following the discontinuity in the habitat structure of the landscape (Fischer et al. 2008; Holling 1992). This hypothesis predicts that smaller bodied species are more dominant in structurally complex landscapes with fine-grained heterogeneity, which is often associated with habitats having a high proportion of perennial native vegetation (e.g., woodlands). Conversely, larger bodied species are predicted to be more dominant in simpler landscapes with coarse-grained heterogeneity, such as habitats with a high proportion of annual vegetation (e.g., crop monocultures) (Fischer et al. 2008; Holling 1992).

The size–grain hypothesis also predicts smaller species to be associated with complex, less disturbed habitats (Kaspari and Weiser 1999), and has been specifically linked to movement mechanisms (Fischer et al. 2008; Kaspari and Weiser 1999). This hypothesis predicts that smaller species (often with proportionately shorter legs) have a functional advantage of being able to move through fine-grained environments, while movements of larger species are impeded (Gibb and Parr 2010; Kaspari and Weiser 1999). Conversely,

the size–grain hypothesis predicts that larger species are favoured in simpler, more disturbed habitats due to advantages from their higher robustness and dispersal ability (particularly greater leg length) in using open environments (Barton et al. 2011; Gibb and Parr 2010; Kaspari and Weiser 1999) (but see Teuscher et al. 2009, which could not support the size–grain hypothesis for several taxonomic groups). In open habitats, larger species are generally able to move rapidly while foraging or escaping predation (Kaspari and Weiser 1999), and can withstand higher desiccation stress from adverse climatic conditions (Barton et al. 2011; Kaspari 1993; Ribera et al. 2001). Besides movement, relationships between body size and habitat complexity also could be explained by other mechanisms, such as biogeographic and phylogenetic constraints (Allen et al. 2006), relationships between resource use and habitat complexity (Fischer et al. 2008), and the amount supplementary resources (Ries et al. 2004).

While most of the beetles sampled were fully winged, winged species were less common in the interior of woodlands. This result supports predictions that flying ability strongly influences beetle responses to disturbance in fragmented landscapes (Driscoll and Weir 2005). We suggest that although cursorial movements of carabids are more widespread in farmed areas (Hanson et al. 2016), if required, many species can overcome disturbance through flight to a more suitable environment (Gerisch 2011; Thiele 1977). Flying species have likely persisted in our agricultural landscape due to their ability to colonise scattered habitat patches, thereby accessing a wider range of available resources (Driscoll and Weir 2005; Gerisch 2011; Ribera et al. 2001; Tschardt et al. 2012). Our species-level data also suggest that species in woodlands might be dispersal-limited woodland specialists (e.g., small, flightless *Amblystomus* sp. C252), which may be susceptible to further habitat loss (Ribera et al. 2001; Tschardt et al. 2005).

Effects of vegetation structure on body size, body shape and flying ability

Body size

Interestingly, associations between vegetation structure and body size in our study also broadly support the textural-discontinuity (Holling 1992) and size–grain hypotheses (Kaspari and Weiser 1999) at small microhabitat scales. We found that larger body sizes were associated with lower litter cover and more bare ground (Fig. 2a), which are vegetation metrics sometimes used to characterize low habitat heterogeneity and high disturbance (Eyre et al. 2013; Ribera et al. 2001; Rouabah et al. 2015). These findings are also consistent with the hunting efficiency hypothesis, which predicts that larger predators would prefer more open microhabitats

(Brose 2003). We found, however, that total herbaceous cover was positively associated with body size (Fig. 2a). This suggests that total herbaceous cover might be a better indicator of the amount of available food or habitat resources than the level of vertical or horizontal habitat complexity (Kaspari and Weiser 1999; Parr et al. 2003).

When considered as additive effects, the vegetation variables explained most of the edge responses of body size to different farmland types (cf. Fig. 1a,b). These results support the previous studies on the influences of multiple vegetation and environmental attributes on carabid traits, through changes in habitat complexity, disturbance (Gerisch 2011; Ribera et al. 2001; Thiele 1977), or resource availability (Eyre et al. 2013; Rouabah et al. 2015). For example, we found larger species associated with low levels of litter in fallows (i.e., lower structural complexity), most likely caused by livestock grazing in fallows (cf. Fig. 1a, Online Resource 1: Fig. S3b, Fig. S4a). We also identified significant interactive effects of farmland use and distance from edges on all vegetation structural variables (Online Resource 1: Table S6). Therefore, the carabid trait responses we observed could also be interpreted as being secondary effects of the response of vegetation structure to farmland use and edge effects.

While vegetation structure was able to explain some of the underlying differences in carabid body size, there was residual variation in the relationship between body size and the interactive effects of farmland use and distance from edges (cf. Fig. 1a, b). This unexplained variability might be due to land management (e.g., soil tillage or pesticide use; Winqvist et al. 2014) or environmental factors (e.g., microclimate, Kaspari 1993; soil moisture, Thiele 1977) not measured in our study. Here, we highlight three notable patterns of body size associations with farmland use and edge effects that could not be fully explained by vegetation structure.

First, after accounting for effects of vegetation structure, we still found larger species in crops and fallows than woodlands. This is a surprising result, because, irrespective of vegetation structure, larger species have been found to be more vulnerable to increased habitat disturbance in intensively farmed areas, due to their longer development times and lower reproduction rates (Blake et al. 1994; Lovei and Sunderland 1996; Ribera et al. 2001). In agroecosystems, disturbance and primary productivity are thought to be key determinants of carabid activity and assemblage patterns (Eyre et al. 2013; Ribera et al. 2001; Thiele 1977). While productive farmlands can provide plentiful foraging resources, the availability of resources is short-lived in frequently disturbed agroecosystems and thus not accessible to higher trophic levels (Blake et al. 1994; Ribera et al. 2001). This has led to higher activity of larger carabid species in farms with high productivity and low to medium management intensity in England (Eyre et al. 2013). Farmlands in

our study region are perhaps better characterised as having low to moderate levels of disturbance, due to the soil conservation practices in the area (i.e., reduced tillage and increased stubble retention). Given that body size is positively associated with predation rates (Rusch et al. 2015), increased intensification of cultivation practices in this region may be to the detriment of larger carabid species and have profound implications for pest control in farmlands. Other ecosystem functions, such as the availability of large beetle prey for birds may also be affected (Blake et al. 1994).

Second, we found that vegetation structure could account for the occurrence of smaller species in the interior of woodlands adjacent to crops, but not in the interior of woodlands adjacent to plantings, fallow and the woody debris treatment (cf. Fig. 1a, b). This result is comparable to literature on the effects of surrounding farmlands on beetle assemblages within non-cropped or native habitat patches (Driscoll et al. 2013; Eyre et al. 2016; Tschantke et al. 2012). For example, Eyre et al. (2016) found that surrounding crop cover significantly affected carabid abundance in non-crop habitats, with more larger, non-flying species, where crop management intensity was reduced. Vegetation structure might be a discernible explanatory factor filtering towards smaller sized species in woodlands adjoining crops (e.g., following the textural-discontinuity hypothesis previously discussed), because long-term cropping in our study region could be regarded as an established component of the landscape (Eyre et al. 2016). In comparison, plantings, fallow rotation, and the woody debris treatment might be regarded as relatively novel, less disturbed landscape components that might, therefore, contributed to additional biotic or abiotic factors. For example, long-distance spillover of competitive or predatory fauna from these adjoining farmlands into the woodland interior (perhaps due to higher edge permeability; Rand et al. 2006) might have led to a reduction in larger carabids.

Third, we found that vegetation structure did not account for the occurrence of smaller species near woodland edges adjacent to plantings (cf. Fig. 1a, b). For this pattern, we speculate that high bird activity in plantings (Munro et al. 2007) might have led to their spillover into adjacent woodlands and increases in foraging rates of large beetles at all distances within the woodlands. More work is needed to investigate whether restoration plantings might act as ecological traps (Battin 2004) for larger sized beetles in agricultural landscapes.

Body shape

We found interpretable links between the structuring of body-shape-related traits and three ecological functions in our PCA, which supports previous beetle morphometric studies (Barton et al. 2011; Ribera et al. 1999; Winqvist

et al. 2014). The largest morphological variations in Carabidae are, for example, typically linked to specialized modes of nutrition (Thiele 1977). In our study, the compound axes Dim.2 was related to diet (increasing head width), Dim.3 to robustness (increasing elytra width), and Dim.4 to visual ability (increasing eye protrusion).

We found that vegetation structure was a good predictor of body-shape-related traits associated with diet (Dim.2), robustness (Dim.3), and visual ability (Dim.4), whereas we did not find interactive effects between these traits and farmland use or distance from edges. Our findings suggest that—regardless of land-use context—vegetation variables measured in our study adequately captured changes to environmental conditions that explained body-shape-related trait responses. These results support studies on the key influence of small-scale changes in vegetation structure on morphological traits (Barton et al. 2011; Gibb and Parr 2013; Rouabah et al. 2015; Winqvist et al. 2014). Our results highlight the importance of considering multiple shape-related traits beyond body size (Barton et al. 2011; Öckinger et al. 2010), because they may better predict species responses to landscape changes (McGill et al. 2006).

Higher values of Dim.2 (diet) with higher vegetation height and lower total herbaceous cover (Fig. 2a) may be explained by two different processes. First, greater occurrence of species with wider heads (e.g., *Egadroma* sp. C086, *Pericompsus* sp. C164, and *Simodontus* sp. C039; Online Resource 1: Table S5, Figs. S2 and S5) may be due to the availability of larger prey associated with increased productivity of taller vegetation (Forsythe 1987; Weiser and Kaspari 2006). Second, species with wider heads (e.g., *Amblystomus* sp. C252; Online Resource 1: Table S5, Figs. S2 and S5) may be disadvantaged in physically navigating through more complex microhabitats, where there is higher total herbaceous cover (Gibb et al. 2015).

We identified a negative association between Dim.3 (robustness) and bare ground cover (Fig. 2a). This result was inconsistent with predictions of more robust species in simpler and more disturbed areas (Barton et al. 2011; Kaspari and Weiser 1999; Wiescher et al. 2012). Our species composition data show that this result may be related to an increase in narrow-shaped *Notiobia* sp. C293 with increased bare ground, although we also found increased occurrence of a relatively robust *G. multipunctatus* with increased bare ground (Online Resource 1: Table S5, Figs. S2 and S5). It could be that elytra width also represents life-history traits outside of robustness for different species, such as some species with wider elytra having stronger flying ability, and other narrower bodied species being associated with faster running speeds which might be advantageous in open habitats (Gibb et al. 2015).

Positive associations between Dim.4 (visual ability) and vegetation height (Fig. 2a) is consistent with a study

that found ants adapted to having increased sensory abilities (including larger eye widths) in more complex habitats due to perceptually demanding conditions in these habitats (Yates et al. 2014). For beetles, however, simpler microhabitats have previously been found to contain more diurnal visual hunters with larger eye protrusion and surface area than in complex microhabitats (Fountain-Jones et al. 2015; Talarico et al. 2011).

Flying ability

We found higher occurrence of wingless or brachypterous species in areas with increased vegetation height, and higher occurrence of fully winged species in areas with increased bare ground (Fig. 2b). These results are consistent with studies that have found less flight-capable arthropod species in denser vegetation, where more stable habitat conditions favoured species with lower mobility (Kotze and O'Hara 2003; Shibuya et al. 2014). We suggest that flightless species might be particularly disadvantaged in cultivated farmlands due to reduced vegetation structural complexity at local scales.

Conclusions

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

Our findings indicate potential implications of land-use changes on trait-mediated ecological functions of carabid

species across both managed and unmanaged parts of fragmented farming landscapes. This includes, for example, predation of differently sized invertebrate prey by beetles, or the availability of varying beetle sizes as food for other arthropod and vertebrate predators, in areas of contrasting land use. We suggest maintaining adequate heterogeneity in land uses and vegetation structural attributes (e.g., by incorporating low-intensity land uses or reducing weeds that might lead to homogenised vegetation) as a way of supporting a range of different species sizes and traits across the landscape, which may promote higher landscape-level diversity (Tscharrntke et al. 2005) and increased variety of ecological functions (Rouabah et al. 2015; Wood et al. 2015).

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Author contribution statement KN and DAD conceived the ideas and design for overall experiment, KN, PB, and SaM conceived and developed traits methodology, KN analysed data with statistical input from WB and MJE, KN and MJE conducted lab work, KN conducted fieldwork and led manuscript writing, and all authors revised the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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