Rothamsted Repository Download

A - Papers appearing in refereed journals

Jowett, K., Milne, A. E., Metcalfe, H., Hassall, K. L., Potts, S. G., Senapathi, D. and Storkey, J. 2019. Species matter when considering landscape effects on carabid distributions. *Agriculture, Ecosystems & Environment.* 285 (2019), p. 106631.

The publisher's version can be accessed at:

- https://dx.doi.org/10.1016/j.agee.2019.106631
- https://www.sciencedirect.com/science/article/pii/S0167880919302476

The output can be accessed at: https://repository.rothamsted.ac.uk/item/8wyx8/species-matter-when-considering-landscape-effects-on-carabid-distributions.

Species matter when considering landscape effects on carabid distributions

Kelly Jowett[a,b,*], Alice E. Milne[a], Helen Metcalfe[a], Kirsty L. Hassall[a], Simon G. Potts[b],
Deepa Senapathi[b], Jonathan Storkey[a]

[a] *Sustainable Agricultural Sciences, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK*
[b] *Centre for Agri-Environmental Research, School of Agriculture Policy and Development, University of Reading, Reading, Berkshire RG6 6AR, UK*

ABSTRACT

Increasing the abundance and diversity of carabid beetles is a common objective of farm habitat management to deliver sustainable pest control. Carabid spatial distributions in relation to crop areas are important to the delivery of this ecosystem service.

We used pitfall count data at distances from edge habitats into crop centres, from farm sites across the UK, to determine the effects of in-field and adjacent environmental features on carabid abundance and diversity.

Overall carabid abundance increased towards the crop centre, whilst species richness and diversity decreased. The analyses of carabid abundance based on all the species pooled together strongly reflected the behaviour of the most abundant species. Species preferences varied by crop, soil type, and environmental features. For instance, some species were positively associated with habitats such as margins, while others responded negatively. This contrast in individual species models highlights the limitations on pooled models in elucidating responses.

Studies informing farm-habitat design should consider individual species' preferences for effective enhancement of pest control services. Diverse cropping and landscape heterogeneity at the farm scale can benefit the varied preferences of individual species, help build diverse communities and, potentially increase service resilience and stability over time.

1. Introduction

Carabid beetles, as ubiquitous polyphagous predators, are much studied in agro-ecosystems. Research has shown their potential to control pest arthropods and weed seeds in crop areas, leading to the inclusion of management measures to boost carabid abundances on farms (Kromp, 1999). Landscape features such as hedgerows and field margins are presumed to provide refuge, breeding and hibernation habitats, and food resource stability; therefore, ensuring viable populations in proximity to crop areas (Thomas et al., 2002). The European Commission and member states have made policy commitments towards the sustainable use of pesticides (EC, 2009 Directive 2009/128/ EC, and National Action Plans: EC, 2018) to support more efficient food production and reduce negative environmental impacts. To help deliver on this, effective management solutions to enhance natural pest regulation need to be developed (Petit et al., 2018).

Approximately 350 species of carabid reside in the UK, with widely differing characteristics, environmental needs and preferences. Carabids inhabiting agro-ecosystems are polyphagous generalists, exploiting the range of disturbed agroecosystems (Thiele, 1977). Previous work has focussed on within field factors that drive carabid community structure, for example agricultural inputs (Garratt et al., 2011) and the presence of field margins (Woodcock et al., 2007). Since a common justification of many agricultural studies is the delivery of ecosystem services by carabids, the literature has focussed on the metrics this utility is dependent on: overall abundance, diversity, and spatial distribution. Overall abundance is a major focus, as it affects the quantity of service provision (Kotze et al., 2011; Pennekamp et al., 2018). Diversity is thought to affect the quality, stability, and resilience of provision, by the differential predation, environmental tolerances and complementarity of species (Petit et al., 2018). Distribution impacts the provision in relation to service requirements spatially (Holland et al., 2005; Weibull et al., 2003).

As well as in-field factors, boundary habitats and adjacent environments also significantly impact carabid abundance and community composition (Fahrig and Jonsen, 1998; Holland et al., 2004). Yet a key aspect for the delivery of pest-control services is the role these landscape features play in determining the carabid species that are

---

found in the crop determined by the degree of spill over (Holland et al., 2009; Petit et al., 2018). For instance, the presence of certain types of carabids at the field edge may not be strongly associated with the species distribution and abundance of those foraging within crop areas (Crowder and Jabbourb, 2014; Holland et al., 2005). Carabid abundance by distance from the crop edge has been extensively studied to explore ecological edge effects (Koivula et al., 2004), yet until recently literature focussed on the plot-scale effects of management, irrespective of landscape composition (Booij, 1994; Petit et al., 2018). Recent work, linking landscape composition to in-crop community structure (Boetzl et al., 2018; Gallé et al., 2018), lacks replication over multiple crops and sites. Meta-analyses have drawn general ecological conclusions at a landscape scale (Karp et al., 2018; Lichtenberg et al., 2017), but these fail to capture fine-scale nuances and interactions. The grouping of ecologically dissimilar species and methodologies into broad categories potentially loses the distinctions and details necessary for farm-scale specific interpretations. For example, Bianchi et al. (2006) found that complex landscapes enhanced natural enemy pest control in 74% of studies across multiple arthropod groups but, for carabids, landscape composition had no apparent effect. This is likely due to the loss of power to separate out the influence of other landscape factors, such as the relative importance of landscape configuration on carabid distribution and infield management (Fusser et al., 2018; Winqvist et al., 2011). Therefore, to determine whether complex landscapes enhance natural enemy pest control for such diverse taxa, the retention of site specifics could disentangle complex interactions to enable more informative conclusions to be drawn.

In attempting to disentangle these complex landscape effects on carabids, studies tend to focus at either the narrow or broad end of the study spectrum, such as the plot to field scale, or landscape to regional scale, respectively. Brooks et al. (2008) studied national scale distributions; finding carabid meta-communities structured by dynamics operating at two spatial scales: at a local scale, along a resource gradient determined by crop type; and at a landscape scale along a longitudinal gradient. Woodcock et al. (2014) considered national patterns of functional diversity, highlighting correlations between carabids and landscape cover of semi-natural habitats and linking this to extinctions ordered by body size and dispersal ability.

There remain relatively few studies covering the distribution of carabids at the mid-scale (field to landscape), which we define as the *farm-scale* integrating both cropped areas and semi-natural features (Kotze et al., 2011). This scale is important when considering how to manage better the population dynamics and community composition of carabids (Brooks et al., 2008; Kotze et al., 2011). Within the context of this knowledge gap, Labruyere et al. (2016) found that crop type and management intensity affected carabid community composition at the plot scale, whilst neighbouring habitat (grassland or oilseed rape (OSR)) had an effect at the farm-scale, and landscape scale. However, additional evidence is required to inform management decisions at the farm-scale to improve the efficacy of habitat management to deliver ecosystem services from carabids. For example, the optimal arrangement of semi-natural habitat in relation to different crop types, enabling carabids to follow crop rotations; towards greater service delivery and resilient communities.

Here, we make novel use of the UK Farm-Scale Evaluation (FSE) of Genetically Modified Herbicide Tolerant (GMHT) crops (Firbank et al., 2003; Brooks et al., 2003). The study gathered extensive and detailed survey data on farm habitats, within and adjacent to GMHT and conventional crops. This is the largest dataset on farm-scale distribution of carabids over multiple UK farm sites; and within various crops. In relation to carabids, the FSE data have previously been analysed in five studies (Brooks et al., 2003, 2008, 2012; Woodcock et al., 2014; Labruyere et al., 2016). Here we consider the data from a new perspective and focus on the effect of, previously unpublished, data on neighbouring environmental features on carabid abundance and diversity in cropped fields. In line with more recent understanding and

work, we argue that considering processes at this farm-scale is the most relevant for management decisions aimed at manipulating in-field service delivery (Kotze et al., 2011; Holland et al., 2009; Weibull et al., 2003).

We analysed the data to determine how environmental and management factors interact to affect the in-field abundance and diversity of carabid species, addressing three hypotheses on the relationships between carabids and land use to help inform habitat management and to develop recommendations for carabid mediated pest control.

H1. Carabid abundance, species richness, and diversity decrease with distance from the boundary habitat towards the crop centre.

H2. The relationship of carabid abundance, species richness, and diversity with distance into the field will be contingent on the neighbouring field boundary and habitat. For example: abundance, species richness, and diversity in the crop area are expected to be higher closer to and in the presence of a field margin.

H3. Responses to environmental and management factors will vary by individual carabid species. For example: species associated with woodland habitats are expected to occur more frequently in the presence of a hedge boundary.

2. Materials and methods

2.1. Data

The FSE dataset quantifies weed and invertebrate populations in conventional and GMHT crops and the ecological characteristics of habitats adjacent to these crops in a network of 251 fields in lowland farms across Great Britain from 2000 to 2002 (Firbank et al., 2003). The crops included in the study were spring-sown sugar beet (*Beta vulgaris* L.), maize (*Zea mays* L.), spring OSR (*Brassica napus* L.) and winter OSR (*Brassica napus* L.). The experiment comprised random blocks where each field was a block with treatments (conventional or GMHT) replicated once on half-field units. Each field-crop combination was sampled in a single growing season. Here we use a subset of data from conventional crops, focussing on variables that we expect to affect carabid abundance.

Pitfall trapping was conducted according to the FSE protocol (Brooks et al., 2003) on four transect lines per field at 3 distances: 2, 8, and 32 m into the crop (Fig. 1). Traps were run for 14-day periods three times in 2000, 2001 and 2002, respectively; May to August in spring crops, and September to early July for winter OSR. For each event, carabids were identified to species level and counted.

Environmental factors were grouped to reflect differences in the biology of carabid species, accounting for similar habitat structures and resources in carabid niche space (Thomas et al., 2002). These were: *Adjacent habitat* (Fig. 1), with six levels: crop, ploughed, grassland, semi-natural (including scrub and heath), woodland, and urban; *Hedge*; *Margin*; *Water* (pond or streams); *Road or track*; and *Ditch*; with levels of present or absent. Other in-field factors were *Soil type* – categorised as either Heavy, Medium, Light, or Organic; *Crop type* (with 4 levels as listed above); and *Distance* into crop, with levels categorised as 2, 8 and 32 m.

2.2. Statistical analysis

2.2.1. Pooled-carabid abundance, species richness, and diversity

We analysed only the count data from complete records with information recorded for all environmental factors, leaving 3469 trap occasions, from 992 transects. For each trap occasion we calculated, what we refer to as 'pooled-carabid abundance' (N), i.e. the total number of carabids of any species, and species richness (S), i.e. the number of different species. We fitted the log series model (Eq. (1)) to the data by maximum likelihood to give estimates of Fisher's log-series
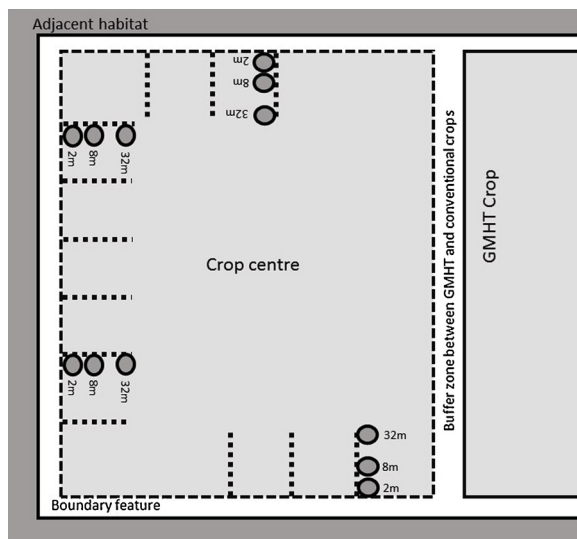
Fig. 1. The experimental layout of the Farm Scale Evaluation. The circles denote trap locations, on dashed transect lines, from boundary feature to crop centre.
Source: Adapted from Firbank et al. (2003).

alpha ($\hat{\alpha}$), a robust and widely used diversity metric (Beck and Schwanghart, 2010; Magurran, 2013)

$$S = \hat{\alpha} \, \log\left(1 + \frac{N}{\hat{\alpha}}\right) \tag{1}$$

We fitted Generalised Linear Mixed effects Models (GLMMs) using the GenStat statistical software package (Payne, 1993) to determine the effect of environmental factors on pooled-carabid abundance (N), richness (S) and species diversity (quantified as $\hat{\alpha}$). We considered the environmental factors *Soil type*, *Crop type*, *Adjacent habitat*, *Hedge*, *Margin*, *Water*, *Road or track*, *Ditch*, and *Distance* into the crop as fixed effects with all two-way interactions. The full random model was defined as *Site*, and nested within each site, *Transect* and nested within each transect, *Visit* (i.e. *Site/Transect/Visit*). We assumed a Poisson distribution for pooled-carabid abundance, species richness and diversity and used a log link function. We estimated the dispersion parameter to account for over dispersion, and set this to one where under dispersion was detected to avoid inflating the significance of hypothesis tests (see Welham et al., 2014). We selected terms using backwards elimination according to the largest *P*-value given by the Kenward–Roger approximate *F*-tests, in some cases it is not possible for the software to estimate the *F*-value so we report the associated Wald test, which is approximate under a large sample approximation. The final predictive model was chosen when all remaining terms gave significant values ($P \leq 0.05$) when dropped from the model.

2.2.2. Frequency and abundance of individual species

Preliminary analysis showed the counts were dominated by a single species, therefore to separate species responses and further investigate the effect of environmental factors and management on abundance we also considered the effect of the explanatory variables at the level of individual species. There were 92 species in the dataset in total, but many were observed extremely infrequently. Therefore, we restricted this analysis to ten species. These were selected to represent the most abundant and frequently trapped species, to account for bias towards aggregative species (Table 1). We fitted separate GLMMs to the data for each of these species, to identify differential responses. We first modelled the presence/absence of each species using a binomial GLMM to understand the characteristics contributing to the probability that each species was present (assuming a logit link function). Conditional on species presence, we then modelled the abundance using a Poisson

GLMM (assuming a log link function).

The structure of the models was similar to that described above (see Section 2.2.1). As before, the dispersion parameter was estimated to account for over-dispersion or fixed to 1 for under dispersion. Terms were selected using backwards elimination as described above.

3. Results

The ten species selected as the most abundant and frequently trapped accounted for nearly 94% of the total counts (Table 1). The order of species ranks between count and trapping frequency was different, reflecting aggregative species: those that occur in fewer locations but with higher abundances where trapped. The catch was heavily dominated by *Pterostichus melanarius* (54% of total carabids counted and identified in 85% of traps).

3.1. Pooled-carabid abundance, species richness, and diversity

The fitted models for pooled-carabid abundance, species richness and diversity are presented in Table 2. Pooled-carabid abundance significantly increased with distance into the crop and varied significantly between crops with most carabids trapped in sugar beet, and least in winter OSR. There was a significant interaction between crop type and distance (Fig. 2a). The highest pooled-carabid abundance was found on light and medium soils, and lowest in organic (Fig. 2b). There were no significant effects of any boundary feature on the pooled carabid abundance.

Species richness decreased with distance into the crop and was significantly greater on soils classified as light or medium and least on organic soil (Fig. 3a). The presence of a margin had a significant effect with a greater number of species present when margins are absent (Fig. 3b).

Diversity, measured as Fisher's α, also decreased into the crop. Diversity varied by crop with the largest diversity in winter OSR and lowest in maize and sugar beet (Fig. 4a). There were interactions between Distance and the Road/Track factor and Ditch (Fig. 4b and c).

3.2. Abundance according to species

In the GLMMs of individual species presence/absence and abundance, the Crop, Distance, and Soil factors were often retained as significant terms (Tables 3 and 4). Generally, more significant interactions and landscape variable terms were retained in the abundance models (Table 4).

The significant terms in the models for *P. melanarius* (Tables 3 and 4) largely correspond with those in the pooled carabid abundance model (Table 2). This reflects the dominance of *P. melanarius* in the total catch (Table 1). Fig. 5 illustrates the dominance of *P. melanarius* across crops and distances. It can be seen that by discounting *P. melanarius*, the highest pooled-carabid abundances would be less biased to 32 m distances and the sugar beet crop.

The direction of response differed between species for factors identified as significant in the models (Figs. 5–7). Most species showed a decrease in abundance and/or probability of occurrence from crop edge to centre (although for some species this was crop dependent), whilst some, notably *P. melanarius*, increased in abundance at the crop centre (Figs. 5 and 6). The predictions from the individual species models demonstrate differences in response between species that are lost in the typical pooled analyses, whilst infield habitats are key to presence/absence and abundance, the specifics of responses vary. Responses are stronger in the presence/absence models, suggesting that the in-crop environment is most influential in the presence of species. Again, we note the effect of pooled counts in obscuring details of distributions: *P. melanarius* is most abundant in sugar beet, and least in Winter OSR; the pattern shown by the overall abundance (Fig. 5). This pattern does not hold true for all species (Fig. 6).

Table 1

Summary statistics for the ten most common species of carabid in the FSE. These ten species were selected for further analysis based on abundance and frequency of trapping.

Species	Count	% of total	Occasions trapped	% of traps	Mean per trap	Std. Dev	Variance	Skew
Pterostichus melanarius	106,589	53.8	2933	84.6	30.40	52.38	2744	3.04
Pterostichus madidus	38,353	19.4	1542	44.5	11.02	37.25	1388	6.51
Harpalus rufipes	7799	3.9	1160	33.4	2.23	6.98	48.65	6.63
Bembidion lampros	4788	2.4	973	28.0	1.37	5.66	32.08	10.05
Pterostichus niger	8165	4.1	961	27.7	2.27	7.63	58.14	6.05
Agonum dorsale	2121	1.0	805	23.2	0.602	1.81	3.29	5.84
Trechus quadristriatus	2517	1.3	739	21.3	0.70	2.61	6.80	7.78
Calathus fuscipes	3894	2.0	700	20.2	1.09	4.442	19.73	8.34
Nebria brevicollis	6630	3.3	643	18.5	1.83	12.91	166.80	16.97
Bembidion tetracolum	5531	2.8	466	13.4	1.58	10.76	115.80	13.21
Total top ten	186,387	94.1	3469					
Total overall	198,051							

Table 2

GLMM final terms and significance for species richness, and diversity.

	Main effects									Interactions			
	Hedge	Margin	Water	Adjacent habitat	Road or Track	Ditch	Crop	Distance	Soil category	Distance & Crop	Distance & Soil category	Distance & Road/Track	Distance & Ditch
Pooled-carabid abundance							***	***	***	***	***		
Wald							23.07	45.24	11.56	17.39	19.32		
d.f.							3	2	3	6	6		
Species richness		**						***	***				
Wald		5.60						39.74	16.44				
d.f.		1						2	3				
Diversity (Fisher's α)					NS	NS	***	***		***		***	***
Wald					1.03	0.68	13.13	21.01		17.35		14.69	16.71
d.f.						1	3	2		6		4	2

NS term included in model but not significant.

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

Species responses also varied by landscape features. For Margin, some species were predicted to have a greater abundance near the crop edge in the presence of a margin (*Bembidion lampros*, *Nebria brevicollis*), whilst some were predicted to be less abundant (*Trechus quadristriatus*) (Fig. 7). In terms of the interaction of adjacent habitat with distance into the field, we observed different responses of individual carabid species to urban, ploughed, and woodland adjacent habitats; yet less marked differences in predicted abundances in response to adjacent crop and grassland habitats (Fig. 8). A high abundance close to the field edge with a steep negative gradient into the field is indicative of a strong preference to the adjacent habitat with spill over only to short distances into the field (for example *Bembidion tetracolum* next to semi-
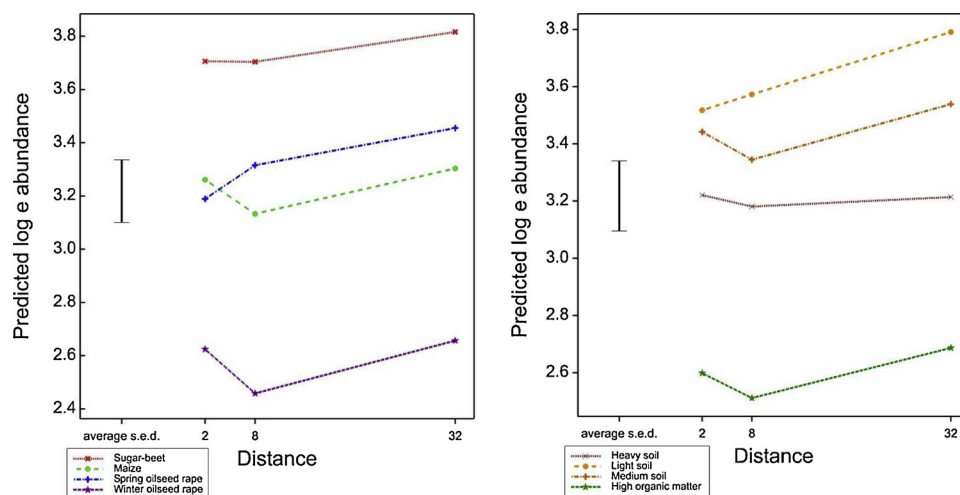

Fig. 2. Pooled carabid abundance predictions plotted against distance into crop according to (a) crop type and (b) soil category. The vertical bar shows the average standard error of the difference.
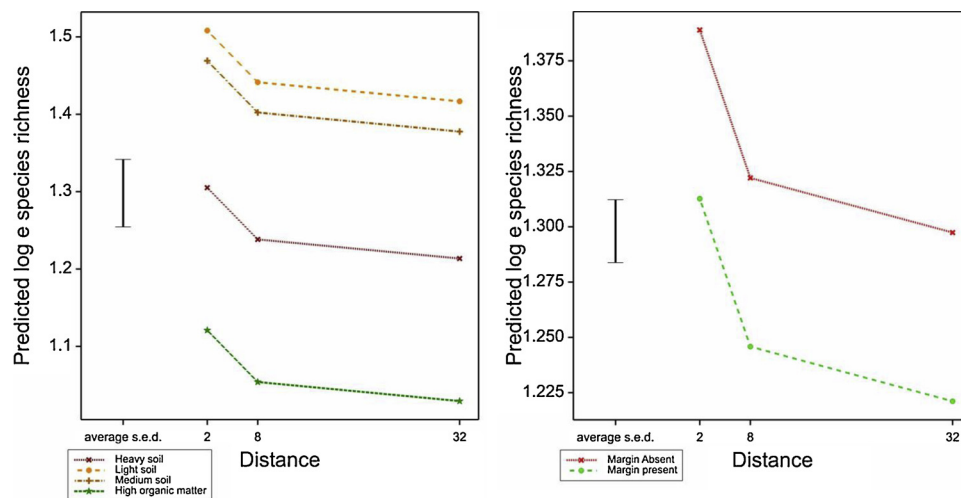
Fig. 3. Species richness predictions plotted against distance into the crop according to (a) soil category and (b) the presence of a margin. The vertical bar shows the average standard error of difference.

natural habitat). In contrast, the consistently positive gradients for *P. melanarius* confirm its preference for the cropped field centre habitat with some evidence for an adjacent ploughed field reducing the local scale population size.

4. Discussion

4.1. H1: Carabid abundance, species richness, and diversity decrease with distance from the boundary habitat towards the crop centre

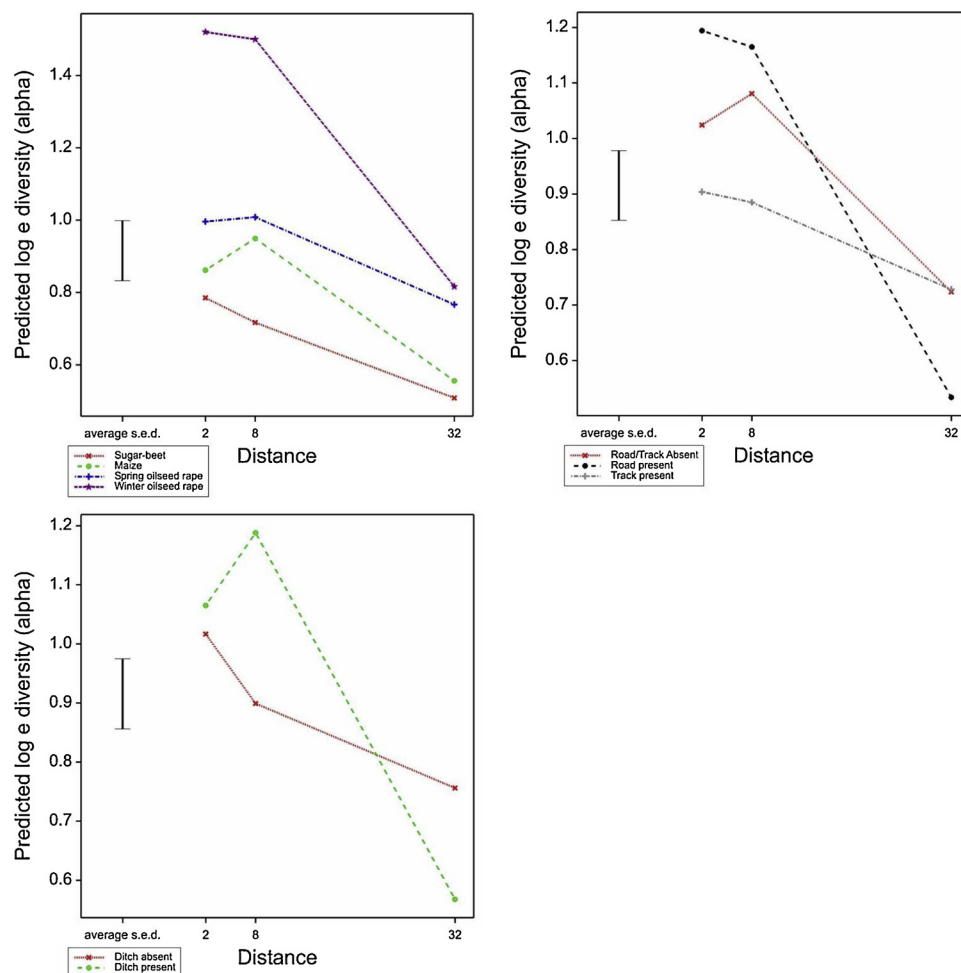We found that in contrast to Hypothesis 1, pooled-abundance of

Fig. 4. Diversity (Fisher's alpha) predictions plotted against distance into crop according to (a) crop type, (b) the presence of roads or tracks (Road/Track factor) and (c) the presence of a ditch. The vertical line shows the approximate average standard error of difference.

Table 3
GLMM of factors upon presence/absence, by individual species.

Main effects

	Hedge	Margin	Water	Adjacent	Road or Track	Ditch	Crop	Distance	Soil category
P. melanarius	NS	NS	NS	NS	NS		***	NS	NS
P. madidus			*				NS	***	***
H. rufipes							***	***	**
B. lampros		NS	NS	NS		*	*		
P. niger	NS	NS	NS				***	NS	
A. dorsale		NS		NS			*	***	NS
T. quadristriatus		NS		NS	NS		NS	***	NS
C. fuscipes	NS	NS		NS	NS		*	***	
N. brevicollis						NS	***	***	
B. tetracolum	NS		NS	NS			*	**	NS

Interactions

	Distance & Crop	Distance & Soil category	Distance & Road/Track	Distance & Ditch	Distance & Adjacent	Distance & Hedge	Distance & Water	Distance & Margin	Crop & Adjacent	Crop & Soil category	Crop & Hedge	Crop & Margin	Adjacent & Soil category	Water & Adjacent	Water & Road/Track
P. melanarius										***					NS
P. madidus	**														
H. rufipes	***														
B. lampros							**	NS							
P. niger						NS	***	*							
A. dorsale		***			**			***				NS		*	
T. quadristriatus	**	***						***							
C. fuscipes	*		*		***	**		***		*					
N. brevicollis	*			**					**				*		
B. tetracolum	**	**									**				

NS term included in model but not significant.

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

6

Table 4
GLMM of factors upon abundance where present, by individual species.

Main effects

	Hedge	Margin	Water	Adjacent	Road or Track	Ditch	Crop	Distance	Soil category
P. melanarius				NS	NS		***	***	NS
P. madidus	NS	NS		NS	NS		NS	NS	NS
H. rufipes	NS		NS	*		NS	NS	**	NS
B. lampros	NS	NS	NS	NS	NS		**	NS	***
P. niger[†]	NS		NS	*	NS			**	NS
A. dorsale			NS					***	
T. quadristriatus		NS		NS	NS				NS
C. fuscipes	NS	NS		NS			*	NS	NS
N. brevicollis		NS					NS	***	
B. tetracolum	NS			NS	NS			NS	

Interactions

	Distance & Crop	Distance & Soil category	Distance & Road/Track	Distance & Margin	Distance & Adjacent	Distance & Hedge	Distance & Water	Hedge & Adjacent
P. melanarius	***	***	***		NS			
P. madidus	***	***	NS		***			
H. rufipes	***	***		**	***			**
B. lampros	**	***		**	***	***	***	
P. niger[†]						NS	NS	
A. dorsale			***	***	***		***	***
T. quadristriatus		***			***			
C. fuscipes	*	**			***	NS		
N. brevicollis	***			***				
B. tetracolum					***	***		

NS term included in model but not significant.

* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$. [†] Site.transect random term was dropped due to zero variance component.
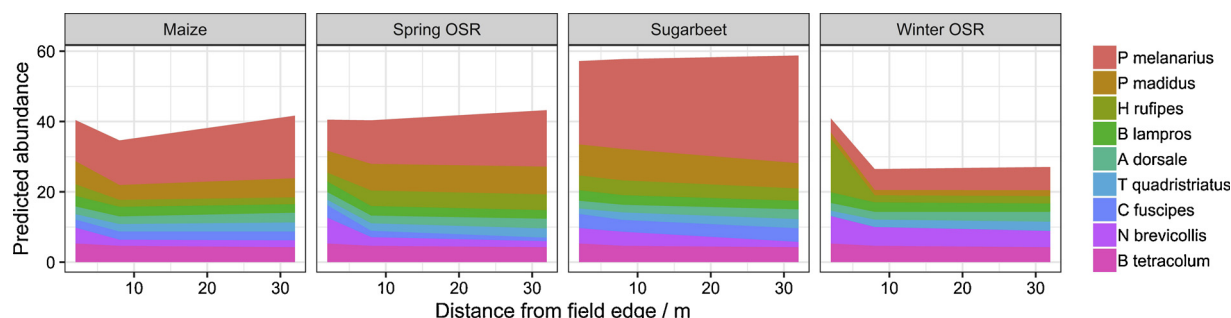
Fig. 5. Overall abundance predictions from the individual GLMMs by Distance into crop, stacked by Species. Predictions are averaged over all levels of other terms included in the model (see Table 3).

carabids increased towards the centre of the field. However, the overall picture is biased by the dominance of *P. melanarius* in catches. This species is predatory, aggregating in crop areas following pest distributions (Warner et al., 2008) and we would predict this would have a positive effect on the delivery of ecosystem services into field centres. However, if we consider predator diversity to be an important component of ecosystem services (Greenop et al., 2018), the increasing dominance of a single species away from field edges may compromise the resilience of service delivery; the abundance of most other major species reduced with distance into the crop. However, interactions between distance into crop and other factors such as soil category and

crop type indicate that there is not a simple response to distance even within a species. For example *Harpalus rufipes* is more abundant near the edge in Winter oilseed rape, yet more abundant towards the centre in Spring oilseed rape. Since these crops are similar in structure, this suggests temporal influence of management or resources is crucial (as trapping was carried out at different times in winter and spring crops) and species with differing habitat requirements may be delivering predation services at different times of the cropping season. For example, relative weed seed availability in crop areas (Petit et al., 2014).

The importance of species level differences in the response to distance into the crop is particularly important when considering the
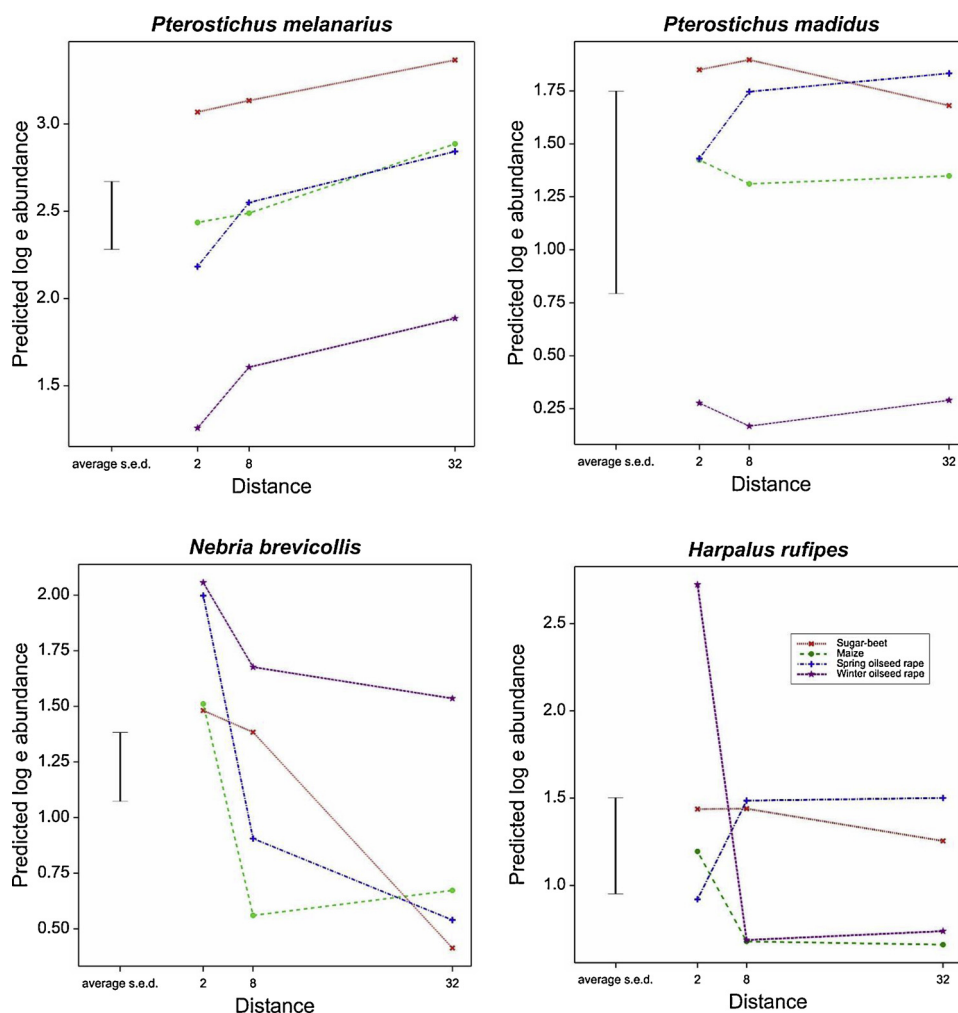

Fig. 6. Abundance predictions by distance according to crop type for species: (a) *P. melanarius*, (b) *P. madidus*, (c) *N. brevicollis* and (d) *H. rufipes*. The vertical line shows the approximate average standard error of difference.
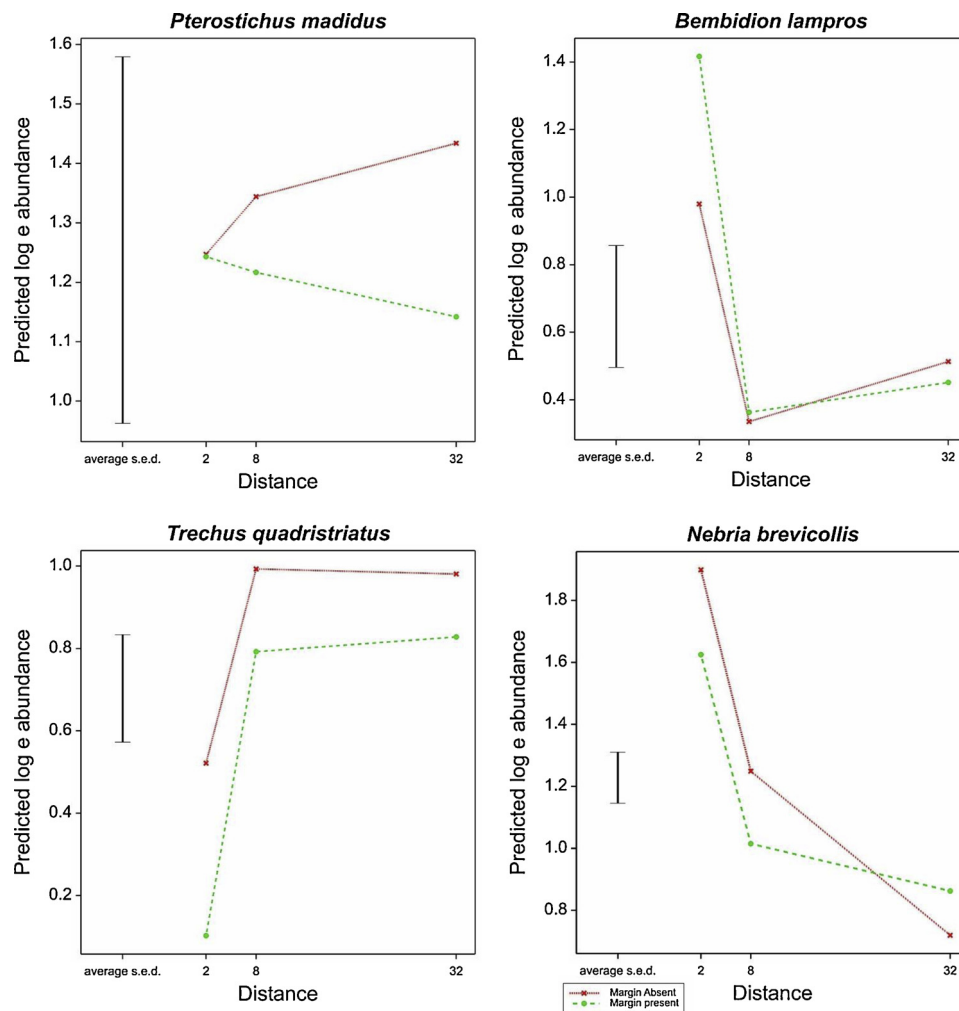
Fig. 7. Abundance predictions by distance according to margin presence/absence, for species: (a) *P. madidus*, (b) *B. lampros*, (c) *T. quadristriatus* and (d) *N. brevicollis*. The vertical line shows the approximate average standard error of difference.

implementation of agri-environment options as not all species will respond in the same way. Boetzl et al. (2018) investigated abundances by distance into crops and found evidence for distance decay, suggesting that carabid abundances were increased in fields of oilseed rape adjacent to agri-environment options. However, our results indicate that their approach of considering pooled carabid abundances may be obscuring underlying trends, particularly if the counts are dominated by one or two species. This highlights an advantage of using the FSE dataset that includes data from multiple crops and regions, capturing variability in responses between contrasting species pools and supporting Hypothesis 3. The most abundant species in their study were smaller, more flight dispersive species in contrast to *P. melanarius* which is predominantly ground dispersive. However, we also note that in our data the greatest distance into the crop was 32 m, which may not constitute crop centre: Boetzl et al. (2018) extended distance to around 60 m.

Species richness and species diversity were shown to decrease towards the centre of the crop supporting Hypothesis 1. These observations agree with the literature on edge effects: with species of both overlapping habitats co-occurring in the peripheral zones (Bianchi et al., 2006; Saska et al., 2007). This reflects the requirements of carabids in terms of providing habitats for aestivation and hibernation, and stable food and shelter, so dictating accumulations of species where these resources are most likely to co-occur (Thiele, 1977).

4.2. H2: The relationship of carabid abundance, species richness, and diversity with distance into the field will be contingent on the neighbouring field boundary and habitat

We found no significant interactions between landscape features and distance in the models of pooled-carabid abundance and species richness indicating that the spillover of carabids from off-crop habitats into the field is limited. However, in the diversity model we did observe significant interactions between distance and landscape features that represent a barrier or corridor for many species. This supports the theory that the carabid community structure is driven by a combination of spatial mass effects from corridors, or the prevention of spatial mass effects across species specific barriers, from adjacent habitats. The lack of such effects in the species richness models may be accounted for by the nature of this measure showing only the total count of species, and not incorporating evenness, for example a habitat may be species rich but not diverse if dominated by certain species (Magurran, 2013; Shmida and Wilson 1985).

The only environmental feature retained in the pooled-carabid models was margin, yet this did not interact with distance to support Hypothesis 2. Margins, with relatively diverse and stable resources, are generally thought to support more species and higher abundances (Weibull et al., 2003). However, we found species richness was lower in the presence of a margin. This may be due to the margin acting as a sink, providing stable resources for a greater range of species than the habitat afforded within the crop. Fusser et al. (2018) and Anjum-Zubair
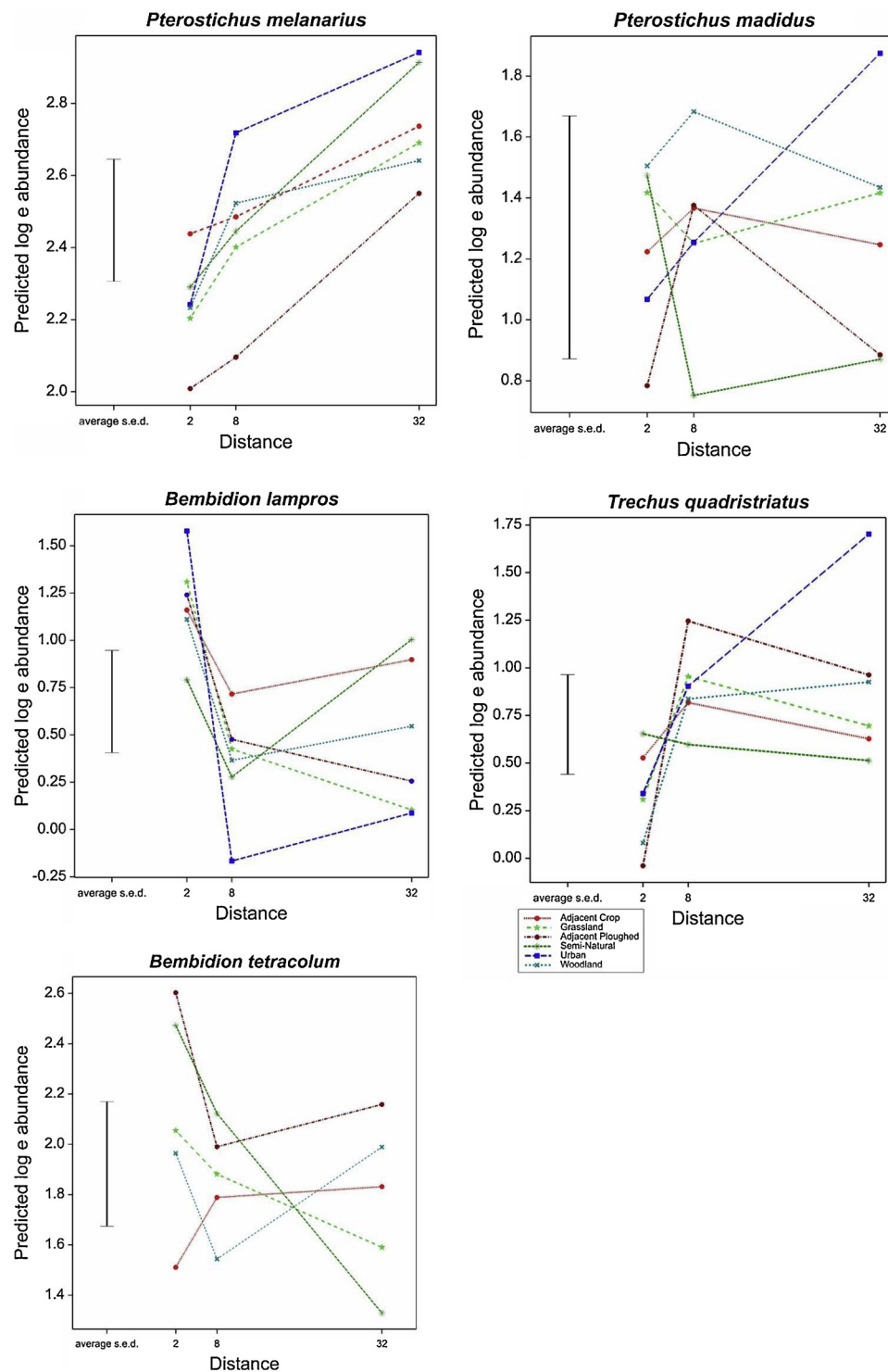
Fig. 8. Abundance predictions for by distance into crop according to adjacent habitat, for species: (a) *P. melanarius*, (b) *P. madidus*, (c) *B. lampros*, (d) *T. quadristriatus* and (e) *B. tetracolum*. The vertical line shows the approximate average standard error of difference.

et al. (2010) found carabid abundances to be higher in the field centre than near margins, but lacked comparative margin samples to make causal conclusions.

4.3. H3: Responses to environmental and management factors will vary by individual carabid species

The limited interactions between environmental features and Distance into crop in the pooled-carabid abundance and species

richness models suggest rejection of Hypothesis 2. This contrasts with the role of spatial mass effects described by Metcalfe et al. (2019) for arable plants, indicating that the classic view of spillover from agro-ecological habitats cannot be extended from the passive dispersal of weeds to actively dispersing invertebrates. However, the individual species models show that all environmental features were important determinants of carabid presence and abundances and often interact with distance.

When we consider the predictions from the individual species

models where there are interactions between Margin and Distance, an important general pattern emerges – responses are different for different species. For instance, in the presence of a margin, our models predicted that *B. lampros* would be more abundant at 2 m (spillover zone), yet *T. quadristriatus* and *N. brevicollis* would be less abundant; with divergent patterns of distribution towards crop centres. When taken in context of management design, the utility of margins to ensure spillover of predation services into crop areas must be considered, especially given that different species may carry out desirable services in those areas.

Most notably in the consideration of Hypothesis 2, for many species there was an interaction between adjacent habitat and distance into crop, suggesting that landscape configuration should be taken into in management design. However, on examination of model predictions we see that species' differences mean that one size fits all recommendations cannot be made. For example, *P. melanarius* and *P. madidus*, although morphologically similar, display divergent responses to adjacent habitats, likely due to niche differentiation; *P. madidus* has a known preference for wooded habitats (Luff, 1998). *B. lampros* and *T. quadristriatus*, are likewise similar in their small size and flight dispersal (Luff, 1998), yet the patterns of abundance by distance are broadly reversed in interaction with most adjacent habitats. The pattern across these models appears to tell that for adjacent habitats with a similar vegetative structure to the crop environment (i.e. crop, and grassland), the response is less markedly divergent, representing a somewhat consistent matrix. Conversely, urban and woodland habitats, where the vegetative structure is very different to the cropped field are where we most often observe edge effect. This may be interpreted as landscape factors filtering the species pool.

Across the individual species models we found that there were significant interactions between distance and landscape features, particularly in the abundance models. For every species, at least one model related a landscape feature to the distance into the crop. This strongly supports Hypothesis 2, and underlines the importance of examining the effects of these variables when considering management. As active dispersers, carabids can search out resources for daily and seasonal needs – yet the parameters governing which resources guide their dispersal, and physically affect their dispersal, varies species to species (Luff, 1998). The assumption of proximity effects on distribution has extended into management design (Marshall and Moonen, 2002), backed by numerous studies correlating abundance of desirable species with semi-natural habitats (Bianchi et al., 2006). However, our results indicate more complex interactions of mass effects, niche differentiation, coexistence, and resource partitioning theories similar to those reported in Shmida and Wilson (1985) – this reportedly generic genus, in practice, demonstrating different actualised distributions than may be extended from their preferences when considered grouped as a whole (Holland et al., 2009).

The significance of the in-field habitat in our models, as represented by crop and soil factors, conformed to expectations from the literature of their importance to key carabid resource needs (Kotze et al., 2011). Crop was a significant factor in the pooled abundance and diversity models, and across the majority of species models. This reflects the differential resources and structure of the crop habitats in question. General ecological theory supports increased species richness and diversity with diverse habitat structure and abundant food resources (Davies et al., 2012). Differing crops are also subject to differing management which can interact with the biological needs of resident species, for instance the timing of cultivation relative to presence of eggs and larvae in the soil can be important in determining whether the species can complete its life-cycle in that crop type. The significance of crop further emphasises the necessity to manage carabids with contrasting ecological requirements at the farm scale to deliver ecosystem services across the range of crops grown, as management may change areas from source to sink across the year, and if managed strategically, perhaps by staggering resource across space and time, populations may

persist and repopulate effectively (Kromp, 1999; Thorbek and Bilde, 2004; Weibull et al., 2003). Soil is known to impact greatly on carabids, due to food web and habitat effects, most crucially on (soil dwelling) larvae (Kotze et al., 2011). Our results show that Soil is significant in explaining species richness and abundance, but not diversity.

Particular distinctions are seen in abundance by distance in different crops. *H. rufipes* is clearly more abundant near the edge of the crop in Winter OSR. Brooks et al. (2012) linked *H. rufipes* with larger seeded spring germinating weeds, which were shown to be less abundant than other weed functional groups in Winter oilseed rape. More generally the Brooks et al. study demonstrated preferences in different functional groups of carabids between invertebrate and weed food resources; shifting in omnivores over time due to resource availability. This supports our findings in relation to *H. rufipes* as foraging activity based on resources, not structure of crop; but does not account for those species distinctions we observe in our models, between such similar carabids as *P. melanarius* and *P. madidus*. Holland et al. (2004) examined the spatial dynamics of *P. melanarius* and *P. madidus*; finding both species were associated with margins early in the year, yet aggregated differentially in the crops over time. Furthermore, the authors found that *P. madidus* crossed boundaries 'more frequently' than *P. melanarius*. Clearly these *Pterostichus* species – assumed by much literature to have similar distributions based upon morphologies, respond differentially to landscape factors.

In the individual species abundance models, landscape variables are retained more often than when we consider presence/absence. This reflects the influence that these variables have upon breeding and survivorship. For example, Luff (1998) describes *Pterostichus niger*'s preference for damp grassland and woodland habitats, which is seen in the retention of hedge, water and adjacent habitat in the abundance model (Table 4). This clarifies the above lack of evidence for Hypothesis 2 under the pooled abundance model. Environmental features were associated with abundances, however this was varied greatly by species; an effect that is lost when considering only pooled carabid abundance.

The individual species models elucidate the influence of environmental features on the distribution of carabid species. *P. niger* was more likely to be observed in pitfalls with a ditch at the boundary, suggesting this species use ditches as a corridor. *P. melanarius* appears to associate with tracks which may be explained by its preference for hunting in open habitats (Holland et al., 2004; Luff, 1998); whilst it is less abundant near roads. When *P. melanarius* is considered in context with *B. lampros*, a primarily flight dispersive species (Luff, 1998; Thiele, 1977); the influence of running dispersal, seems to be indicated. *B. lampros*'s higher abundance near the edge in association with urban adjacent habitats may represent colonisation where other species' lower abundances leave a gap in exploitation of resources. Flight dispersal may render the urban environment less of a barrier, and support quicker recolonisation for this species after agricultural disturbances (Davies et al., 2012).

We have shown that the configuration of environmental features at a farm-scale affects the species present and their abundances. This supports Hypothesis 3, and indicates that the picture afforded by pooled-carabid abundance loses accuracy due to the diverse preferences and tolerances of individual species where boundary and adjacent environmental features act by sorting the species pool found in the field. This is likely to impact functional diversity, and the traits of particular species assemblages may have considerable impact on the extent of ecosystem service delivery.

5. Management implications

Understanding the multiple effects of environmental and management factors upon overall abundance, and spatial distribution (e.g. spillover distances into the crop) are key to the design of effective management for pest control. Recent innovations in agri-environmental

measures have worked on the assumption of spillover (Rand et al., 2006); however, the findings of this study are not consistent with this simplistic idea. We argue that managing landscape features crucial to carabid's daily (for example weed seed food resource) and seasonal needs (for example hibernation in hedgerows) (Thomas et al., 2002) are the most important consideration when seeking to maintain ecosystem service delivery at the individual field scale. Our results suggest the importance of considering this at a farm scale, to account for the differing response of species (which may each be providing different ecosystem services) to environmental factors.

Our findings suggest that plot scale immediacy of these habitat and dispersal resources affects movements in the crop, but that species' responses vary markedly with landscape variables. Therefore fine-scale service delivery may not be determined solely by the proximity of refuge habitats; an argument supported by the limited benefit of margins on in-crop carabid abundance in the neighbouring field observed in this large dataset. The effect of species preferences is likely to have the effect of balancing out the benefits of measures such as margins and hedges – with some species responding positively, and some negatively. What is needed to transform our findings into practical applications of management interventions is the integration of species preferences with the service provision desired in space and time (i.e. matching supply and demand of pest regulation services). In the absence of rigorous data on this (Kotze et al., 2011), a simple recommendation is that a diversity in habitat provision, relative to landscape features, can provide multiple habitats for individual species to thrive – in essence, maximising habitat diversity for carabid diversity.

With even a limited species pool of the ten species considered in this study, it is evident that in any combination of crop, soil and landscape attributes; one or more species is likely to thrive. Our analyses show that diversity and species richness are strongly linked to the boundary of the field, and more crucially to the crop – this suggests that multiple crop types at a farm scale can be most advantageous. Given the mobility of this group of ecosystem service providers, there may be potential to manipulate carabid distributions through the year by the placement of crops in relation to each other and the surrounding landscape. We suggest this would be most effective by avoiding block cropping and maximising the interfaces between crops to enable populations to move with favoured crops through the rotation.

There is scope from this work to tailor farm habitat management to enhance the abundance of specific desirable species in a given location; yet current understanding falls short of directly linking this to pest regulation services. Further knowledge on the actual levels of pest control service provision by individual species is needed, along with their specific lifecycle needs. Desirable species assemblages could be encouraged by providing appropriate resources in time as well as space; for example, weed seeds of preferred species set in margins at key times for population persistence of *H. rufipes*; in farms where weed seed predation is desirable.

We show that important relationships between carabids and habitats can be missed if a study only considers a limited number of scales, on single crops, and single species. The overwhelming influence of species identity as a factor modulating interactions with habitats challenges the applicability of previous recommendations on general management practices based on limited data.

For example Boetzl et al. (2018) studied carabid beetle assemblages in OSR fields relative to four types of similar semi-natural adjacent habitats. The authors used the strong distance decay exhibited by the communities they sampled as a basis for a general recommendation for small field sizes or agri-environment scheme options inside fields based. This community (as discussed above), typical of the OSR in their region, and with limited inclusion of other landscape factors – may not be as widely applicable for recommendations, for example cropped wheat in a tree and scrub rich landscape.

Furthermore, this may explain the conflict of various studies on the effects of certain landscape factors. Even as polyphagous generalists,

carabids display vastly variable realised niches over space and time. Though widely recognised in environmental scientific theory, the bias of carabid species differences appears to be inadequately accounted for. Though some efforts are made by measures of species richness and diversity – and some approaches attempt to disentangle species differences by use of traits and functional diversity (Magurran, 2004), we counter that such analyses may be missing vital distinctions. As discussed above, *P. melanarius* and *P. madidus* are morphologically similar and identical in many trait groupings, yet display different preferences. This can have a great impact on extensions – in fact the general assumption that tussocky grass margins benefit carabids in general may be inaccurate for many species of potential benefit in specific farming systems – such as *H. rufipes*; discussed above (Saska et al., 2007; Weibull et al., 2003; Woodcock et al., 2007).

We conclude that in any given study of carabids, dominant species and differing assemblages are likely to bias inferences and general conclusions, if data is pooled. Though this genus is extensively studied, more work still is needed particularly at the species level, to enable effective utilisation for natural enemy pest control.

Authors' contributions

KJ and JS conceived and designed the study. The research and analysis was performed by KJ with input from HM, AEM, and KLH. All authors contributed to interpretation of results and writing the manuscript.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at https://doi.org/10.1016/j.agee.2019.106631.

References

Anjum-Zubair, M., Schmidt-Entling, M.H., Querner, P., Frank, T., 2010. Influence of within-field position and adjoining habitat on carabid beetle assemblages in winter wheat. Agric. For. Entomol. 12, 301–306.

Beck, J., Schwanghart, W., 2010. Comparing measures of species diversity from incomplete inventories: an update. Methods Ecol. Evol. 1 (1), 38–44.

Bianchi, F.J., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. B: Biol. Sci. 273 (1595), 1715–1727.

Brooks, D.R., Storkey, J., Clark, S.J., Firbank, L.G., Petit, S., Woiwod, I.P., 2012. Trophic links between functional groups of arable plants and beetles are stable at a national scale. J. Anim. Ecol. 81 (1), 4–13. https://doi.org/10.1111/j.1365-2656.2011.01897.x.

Brooks, D.R., Bohan, D.A., Champion, G.T., Haughton, A.J., Hawes, C., Heard, M.S., Clark, S.J., …, Rothery, P., 2003. Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. I. Soil-surface-active invertebrates. Philos. Trans. R. Soc. Lond. B: Biol. Sci. 358 (1439), 1847–1862. https://doi.org/10.1098/rstb.2003.1407.

Brooks, D.R., Perry, J.N., Clark, S.J., Heard, M.S., Firbank, L.G., Holdgate, R., Shortall, C.R., …, Woiwod, I.P., 2008. National-scale metacommunity dynamics of carabid beetles in UK farmland. J. Anim. Ecol. 77, 265–274. https://doi.org/10.1111/j.1365-2656.2007.01331.x.

Boetzl, F.A., Krimmer, E., Krauss, J., Steffan-Dewenter, I., 2018. Agri-environmental schemes promote ground-dwelling predators in adjacent oilseed rape fields: diversity, species traits and distance-decay functions. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.13162.

Booij, K., 1994. Diversity patterns in carabid assemblages in relation to crops and farming systems. In: In: Desender, K., Dufrêne, M., Loreau, M., Luff, M.L., Maelfait, J.P. (Eds.), 2013. Carabid Beetles: Ecology and Evolution, vol. 51. Springer Science & Business

Media, pp. 425–431. https://doi.org/10.1007/978-94-017-0968-2_64.

Council Directive, 2009/128/EC of 21 October 2009 Establishing a Framework for Community Action to Achieve the Sustainable Use of Pesticides.

Crowder, D.W., Jabbourb, R., 2014. Relationships between biodiversity and biological control in agroecosystems: current status and future challenges. Biol. Control 75 (August), 8–17. https://doi.org/10.1016/j.biocontrol.2013.10.010.

Davies, N.B., Krebs, J.R., West, S.A., 2012. An Introduction to Behavioural Ecology. John Wiley & Sons.

EC, 2018. Pesticide National Action Plans [19/10/18]. Available at: https://ec.europa.eu/food/plant/pesticides/sustainable_use_pesticides/nap_en.

Fahrig, L., Jonsen, I., 1998. Effect of habitat patch characteristics on abundance and diversity of insects in an agricultural landscape. Ecosystems 1 (2), 197–205. https://doi.org/10.1007/s100219900015.

Firbank, L.G., Heard, M.S., Woiwod, I.P., Hawes, C., Haughton, A.J., Champion, G.T., Scott, R.J., …, May, M.J., 2003. An introduction to the Farm-Scale Evaluations of genetically modified herbicide-tolerant crops. J. Appl. Ecol. 40 (1), 2–16. https://doi.org/10.1046/j.1365-2664.2003.00787.x.

Fusser, M.S., Holland, J.M., Jeanneret, P., Pfister, S.C., Entling, M.H., Schirmel, J., 2018. Interactive effects of local and landscape factors on farmland carabids. Agric. For. Entomol. https://doi.org/10.1111/afe.12288.

Gallé, R., Happe, A.K., Baillod, A.B., Tscharntke, T., Batáry, P., 2018. Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.13257.

Garratt, M.P.D., Wright, D.J., Leather, S.R., 2011. The effects of farming system and fertilisers on pests and natural enemies: a synthesis of current research. Agric. Ecosyst. Environ. 141 (3–4), 261–270. https://doi.org/10.1016/j.agee.2011.03.014.

Greenop, A., Woodcock, B.A., Wilby, A., Cook, S.M., Pywell, R.F., 2018. Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. Ecology 99 (8), 1771–1782.

Holland, J.M., Begbie, M., Birkett, T., Southway, S., Thomas, S.R., Alexander, C.J., Thomas, C.F.G., 2004. The spatial dynamics and movement of *Pterostichus melanarius* and *P. madidus* (Carabidae) between and within arable fields in the UK. Int. J. Ecol. Environ. Sci. 30, 35–50.

Holland, J.M., Birkett, T., Southway, S., 2009. Contrasting the farm-scale spatio-temporal dynamics of boundary and field overwintering predatory beetles in arable crops. Biocontrol 54 (1), 19–33. https://doi.org/10.1007/s10526-008-9152-2.

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

Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., …, O'Rourke, M.E., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proc. Natl. Acad. Sci. U.S.A. 115 (33), E7863–E7870. https://doi.org/10.1073/pnas.1800042115.

Kenward, M.G., Roger, J.H., 1997. Small sample inference for fixed effects from restricted maximum likelihood. Biometrics 53, 983–997.

Koivula, M., Hyyryläinen, V., Soininen, E., 2004. Carabid beetles (Coleoptera: Carabidae) at forest-farmland edges in southern Finland. J. Insect Conserv. 8 (4), 297–309. https://doi.org/10.1007/s10841-004-0296-9.

Kotze, D.J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M.J., Lövei, G.L., …, Pizzolotto, R., 2011. Forty years of carabid beetle research in Europe–from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. ZooKeys (100), 55. https://doi.org/10.3897/zookeys.100.1523.

Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agric. Ecosyst. Environ. 74 (June (1–3)), 187–228. https://doi.org/10.1016/B978-0-444-50019-9.50014-5.

Labruyere, S., Bohan, D.A., Biju-Duval, L., Ricci, B., Petit, S., 2016. Local, neighbor and landscape effects on the abundance of weed seed-eating carabids in arable fields: a nationwide analysis. Basic Appl. Ecol. 17 (3), 230–239. https://doi.org/10.1016/j.baae.2015.10.008.

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R.,

Bosque-Pérez, N.A., …, Winfree, R., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Global Change Biol. 23 (11), 4946–4957. https://doi.org/10.1111/gcb.13714.

Luff, M.L., 1998. Provisional Atlas of the Ground Beetles (Coleoptera, Carabidae) of Britain. Biological Records Centre Institute of Terrestrial Ecology.

Magurran, A.E., 2013. Measuring Biological Diversity. John Wiley & Sons.

Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agric. Ecosyst. Environ. 89 (1–2), 5–21. https://doi.org/10.1016/S0167-8809(01)00315-2.

Metcalfe, H., Hassall, K.L., Boinot, S., Storkey, J., 2019. The contribution of spatial mass effects to plant diversity in arable fields. J. Appl. Ecol. 56, 1560–1574.

Payne, R.W. (Ed.), 1993. Genstat 5 Release 3 Reference Manual. Oxford University Press.

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., Fronhofer, E.A., …, Greene, S., 2018. Biodiversity increases and decreases ecosystem stability. Nature 563, 109–112.

Petit, S., Bohan, D.A., Dijon, A., 2018. The use of insects in integrated weed management. Integrated Weed Management For Sustainable Agriculture. Burleigh Dodds Science Publishing, pp. 453–468. https://doi.org/10.19103/AS.2017.0025.23.

Petit, S., Boursault, A., Bohan, D.A., 2014. Weed seed choice by carabid beetles (Coleoptera: Carabidae): linking field measurements with laboratory diet assessments. Eur. J. Entomol. 111 (5). https://doi.org/10.14411/eje.2014.086.

Rand, T.A., Tylianakis, J.M., Tscharntke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecol. Lett. 9 (5), 603–614. https://doi.org/10.1111/j.1461-0248.2006.00911.x.

Saska, P., Vodde, M., Heijerman, T., Westerman, P., van der Werf, W., 2007. The significance of a grassy field boundary for the spatial distribution of carabids within two cereal fields. Agric. Ecosyst. Environ. 122, 427–434.

Shmida, A.V.I., Wilson, M.V., 1985. Biological determinants of species diversity. J. Biogeogry. 1–20.

Thiele, H.U., 1977. Carabid Beetles in Their Environments: A Study on Habit Selection by Adaptations in Physiology and Behaviour (Translated by Joy Wieser). Springer-Verlag.

Thomas, C.G., Holland, J.M., Brown, N.J., 2002. The spatial distribution of carabid beetles in agricultural landscapes. The Agroecology of Carabid Beetles. Intercept, Andover, pp. 305–344.

Thorbek, P., Bilde, T., 2004. Reduced numbers of generalist arthropod predators after crop management. J. Appl. Ecol. 41, 526–538.

Warner, D.J., Allen-Williams, L.J., Warrington, S., Ferguson, A.W., Williams, I.H., 2008. Implications for conservation biocontrol of spatio-temporal relationships between carabid beetles and coleopterous pests in winter oilseed rape. Agric. For. Entomol. 10 (4), 375–387. https://doi.org/10.1111/j.1461-9563.2008.00391.x.

Weibull, A.C., Östman, Ö., Granqvist, Å., 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. Biodivers. Conserv. 12 (7), 1335–1355. https://doi.org/10.1023/A:1023617117780.

Welham, S.J., Gezan, S.A., Clark, S.J., Mead, A., 2014. Statistical Methods in Biology: Design and Analysis of Experiments and Regression. Chapman and Hall/CRC.

Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Pärt, T., 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. J. Appl. Ecol. 48 (3), 570–579. https://doi.org/10.1111/j.1365-2664.2010.01950.x.

Woodcock, B.A., Potts, S.G., Westbury, D.B., Ramsay, A.J., Lambert, M., Harris, S.J., Brown, V.K., 2007. The importance of sward architectural complexity in structuring predatory and phytophagous invertebrate assemblages. Ecol. Entomol. 32, 302–311. https://doi.org/10.1111/j.1365-2311.2007.00869.x.

Woodcock, B.A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A.J., Heard, M.S., Roy, D.B., Pywell, R.F., 2014. National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. J. Appl. Ecol. 51 (1), 142–151. https://doi.org/10.1111/1365-2664.12171.