

Crop cover the principal influence on non-crop ground beetle (Coleoptera, Carabidae) activity and assemblages at the farm scale in a long-term assessment

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Abstract

Ground beetle data were generated using pitfall traps in the 17-year period from 1993 to 2009 and used to investigate the effects of changes in surrounding crop cover on beetle activity and assemblages, together with the effects of weather variability. Beetles were recorded from non-crop field margins (overgrown hedges). Crop cover changes explained far more variation in the beetle assemblages recorded than did temperature and rainfall variation. A reduction in management intensity and disturbance in the crops surrounding the traps, especially the introduction and development of willow coppice, was concomitant with changes in individual species activity and assemblage composition of beetles trapped in non-crop habitat. There were no consistent patterns in either overall beetle activity or in the number of species recorded over the 17-year period, but there was a clear change from assemblages dominated by smaller species with higher dispersal capability to ones with larger beetles with less dispersal potential and a preference for less disturbed agroecosystems. The influence of surrounding crops on ground beetle activity in non-crop habitat has implications for ecosystem service provision by ground beetles as pest predators. These results are contrary to conventional assumptions and interpretations, which suggest activity of pest predators in crops is influenced primarily by adjacent non-crop habitat. The long-term nature of the assessment was important in elucidation of patterns and trends, and indicated that policies such as agri-environment schemes should take cropping patterns into account when promoting management options that are intended to enhance natural pest control.

Keywords: invertebrates, arable, grassland, willow coppice, hedges, ecosystem services

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Introduction

Land cover, in its broadest sense, has a considerable effect on the distribution of both ground beetle (Carabidae) species and assemblages (Eyre *et al.*, 2003; Woodcock *et al.*, 2014). Within a particular landscape, the extent and type of non-crop habitat, together with spatial relationships among habitat

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patches, have been shown to influence both activity and species richness in the agroecosystem (Schweiger *et al.*, 2005). Ground beetles, an invertebrate group of mainly generalist predators, are abundant throughout most agroecosystems (Holland *et al.*, 2005) and thought to be an important group of beneficial insects contributing to pest control (Symondson *et al.*, 2002).

Differences in agricultural management were thought to influence activity of ground beetles with greater activity in organic wheat crops than in conventional (Mäder *et al.*, 2002), although further work showed few differences (Purtauf *et al.*, 2005). However, crop type has been shown to influence activity with, for instance, Weibull & Östman (2003) reporting greater activity differences between cereal and grass fields than between different cereals. A combination of crop and management differences produced profound effects on both ground beetle activity and species assemblage composition (Eyre *et al.*, 2012). Increased weed cover influences ground beetle activity (Navntoft *et al.*, 2006) and environmental enhancement by vegetation manipulation has been advocated to increase beneficial invertebrate activity by groups such as ground beetles (Landis *et al.*, 2005). The provision of 'beetle banks' (MacLeod *et al.*, 2004), with more permanent vegetation than in cropped fields, has been one approach to increase activity of ground beetles for pest predation in the agroecosystem via manipulation of vegetation cover.

Most investigations on the effects of environmental, agricultural and land management involving ground beetle recording have been short-term (one or two year) projects but surveys carried out over longer time periods are needed to identify changes in ground beetle activity and distribution. One such scheme is the United Kingdom Environmental Change Network (ECN), which has recorded ground beetles in addition to a wide range of other parameters since 1993, at 12 terrestrial sites in the UK (Sykes & Lane, 1996). Morecroft *et al.* (2009) reviewed the range of physical, chemical and biological data recorded from upland and lowland habitats in the ECN, and identified a decline in ground beetles associated with cooler, northern and upland areas, whilst Brooks *et al.* (2012) found varying trends among different habitats.

At one of the terrestrial ECN sites, Drayton Farm in Warwickshire, UK, farm management has mirrored changes in European and UK agricultural and environmental policies since 1992, including the introduction of short-rotation willow coppice as a crop for biomass fuel production and varying European Union rules on set-aside. These data provided an opportunity to examine the effects of relatively large changes in crop cover and management intensity on ground beetle species and assemblages, and to assess the relative importance of these management changes compared with variation in the prevailing environment, specifically temperature and rainfall. The results presented here are based on recording of ground beetles at the Drayton site in the 17 years between 1993 and 2009.

Methods and materials

Study area

The Drayton site (52°11'42"N, 1°45'44"W) is a lowland mixed arable and grassland farm on heavy clay soil overlying limestone and clay drift at an altitude of 40–80 m with mean annual rainfall 630 mm and mean temperature 10.3°C. The study area comprised 73.2 ha within the main farm, of

Table 1. Total area (ha) of each crop type in the study area from 1993 to 2009.

	Arable	Grassland	Set-aside	Willow
1993	38.82	34.34	–	–
1994	41.14	27.62	3.40	–
1995	36.91	27.62	8.63	–
1996	33.31	27.62	9.41	2.82
1997	42.72	27.62	–	2.82
1998	37.94	27.62	4.78	2.82
1999	34.09	27.62	8.63	2.82
2000	48.03	22.31	–	2.82
2001	24.82	22.31	17.09	8.94
2002	24.70	22.31	–	26.15
2003	19.92	22.31	4.78	26.15
2004	16.58	22.31	8.12	26.15
2005	16.07	22.31	8.63	26.15
2006	24.70	22.31	–	26.15
2007	24.70	22.31	–	26.15
2008	19.92	22.31	4.78	26.15
2009	24.70	22.31	–	26.15

which 38.8 ha were arable and 34.3 ha were grassland in 1993. In 1996, the first 2.8 ha of willow coppice was planted but subsequent planting in 2001 and 2002 increased this to 26.2 ha. Up to 17.1 ha of rotational set-aside per annum was present from 1994 to 2005 (table 1).

Sampling

Ground beetles were sampled using standard a standard ECN protocol (Sykes & Lane, 1996). The sampling regime comprised three lines (A–C) of ten pitfall traps each, placed at 10-m intervals along the non-crop field boundaries, each comprising a tall hedge and wet ditch (Supplementary Figure S1). Minimum separation between the ends of the lines was *c.* 30 m. Line C was surrounded by the greatest area of willow coppice and line A the least. Fields either side of line A were, respectively, grassland and arable or set-aside for the duration of the study. A 9.4 ha block of arable land adjacent to line C was converted to willow coppice during 2001–2002, as was a smaller (4.7 ha) field adjacent to line B in 2002 (Supplementary Table S1). Pitfall traps were 7.5 cm diameter polypropylene cups filled with ethylene glycol preservative, located with the top flush with the soil surface. Sampling was carried out from 1993 to 2009 with traps set continuously from the first week of May until the last week of October, with samples collected fortnightly and all carabid species identified and counted. Nomenclature follows Luff (2007).

Annual mean daily air temperatures during the trapping period were derived from hourly dry bulb temperatures recorded from an automatic weather station on the site, as in Eyre *et al.* (2013). Rainfall annual totals for each year's trapping period were recorded from a tipping bucket rain gauge located at the ground level.

Statistical analyses

Analyses were carried out using both individual yearly catches in each of the 30 pitfall traps, a total of 510 species lists, and with pooled annual data from the three lines of ten pitfall traps (A, B, C), a total of 51 lists. Individual yearly catches were used in the first analyses because previous studies have shown independence of both ground beetle and other

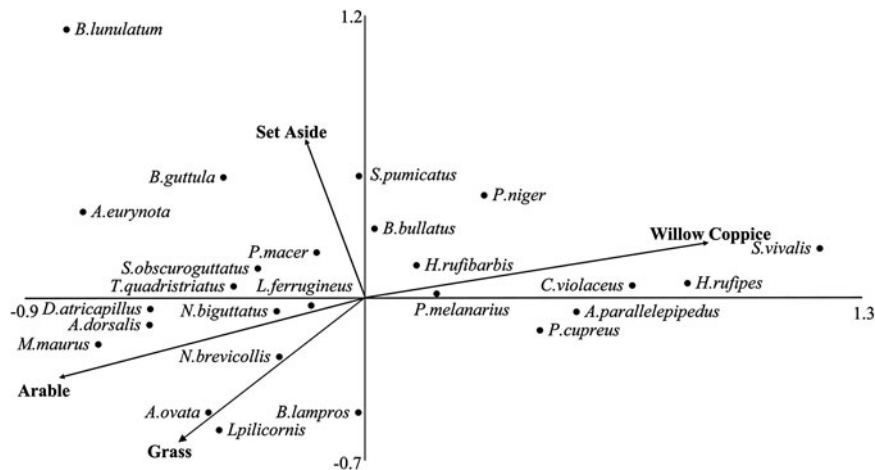


Fig. 1. Biplot derived from the pCCA showing the relationship of ground beetle species to the four main crop cover types.

invertebrate recording at similar distances between traps (Eyre *et al.*, 2009b, 2012). Three sets of analyses were carried out:

- (i) Partial canonical correspondence analysis (pCCA) was applied to determine the relationship of the ground beetle assemblages with the crop cover and weather. The amount of variation explained by the crop cover and weather was analysed by variation partitioning, following the method of Borcard *et al.* (1992) outlined in Legendre & Legendre (1998). A series of pCCAs was applied to ground beetle data from each pitfall trap, together with the cover (i.e. the total area) of each crop (arable, grass or willow coppice) or other vegetation (set-aside) in the study area in the year of sampling (table 1) and the weather variables (rainfall, temperature) specified in turn as environmental variables or covariables. Since land cover explained far more variation than weather, a final pCCA with the weather factors as covariables was used to investigate the influence of the surrounding cover on the ground beetle assemblages, using automatic forward selection of variables and Monte Carlo permutation tests of significance.
- (ii) To identify the main ground beetle assemblages, fuzzy set clustering (Bezdek, 1981) was applied to pooled annual data based on a detrended correspondence analysis (DCA), as in Eyre *et al.* (2003). The site scores on three axes of the ordination were used for the classification.
- (iii) To investigate change in ground beetle assemblages over time, principal response curve (PRC) analysis was applied (Van den Brink & Ter Braak, 1998, 1999). This is a constrained ordination using redundancy analysis that included an interaction term for pitfall line (A, B or C) and year, in addition to partialling out the effect of year. In a conventional ordination plot, the temporal trajectory is often irregular and not parallel with the *x*-axis, making changes over time difficult to interpret. One advantage of PRC is to allow the results to be plotted on a graph with year as the *x*-axis, to gain greater insights into community change with time at the three sets of pitfall traps. The method requires that one site is selected as an unchanging horizontal 'baseline' that forms the *x*-axis: we selected pitfall traps from line B to represent the baseline, because

it was geographically located between lines A and C (Ter Braak & Šmilauer, 2002) and therefore *a priori* might be expected to show intermediate levels of community change. The *y*-axis of a PRC plot (PRC axis 1) indicates the change in the community composition of the samples over time relative to the baseline. PRC plots also indicate the relative abundance of individual species in these samples, via the corresponding species axis, conventionally plotted on the right of the PRC plot. Finally, we used the method of Van den Brink & Ter Braak (1999) to test for significant trapline differences for each year, using 999 permutations.

The pCCAs and DCA were carried out using the CANOCO package (Ter Braak & Šmilauer, 2002) and PRC using R version 3.1 (R Core Team, 2014) with the R package 'vegan' (Oksanen *et al.*, 2008).

Results

A total of 30,139 beetles were trapped, identified to species and counted in the 17 years, with 68 species recorded. The total numbers caught in individual years fluctuated greatly, with the greatest in 2004 (5210) and the fewest in 2009 (373), with the decline of two previously abundant species *Trechus quadristriatus* and *Anchomenus dorsalis* during those 5 years. There was no pattern of catches, with a high number trapped in 1998 (2997) and 1993 (2770) but lower catches in 2001 (522) and 1995 (878). Although the lowest number recorded was in 2009, a high number of species were found (33), close to the most recorded in 2003 (37). The fewest species were found in 2006 (12) and 1997 (20).

The total variation in species composition explained was 7.13%, by land cover 5.23% and by weather 1.48%, with 0.42% explained by the two together. The biplot derived from the pCCA showing the relationship of the 25 most abundant species to the four crop cover types is shown in fig. 1. The major variation along axis 1 represented changes in ground beetle community composition along a trend from those associated with primarily grassland/arable vegetation through to those associated with areas dominated by willow coppice. Secondary variation (axis 2) was mostly related to the effects of set aside and grass fields. Species positively related to the planting of willow coppice, along the positive axis 1, included

Table 2. Mean numbers of ground beetle species in the three groups derived from the fuzzy classification of the 1993–2009 data pooled data (at least a mean of two beetles in a group). Species order is as for the first axis of the ordination and numbers in parentheses are lists in a group.

	Group		
	1 (15)	2 (16)	3 (20)
<i>Microlestes maurus</i>	11	2	1
<i>Amara eurynota</i>	1	3	
<i>Syntomus obscuroguttatus</i>	3	2	
<i>Anchomenus dorsalis</i>	4	202	6
<i>Amara ovata</i>		5	
<i>Nebria brevicollis</i>	52	13	7
<i>Demetrias atricapillus</i>	7	7	1
<i>Loricera pilicornis</i>	5	4	
<i>Trechus quadristriatus</i>	38	189	21
<i>Bembidion obtusum</i>	1	2	
<i>Pterostichus macer</i>	10	1	3
<i>Notiophilus biguttatus</i>	6	3	2
<i>Bembidion lunulatum</i>	2	9	1
<i>Bembidion lampros</i>	5	9	2
<i>Bembidion guttula</i>	5	5	2
<i>Leistus ferrugineus</i>	4	3	2
<i>Harpalus rufibarbis</i>	4	1	2
<i>Leistus spinibarbis</i>	2		1
<i>Badister bullatus</i>	1	3	2
<i>Stomis pumicatus</i>	1	2	2
<i>Trechus obtusus</i>			2
<i>Synuchus vivalis</i>	2		2
<i>Poecilus cupreus</i>	8	13	18
<i>Pterostichus niger</i>	1	1	2
<i>Pterostichus melanarius</i>	58	295	526
<i>Abax parallelepipedus</i>	5	6	18
<i>Carabus violaceus</i>	2	2	7
<i>Harpalus rufipes</i>	3	4	54

Synuchus vivalis, *Abax parallelepipedus*, *Harpalus rufipes* and *Carabus violaceus*, whilst some of those influenced by arable fields, opposite along the negative axis 1, were *Microlestes maurus*, *Demetrias atricapillus* and *A. dorsalis*. Set aside was especially associated with *Bembidion lunulatum* and *Stomis pumicatus*, on axis 2, opposite to species associated with grass fields such as *Bembidion lampros*, *Loricera pilicornis* and *Amara ovata*. The area of willow coppice ($F = 17.35$), grass ($F = 5.53$) and set aside ($F = 4.65$), all had significant effects ($P < 0.002$) on the distribution of species assemblages.

The classification of the 51 pooled species lists produced three groups and the mean number of each species found in the ten traps in each fuzzy classified group is shown in table 2. Thirteen of the 15 lists in group 1 were from line A (pitfalls 1–10), including the first 10 (1993–2002). This line of pitfalls was never adjacent to willow coppice and had the most *Nebria brevicollis*, *M. maurus* and *Pterostichus macer* and the fewest *Pterostichus melanarius* and *H. rufipes*. Of the 16 lists in group 2, nine were from line B and seven were from line C, in a group where all lists were from the period 1993–2001. The lists in this group were characterised by having by far the most *A. dorsalis* and *Trechus quadristriatus* and fewer *N. brevicollis* and *P. macer* than in group 1. Apart from two lists in line C in 1994 and 1995, group 3 lists were from 2002 to 2009, with four lists from line A and seven from both B and C. By far the most *Poecilus cupreus*, *P. melanarius*, *A. parallelepipedus* and *H. rufipes*

were recorded from the traps in these lines, with relatively few *M. maurus*, *A. dorsalis* and *N. brevicollis*.

The results of the PRC analysis are represented in fig. 2, showing the relative change in ground beetle species composition along the three sets of pitfall traps over time, with line B set as the horizontal baseline against which to compare changes. It also shows the relative change in abundance of 15 species over the 17 years, with most change in *P. melanarius*, *A. dorsalis* and *T. quadristriatus*, less, but still considerable, in *H. rufipes* and *A. parallelepipedus* and relatively little in species such as *Pterostichus niger* and *Amara similata*. Beetle species composition from pitfall line A was most dissimilar to that of the baseline in 1993, but this difference gradually reduced over time, particularly after 2005, reflecting the increase in ground beetle species associated with the development of areas of willow coppice. Beetle species composition at pitfall line A was most dissimilar to the others during the assessment. There was a highly significant difference between all three lines of pitfalls throughout the duration of the survey when all three lines were compared simultaneously (table 3). However, after 2002/2003 there were no significant differences in the ground beetle community composition at pitfall lines B and C, the two sets of pitfall traps closest to the willow coppice.

Discussion

Landscape features and crop type influence the distribution of ground beetle assemblages (Purtauf *et al.*, 2005) and generally more species are recorded from cereal fields than from grass (Batáry *et al.*, 2012), but most previous comparisons in the agroecosystem have been in one crop only, usually wheat, a pattern showing no sign of change (Holland *et al.*, 2012; Puech *et al.*, 2014). Given that landscape heterogeneity has a considerable effect on ground beetle activity (Weibull & Östman, 2003), the 17-year Drayton dataset should have, and did, provide insights into the influence of crop and cover changes on beetles recorded from adjacent non-crop habitat. Similarly, Eyre & Leifert (2011) reported that beetle (especially Staphylinidae) activity in fields, itself dependent on crop type, influenced activity in adjacent non-crop habitat, whilst Eyre *et al.* (2013) also found considerable similarities in ground beetle assemblages in crops and field boundaries depending on vegetation structure and amount of disturbance.

The PRCs indicated that the most abundant species showed the greatest changes in activity and that the assemblages from line A traps became similar to those in the baseline line B, with those in line C most similar to the baseline throughout the 17 years. Note that when B and C were compared alone, there were significant community differences in the beetles for the first 10 years of the experiment. These results concur with those of the classification and the frequency table, which showed that activity of such species as *M. maurus* and *N. brevicollis*, not the most abundant, were also considerably reduced as willow coppice developed. One observation is that the most abundant species in group 3 of the classification, made up of assemblages after willow coppice had been introduced, were all large beetles. In the wider environment, agricultural management intensity influences ground beetle species distributions (Eyre, 2006), with small species with high dispersal capability tolerating more intensively managed areas and larger species less inclined to flight more prevalent in less managed landscapes (Ribera *et al.*, 2001). Disturbance at the farm scale has been shown to be more important than

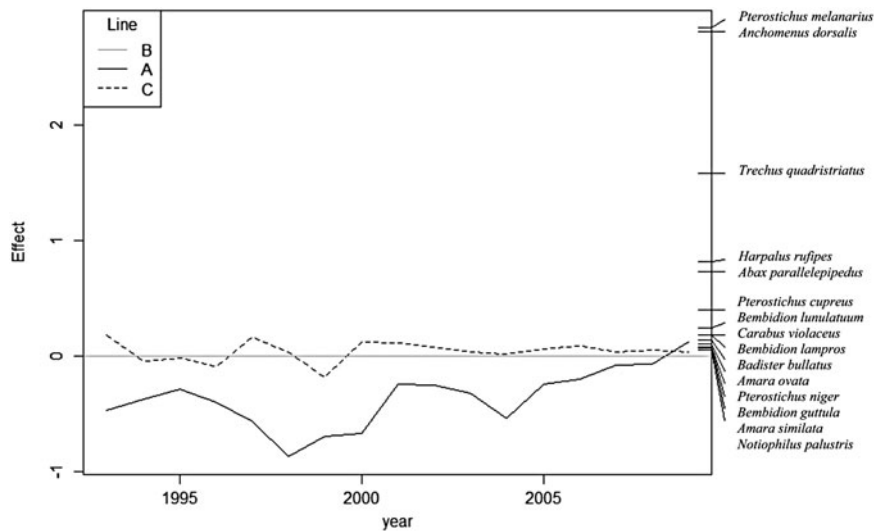


Fig. 2. Summary of the PRC analysis for all three lines of pitfall traps with line B used as baseline, showing the relative change in abundance for 15 ground beetle species.

Table 3. Summary of individual year-wise permutation tests derived from PRC analysis of all three lines (A, B and C) of pitfall traps simultaneously, plus individual pairs of pitfall traps.

Year	F-ratio ABC	P-value ABC	F-ratio BC	P-value BC	F-ratio AB	P-value AB	F-ratio AC	P-value AC
1993	10.327	<0.001	5.518	<0.001	11.400	<0.001	13.817	<0.001
1994	4.193	<0.001	3.230	0.003	5.331	<0.001	4.220	<0.001
1995	5.160	<0.001	2.988	0.002	6.309	<0.001	6.113	<0.001
1996	6.481	<0.001	3.623	0.003	8.828	<0.001	5.809	<0.001
1997	13.600	<0.001	2.954	0.001	15.734	<0.001	22.429	<0.001
1998	15.104	<0.001	1.572	0.118	20.671	<0.001	21.158	<0.001
1999	6.617	<0.001	2.300	0.005	11.694	<0.001	6.477	<0.001
2000	12.188	<0.001	2.703	0.023	14.989	<0.001	17.645	<0.001
2001	4.865	<0.001	3.683	<0.001	4.800	<0.001	5.947	<0.001
2002	5.225	<0.001	2.570	0.006	5.587	<0.001	6.637	<0.001
2003	3.713	<0.001	1.454	0.160	5.090	<0.001	4.306	<0.001
2004	13.539	<0.001	2.759	0.019	15.691	<0.001	21.032	<0.001
2005	4.364	0.001	1.009	0.381	5.739	<0.001	6.351	<0.001
2006	7.035	<0.001	1.161	0.327	7.871	<0.001	14.374	<0.001
2007	3.174	<0.001	0.839	0.528	3.646	<0.001	4.475	<0.001
2008	3.250	0.001	0.853	0.555	3.144	0.006	4.880	<0.001
2009	3.799	<0.001	1.062	0.405	6.035	<0.001	3.818	<0.001

productivity in influencing ground beetle activity and assemblage distribution (Eyre *et al.*, 2013) and it appears that the introduction and development of willow coppice increased the activity of large species such as *A. parallelepipedus*, *P. cupreus* and *C. violaceus* in the adjacent non-crop habitat.

Since ground beetle activity in non-crop habitat was related to changes in the surrounding crops and cover, there are implications for any potential ecosystem services supplied by ground beetles. The presence of semi-natural or other non-crop habitat is generally considered to be beneficial for biological control in cropping systems, as most predatory species require both crop and non-crop areas to persist, and are assumed mainly to inhabit uncultivated areas (Tscharntke *et al.*, 2007). Indeed, the assumption that non-crop habitat such as beetle banks and grassy strips provide overwintering cover and a source of pest predators such as ground beetles is

part of the underlying reasoning for their promotion in some agri-environment schemes (Whittingham, 2011; Holland *et al.*, 2014). However, this might be questioned if beetle activity is crop driven, not the other way around. Eyre *et al.* (2009a) found appropriate ground beetle pest predators in the vegetated margins of vegetable fields, akin to beetle banks, did not disperse into the open fields and had no effect on, in this case, cabbage root fly. Given that non-crop habitat in anything approaching an intensively managed agroecosystem is unlikely to exceed 20% of total cover, it is perhaps not surprising that crop cover and diversity will have an important influence on overall invertebrate activity.

It has been suggested that seasonal 'spillover' effect between habitats is likely to be stronger in the direction from productive to non-productive habitats, due to temporal variation in resource availability (Rand *et al.*, 2006). In our study,

spillover from the fields into the unmanaged field boundaries was indeed apparent, but in this case there was a consistent trend that occurred over a period of years. The results concur with a proposal that species with intermediate dispersal abilities (i.e. the larger carabids) could benefit from long-term temporal changes, whereas those with higher dispersal capabilities are more likely to respond to short-term changes (Driscoll *et al.*, 2013).

The spillover from areas under agricultural management might also have implications for prey populations in non-crop habitat fragments (Rand *et al.*, 2006), an effect compounded by evidence that larger ground beetle species tend to predate smaller ground beetle species (Prasad & Snyder, 2006). The long-term effects of this predation are unknown, and there is a need for more research on both agronomic and ecological effects of spillover from agricultural land to non-crop habitats (Tschardtke *et al.*, 2012).

The lack of any consistent patterns of ground beetle activity or of species numbers recorded at the farm scale at Drayton is not in agreement with the conclusions of Morecroft *et al.* (2009) and Brooks *et al.* (2012) at a national scale, that there were declines in ground beetle 'biodiversity' and populations. However, since pitfall trapping only gives a relative idea of ground beetle activity (or activity density), conclusions concerning populations are inappropriate and should be treated with considerable caution. Pitfall trapping is the best and only method of generating useful and useable ground beetle data (Spence & Niemälä, 1994), but like all sampling methods, it has limitations and population size will be only one reason for pitfall trap catch fluctuation. The results at Drayton concur with those of Taylor & Morecroft (2009), using a 12-year dataset at the farm scale that there was no overall trend in beetle abundance or species richness.

This study has shown that local changes in farm management that affect the agricultural landscape can have a clear influence on ground beetle species assemblages over a period of years and that these effects are much stronger than annual variation in temperature and rainfall. One important consideration is that the long-term nature of the assessment was crucial in showing patterns and trends, indicating that longer sampling periods than those usually employed in invertebrate assessments in the agroecosystem will provide new and more useful conclusions. Other factors such as sampling in more than one crop, together with an understanding of the need for longer sampling periods, would provide a more holistic approach to research. This is important because conclusions reached from work in intensively managed agroecosystems may have little credence in other landscapes.

Supplementary material

The supplementary material for this article can be found at <http://dx.doi.org/10.1017/S0007485315001054>

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References

- Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. & Tschardtke, T. (2012) Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agriculture Ecosystems & Environment* **146**, 130–136.
- Bezdek, J.C. (1981) *Pattern Recognition with Fuzzy Objective Algorithms*. New York, Plenum Press.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology* **73**, 1045–1055.
- Brooks, D.R., Bater, J.E., Clark, S.J., Monteith, D.T., Andrews, C., Corbett, S.J., Beaumont, D.A. & Chapman, J.W. (2012) Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology* **49**, 1002–1019.
- Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B. & Smith, A.L. (2013) Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution* **28**, 605–613.
- Eyre, M.D. (2006) A strategic interpretation of beetle (Coleoptera) assemblages, biotopes, habitats and distribution, and the conservation implications. *Journal of Insect Conservation* **10**, 151–160.
- Eyre, M.D. & Leifert, C. (2011) Crop and field boundary influences on the activity of a wide-range of beneficial invertebrate groups on a split conventional: organic farm in northern England. *Bulletin of Entomological Research* **101**, 135–144.
- Eyre, M.D., Luff, M.L. & Leifert, C. (2013) Crop, field boundary, productivity and disturbance influences on ground beetles (Coleoptera, Carabidae) in the agroecosystem. *Agriculture Ecosystems & Environment* **165**, 60–67.
- Eyre, M.D., Labanowska-Bury, D., Avayanos, J.G., White, R. & Leifert, C. (2009a) Ground beetles (Coleoptera, Carabidae) in an intensively managed vegetable crop landscape in eastern England. *Agriculture Ecosystems & Environment* **131**, 340–346.
- Eyre, M.D., Luff, M.L., Atlihan, R. & Leifert, C. (2012) Ground beetle species (Carabidae, Coleoptera) activity and richness in relation to crop type, fertility management and crop protection in a farm management comparison trial. *Annals of Applied Biology* **161**, 169–179.
- Eyre, M.D., Luff, M.L., Staley, J.R. & Telfer, M.G. (2003) The relationship between British ground beetles (Coleoptera, Carabidae) and land cover. *Journal of Biogeography* **30**, 719–730.
- Eyre, M.D., Sanderson, R.A., Shotton, P.N. & Leifert, C. (2009b) Investigating the effects of crop type, fertility management and crop protection on the activity of beneficial invertebrates in an extensive farm management comparison trial. *Annals of Applied Biology* **155**, 267–276.
- Holland, J.M., Thomas, C.F.G., Birkett, T., Southway, S. & Oaten, H. (2005) Farm-scale spatiotemporal dynamics of predatory beetles in arable crops. *Journal of Applied Ecology* **42**, 1140–1152.
- Holland, J.M., Oaten, H., Moreby, S., Birkett, T., Simper, S., Southway, S. & Smith, B.M. (2012) Agri-environment scheme enhancing ecosystem services: a demonstration of improved biological control in cereal crops. *Agriculture Ecosystems & Environment* **155**, 147–172.

- Holland, J.M., Storkey, J., Lutman, P.J.W., Birkett, T.C., Simper, J. & Aebischer, N.J. (2014) Utilisation of agri-environment scheme habitats to enhance invertebrate ecosystem service providers. *Agriculture Ecosystems & Environment* **183**, 103–109.
- Landis, D.A., Menalled, F.D., Costamagna, A.C. & Wilkinson, T.K. (2005) Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science* **53**, 902–908.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. 2nd edn. Amsterdam, Elsevier Scientific Publishing Company.
- Luff, M.L. (2007) The carabidae (ground beetles) of Britain and Ireland. *Handbook for the Identification of British Insects*, 2nd edn. **4**(2), 1–247.
- MacLeod, A., Wratten, S.D., Sotherton, N.W. & Thomas, M.B. (2004) 'Beetle banks' as refuges for beneficial arthropods in farmland: long-term changes in predator communities and habitat. *Agricultural and Forest Entomology* **6**, 147–154.
- Mäder, P., Fliessbach, A., Dubois, D., Gunst, L., Fried, P. & Niggli, U. (2002) Soil fertility and biodiversity in organic farming. *Science* **296**, 1694–1697.
- Morecroft, M.D., Bealey, C.E., Beaumont, D.A., Benham, S., Brooks, D.R., Burt, T.P., Critchley, C.N.R., Dick, J., Littlewood, N.A., Monteith, D.T., Scott, W.A., Smith, R.I., Walmsley, C. & Watson, H. (2009) The UK environmental change network: emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation* **142**, 2814–2832.
- Navntoft, S., Esbjerg, P. & Riedel, W. (2006) Effects of reduced pesticide dosages on carabids (Coleoptera: Carabidae) in winter wheat. *Agricultural and Forest Entomology* **8**, 57–62.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2008) The vegan package – Community Ecology Package for R. Available online at <http://vegan.r-forge.r-project.org/>
- Puech, C., Baudry, J., Joannon, A., Poggi, S. & Aviron, S. (2014) Organic vs. conventional farming dichotomy: does it make sense for natural enemies? *Agriculture Ecosystems & Environment* **194**, 48–57.
- Prasad, R.P. & Snyder, W.E. (2006) Polyphagy complicates conservation biological control that targets generalist predators. *Journal of Applied Ecology* **43**, 343–352.
- Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tschardtke, T. & Wolters, V. (2005) Landscape context of organic and conventional farms: influences on carabid beetle diversity. *Agriculture Ecosystems & Environment* **108**, 165–174.
- R Core Team (2014) *R: A language and environment for statistical computing*. Vienna, Austria, R Foundation for Statistical Computing. Available online at <http://www.R-project.org/>
- Rand, T.A., Tylianakis, J.M. & Tschardtke, T. (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters* **9**, 603–614.
- Ribera, I., Doleded, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology* **82**, 1112–1129.
- Schweiger, O., Maelfait, J.P., Van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M. & Bugter, R. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *Journal of Applied Ecology* **42**, 1129–1139.
- Spence, J.R. & Niemälä, J.K. (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *Canadian Entomologist* **126**, 881–894.
- Sykes, J.M. & Lane, A.M.J. (1996) *The UK Environmental Change Network: Protocols for Standard Measurements at Terrestrial Sites*. London, The Stationery Office.
- Symondson, W.O.C., Sunderland, K.D. & Geenstone, M.H. (2002) Can generalist predators be effective biocontrol agents?. *Annual Review of Entomology* **47**, 561–594.
- Taylor, M.E. & Morecroft, M.D. (2009) Effects of agri-environment schemes in a long-term ecological time series. *Agriculture Ecosystems & Environment* **130**, 9–15.
- Ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4.5)*. Wageningen, Centre for Biometry.
- Tschardtke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S. & Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control* **43**, 294–309.
- Tschardtke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Frund, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biological Reviews* **87**, 661–685.
- Van den Brink, P.J. & Ter Braak, C.J.F. (1998) Multivariate analysis of stress in experimental ecosystems by principal response curves and similarity analysis. *Aquatic Ecology* **32**, 163–178.
- Van den Brink, P.J. & Ter Braak, C.J.F. (1999) Principal response curves: analysis of time-dependent multivariate responses of a biological community to stress. *Environmental & Toxicological Chemistry* **18**, 138–145.
- Weibull, A.C. & Östman, O. (2003) Species composition in agroecosystems: the effect of landscape, habitat, and farm management. *Basic & Applied Ecology* **4**, 349–361.
- Whittingham, M.J. (2011) The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *Journal of Applied Ecology* **48**, 509–513.
- 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. *Journal of Applied Ecology* **51**, 142–151.