Above- and below-ground assessment of carabid community responses to crop type and tillage

Kelly Jowett*† [ID] **, Alice E. Milne*****, Dion Garrett***†**, Simon G. Potts**‡**, Deepa Senapathi**‡ **and Jonathan Storkey***

**Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK,* †*University of Warwick, Coventry, CV4 7AL, UK and* ‡*Centre for Agri-Environmental Research, School of Agriculture Policy and Development, University of Reading, Reading, RG6 6AR, UK*

Abstract

1 Carabid beetles are major predators in agro-ecosystems. The composition of their communities within crop environments governs the pest control services they provide. An understudied aspect is the distribution of predacious carabid larvae in the soil.

2 We used novel subterranean trapping with standard pitfall trapping, within a multi-crop rotation experiment, to assess the responses of above- and below-ground carabid communities to management practices.

3 Crop and trap type significantly affected pooled carabid abundance with an interaction of the two, the highest numbers of carabids were caught in subterranean traps in barley under sown with grass.

4 Trap type accounted for the most variance observed in carabid community composition, followed by crop.

5 Tillage responses were only apparent at the species level for three of the eight species modelled.

6 Responses to crop type varied by species. Most species had higher abundance in under-sown barley, than grass, wheat and barley. Crop differences were greater in the subterranean trap data. For predaceous larvae, standard pitfalls showed lowest abundances in under-sown barley, yet subterranean traps revealed abundances to be highest in this crop.

7 Comprehensive estimation of ecosystem services should incorporate both above- and below-ground community appraisal, to inform appropriate management.

Keywords Agricultural management, arable fields, biological pest control, carabid beetles, ecosystem functions, tillage, trapping methodology.

Introduction

Carabid beetles, as ubiquitous and generally polyphagous predators, are much studied in agro-ecosystems. Research has shown their potential utility to control pest arthropods and weed seeds in crop areas, leading to the development of management measures to boost carabid abundance in farm habitats (Kromp, 1999; Tscharntke *et al.*, 2007; Petit *et al.*, 2018a). Furthermore, there is a general consensus that a diverse carabid community will provide more stable and increased natural pest regulation in agricultural crops (Bianchi *et al.*, 2006; Bommarco *et al.*, 2018). The presence of carabids in crop areas largely depends on the resources available in these areas, which is modified by farm management practices (Thomas *et al.*, 2002). This may vary

Correspondence: Kelly Jowett, Sustainable Agricultural Sciences, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK.
e-mail: kelly.jowett@rothamsted.ac.uk

considerably by species; therefore, to design models and management to boost populations or increase biodiversity, it is important to understand the needs of carabid beetles, at a biological and behavioural level (Kleijn & Sutherland, 2003; Petit *et al.*, 2018b; Jowett *et al.*, 2019).

One large biological, and indeed behavioural, knowledge gap exists around the immature life-stages of carabids. Carabid larvae are principally soil-dwelling, especially those species inhabiting agro-ecosystems (Luff & Larsson, 1993). Though some species may move metres down into the soil, most live near the surface (top 50 cm) feeding on the biota of the top soil horizons. Larvae are predominantly carnivorous, even when the adults are granivorous (Sasakawa *et al.*, 2010); and have even been observed climbing up crop plants to feed on invertebrate pests (Suenaga & Hamamura, 1998). Some species such as *Harpalus rufipes* (De Geer, 1778), however, specialise in weed seed predation, collecting seeds in burrows for consumption (Traugott, 1998). Since a

large proportion of crop pests have at least one life-stage inhabiting topsoil layers (Ratnadass *et al.*, 2006), and weed seeds cycle in this soil level (Petit *et al.*, 2018a), carabid larvae comprise a large proportion of natural enemy pest-control in crops.

Some studies have shown predation of key crop pests by carabid larvae (*e.g.* Symondson, 2004), yet most studies on larvae are laboratory based, and suffer from the bias inherent in artificial environments when considering actualised predation and preferences (Suenaga & Hamamura, 1998; Thomas *et al.*, 2009). Much work on larvae is based on assumptions from morphology and analogous organisms, and extended from limited data (Kotze *et al.*, 2011). To gain a fuller, and more accurate picture of carabid predation we must incorporate data on the relative abundance and occurrence of carabids at all life stages within arable fields.

There are around 350 species of carabid in the UK. Though much data exist on the most prevalent carabid species in agro-ecosystems, further knowledge of their occurrence by site, habitat, and crop, would help inform targeted management to increase the efficient provision of services (Thiele, 1977; Kromp, 1999; Tscharntke *et al.*, 2007; Kotze *et al.*, 2011; Redlich *et al.*, 2018). Crucial to these considerations is the community composition of carabids in a given agro-ecosystem. This will be a result of the filtering of species by environmental factors, management and biological interactions leading to large variation in the level of ecosystem services they provide spatially and temporally (Tylianakis & Romo, 2010; Eisenhauer *et al.*, 2019).

The in-field factors that have the greatest influence on carabid communities across all life stages relate to the structure and resources in the habitat. Above-ground, the crop type determines the shelter, microclimate, and food resource availability. As such, this is a key determinate in the abundance and species richness of carabids present (Brooks *et al.*, 2003, 2008; Woodcock *et al.*, 2014). Where two or more crops are grown simultaneously (inter or companion cropping) this would be expected to lead to greater habitat complexity than if crops were grown in monocultures. One example is the practice of establishing grass leys by undersowing the grass into a cereal crop. This method of continuous cropping is thought to improve soil structure and function. Under-sowing may also benefit carabids by providing a greater variety of canopy structure and resources, and through associated reductions in pesticides and disturbance (Clapperton, 2003; Scopel *et al.*, 2013). Grass is also of interest as it is suggested that tussocky grass margins and adjacent grass habitats can boost carabid populations (Holland, 2002; Woodcock *et al.*, 2007; Boetzl *et al.*, 2018). For below-ground structure and resources, crop type also affects rooting structure and associated resources, as well as determining cultivation timings and crucially tillage. Constituting a major disturbance event below-ground, and a reconfiguration of the upper soil level structure and resources, tillage is reported to have a great effect on carabid abundance- particularly to larvae (Baguette & Hance, 1997; Hatten *et al.*, 2007; Lami *et al.*, 2020). Cultivation timings of winter and spring cereals may constitute the largest management effect upon carabids due to the impacts on population processes between autumn and spring breeding (Holland & Luff, 2000; Marrec *et al.*, 2015).

Though the literature on carabids documents the differential responses of carabids by crop, few studies consider the effect of crop on above- and below-ground communities. The majority

of studies use pitfall trapping to collect carabids. These traps are level with the soil surface, so organisms that move across the soil surface will fall in. Fluid (typically a solution of alcohol) is placed in traps to preserve the catch for accurate species identification and to prevent in-trap predation (Wheater *et al.*, 2011). The ease of setting these traps and their reliability have largely standardised reliance on this technique; despite some concerns over bias in species capture towards surface active and more activity-dense individuals (Holland, 2002). Pitfall traps do capture carabid larvae; but the numbers caught are relatively small compared to adults, typically less than 1% of the catch (McGavin, 1997; New, 1998; Hyvarinen *et al.*, 2006). Soil cores are the standard approach for collecting soil-active invertebrates (Smith *et al.*, 2008; Wheater *et al.*, 2011) yet this method may be inefficient for surveying carabid larvae (Bell, personal communication), returning few specimens for much effort and/or cost.

Subterranean pitfall traps offer a third alternative and work on a similar premise of standard pitfalls. They catch active invertebrates in a trap solution, where the trap is set underground, with the trap area delimited by a mesh tube through which soil organisms pass and fall. This allows a catch over time (rather than the snapshot of soil cores); which may return more specimens of soil-active larvae moving to the surface to feed; and is more comparable to pitfall catches (Owen, 1995; Sims & Cole, 2016; Sims & Cole, 2017; Telfer, 2017). Furthermore, the subterranean element of the trap means that it will also capture adult carabids moving through the soil, constituting a differential activity-density measurement to standard pitfalls, and affording a more comprehensive appraisal of the species present and their movements in crop.

In this study, we deployed subterranean and pitfall traps across an existing agricultural experimental platform to assess the effect of crop type and cultivation method on carabid communities. Based on our previous findings (Jowett *et al.*, 2019), we expected that there would be a difference in response to these factors according to species and life stage (larvae *vs.* adults). We aimed to (i) investigate the infield factors influencing carabid abundance, species richness, and diversity, (ii) relate this to individual carabid species and community composition between treatments, and (iii) quantify the differential response of carabid larvae to infield factors.

Methods

Brooms barn large-scale rotation experiment

To explore the impact of crop and tillage on carabid communities, we used a new field-scale experimental platform established on the Rothamsted Research farm at Brooms Barn (Suffolk, U.K.) that has been designed to quantify the impact of alternative cropping systems on a range of agronomic and environmental variables. The experimental platform, known as the large scale rotation experiment (LSRE), was set up in 2017 and has 63 plots each 24×24 m in size, set in a grid of 7 by 9 plots in a single field (Fig. 1). Each plot forms an experimental unit. The main treatments are three crop rotations (3, 5, or 7 years long) and two cultivation strategies (zero tillage *vs.* mouldboard ploughing). Each phase of every rotation is sown every year in both a zero

ZERO TILL Grass / clover	INVERSION Grass / clover	INVERSION Winter wheat	ZERO TILL Soybean	ZERO TILL Winter wheat	INVERSION Spring barley	ZERO TILL Winter wheat
INVERSION Oilseed rape	INVERSION Oilseed rape	ZERO TILL Winter wheat	ZERO TILL Winter wheat	INVERSION Winter wheat	INVERSION Winter wheat	INVERSION Winter wheat
INVERSION Winter wheat	ZERO TILL Oilseed rape	ZERO TILL Winter wheat	INVERSION Grass / clover	ZERO TILL Under-sown Spring barley	INVERSION Oilseed rape	ZERO TILL Oilseed rape
INVERSION Grass / clover	INVERSION Under-sown Spring barley	INVERSION Winter wheat	INVERSION Winter wheat	INVERSION Under-sown Spring barley	ZERO TILL Under-sown Spring barley	INVERSION Winter Wheat
INVERSION Winter wheat	ZERO TILL Grass / clover	INVERSION Soybean	INVERSION Field beans	INVERSION Sugar beet	INVERSION Soybean	ZERO TILL Linseed
ZERO TILL Winter wheat	ZERO TILL Winter wheat	ZERO TILL Winter wheat	INVERSION Spring barley	INVERSION Grass / clover	INVERSION Winter wheat	ZERO TILL Sugar beet
ZERO TILL Spring Barley	ZERO TILL Winter wheat	INVERSION Winter wheat	INVERSION Sugar beet	ZERO TILL Field beans	ZERO TILL Winter wheat	ZERO TILL Grass / clover
ZERO TILL Spring barley	ZERO TILL Grass / clover	ZERO TILL Winter wheat	ZERO TILL Winter wheat	INVERSION Winter wheat	ZERO TILL Field beans	ZERO TILL Oilseed rape
ZERO TILL Winter wheat	INVERSION Field beans	ZERO TILL Soybean	ZERO TILL Oilseed rape	ZERO TILL Sugar beet	INVERSION Oilseed rape	ZERO TILL Grass / clover

Figure 1 A plan and photograph of the Large Scale Rotation Experiment (LSRE) at Brooms Barn Experimental Farm, which is located Suffolk, UK. The plan shows the crops grown and associated tillage type for harvest year 2018. Each plot is 24 × 24 m. Plots with a dashed border were included in the invertebrate trapping Run 1 only, plots with a solid border in Run 2 only, and plots with a double border were included in both runs. The photograph was taken at the time of spring crop drilling [Colour figure can be viewed at wileyonlinelibrary.com].

till or ploughed plot and replicated twice in a fully randomised design (Fig. S1). The first crops were established in autumn 2017 following a preparation crop of winter oats. The main plots were divided into two sub-plots for the implementation of an organic amendment treatment in future years; this treatment is not relevant to the results reported in this paper as the trapping was done before the first application of compost but the traps were always positioned in the sub-plot designated as 'unamended'. Invertebrate sampling was not done on all plots of the platform, but the opportunity was taken in the first cropping year to quantify the effect of different crop types and tillage on carabid assemblages by selecting plots that had replicate treatments in the first year. Using an experimental platform in this way ensured that soil type, field history, and the local carabid species pool were all constant meaning any differences could be attributed to the plot treatments.

Sampling design

The carabid sampling was done in the spring and summer of 2018. Because this was the first cropping year of the experiment, plots in the same crop type could be treated as true replicates (Fig. S1, Table 1). The crops chosen for sampling were selected on the basis of the functional differences we expected to have the biggest effects on carabid communities. We chose to sample carabids in (i) spring barley (*Hordeum vulgare*), (ii) spring barley (*H. vulgare*) under-sown with grass (*Lolium perenne*), (iii) winter wheat (*Triticum aestivum*), and (iv) grass (*L. perenne*) (Table 1). These were chosen to examine the effects of spring and winter crops, and the effects of cultivated grasses (under-sown and main crop) as identified above as having an impact on carabid distributions. For wheat and grass plots, there were six replicates in total, three had a zero till cultivation and three had inversion. For the barley and barley under-sown plots, there were two replicates of each crop by tillage treatment. To control for distance, where possible, plots were chosen for each set of treatment replicates at distances close to the experiment edge.

The experimental unit was therefore the selected plots, represented by the sub-plot of standard nutrition. Each 12 m × 24 m sub-plot was stratified into three 8 m × 12 m grids and one pitfall trap placed at random in each grid (three pseudo replicates). A subterranean trap was subsequently located randomly in each stratum, but at distance of at least a 5 m from any other trap. This made a total of 60 traps of each type across the experiment. These were installed on the fourth May 2018. With a two-month settling in period (Sims & Cole, 2017). We ran two 14-day trap runs (which we refer to as Run 1 and Run 2). Farm operations meant that the two runs did not have identical treatments. Run 1 was set

Table 1 Large scale rotation experiment treatments and runs in which treatments were included (see Fig. S1 for experimental plan)

Treatment	Crop	Run 1	Run 2
Wheat	Winter wheat (*Triticum aestivum*) (cultivar siskin sown 25 September 2017 at 300 seeds m⁻²)	3 replicates with zero till, 3 replicates with inversion	3 replicates with zero till, 3 replicates with inversion
Barley	Spring barley (*Hordeum vulgare*) (cultivar Laurete sown 26 April 2018 at 350 seeds m⁻²)	2 replicates with zero till, 2 replicates with inversion	Not included
Barley under-sown	Spring barley under-sown grass clover mix (*Lolium perenne*, *Trifolium repens*) (cultivar Laurete sown 26 April 2018 at 350 seeds m⁻², grass/clover under-sown at 11.2 kg ha⁻¹ on the same day	2 replicates with zero till, 2 replicates with inversion	2 replicates with zero till, 2 replicates with inversion
Grass	Grass (*Lolium perenne*) 11.2 kg ha⁻¹ sown on 26 April 2018	Not included	3 replicates with zero till, 3 replicates with inversion

16th July and collected 30th July, grass plots were excluded from this run because of plot harvesting. Run 2 was set 30th August and collected 13th September. Grass plots were included in this second run but the Spring barley treatment was dropped due to harvest.

Trap design

The standard pitfall equipment used was 7.5 diameter 10 cm depth cups, set in space holding pipes, with lids raised 4 cm when set (Fig. 2a).

The design of the subterranean trap was based on Owen (1995) (see also Sims & Cole, 2016, 2017; Telfer, 2017). The design is based on a $34 \text{ cm} \times 7$ cm pipe with 3 cut-out sections $20 \text{ cm} \times 4$ cm, bordered by wire mesh of 1.2 cm grid. A closely fitting sample collection pot sits at the base of the trap and collects soil active invertebrates falling through the wire mesh panels. The collection pot has a handle for collection and resetting with a hooked pole. A lid sits on the top, stopping surface active catch (to a depth of 3 cm), while allowing access to empty (Fig. 2b). When unset, a plastic film sleeve was used to block the mesh. This is a novel aspect that reduced setting in times and unintentional catch when not in use. When set, liquid is put in the collection cup. We chose to use a 70:30 ratio of ethanol and water because it preserves samples should we wish to carry out DNA analysis at a later date (Schmidt *et al.*, 2006; Moreau *et al.*, 2013). This liquid was also used in standard pitfalls.

Statistical analysis

Pooled-carabid abundance, species richness, and diversity. Carabid adults were identified to species level (Luff, 1997). Identifying carabid larvae to species level is notoriously difficult. Therefore larvae were classified by size, and predatory morphology classified as (i) seed-eaters or (ii) predatory/omnivorous. During Run 1, drought conditions and particularly high temperatures caused the pitfall trap fluid to dry out in nearly all of the standard pitfall traps, in some cases causing in-trap predation; therefore, we analysed the two runs separately. Although the results from Run 1 need to be interpreted with caution, where they are consistent with the observations in Run 2, they provide valuable supporting evidence.

Some traps (around 1%) were spoiled or data labels incomplete; therefore, we analysed only the count data from complete records with information recorded for all environmental factors, leaving 78 trap occasions in Run 1 and 75 in Run 2. We use the standard proxy measure of activity density to account for abundance. For each trap occasion, we calculated the '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 (Eqn 1) to the data by maximum likelihood to give estimates of Fisher's log-series alpha ($\hat{\alpha}$), which is a robust and widely used diversity metric (Beck and Schwanghart, 2010; Magurran, 2013) that accounts for the effect of total numbers of individuals in a sample on diversity estimates.

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

We fitted linear mixed models (LMMs) using the Genstat statistical software package (Payne, 1993) to determine the effect of environmental factors on (i) pooled-carabid abundance (N), (ii) richness (S), (iii) species diversity (quantified as $\hat{\alpha}$), (iv) carabid larvae (pooled), and (v) abundance of carabids at species level (where sufficient numbers were present). We considered the environmental factors crop type, tillage type, and trap type (denoting hypogeal and epigeal movements) as fixed effects with three-way interactions. The random model was defined as plot, and nested within each plot, trap number (*i.e.* plot˙trap replicate). We log transformed the pooled-abundance and alpha so that residuals conformed to normality. We selected terms using backward elimination according to the largest *P*-value given by the Kenward-Roger approximate *F*-tests. The final predictive model was chosen when all remaining terms gave significant values ($P \leq 0.05$) when dropped from the model.

The effect of crop type and cultivation on carabid community composition was analysed using redundancy analysis (RDA), a constrained principal components analysis using crop type, tillage, and trap type as explanatory variables. Analyses were carried out in Canoco (Smilauer & Leps, 2014) for each run separately using Monte Carlo methods to derive a measure of statistical significance. To avoid the analysis being biased by infrequent species, species were excluded if they were only recorded in a single trap in any given run. The partial effects of each explanatory variable were first quantified, including the other variables as co-variates. All variables with significant partial effects were then included in a combined analysis for each run.
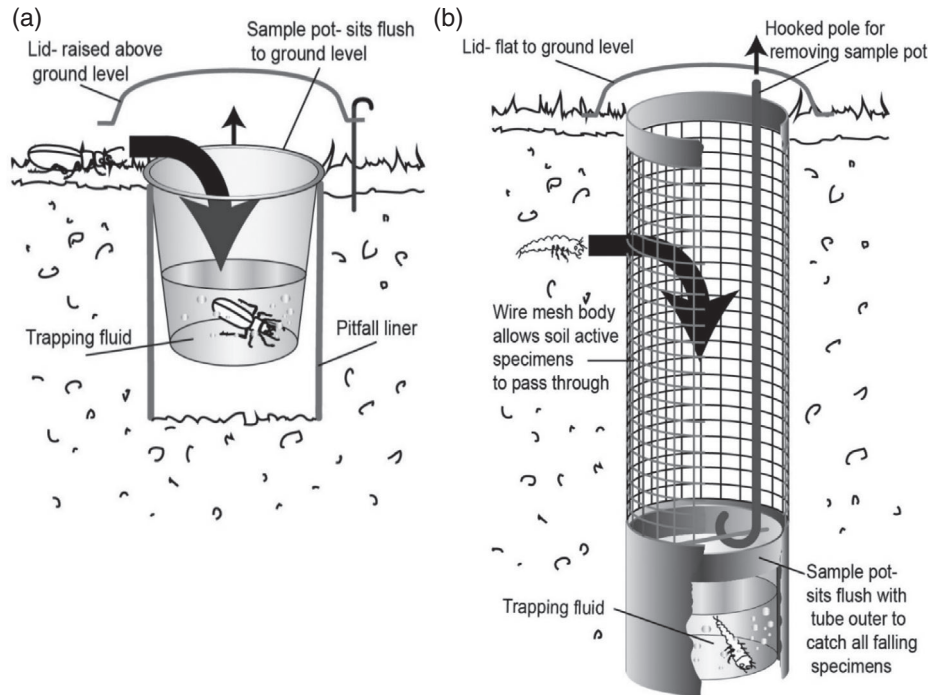
Figure 2 (a) Standard pitfall trap design and setup. Cup 7.5 diameter 10 cm depth. (b) Subterranean pitfall design and setup. Pipe 34 cm × 7 cm with 3 cut-out sections 20 cm × 4 cm, bordered by wire mesh of 1.2 cm grid.

Results

Summary of data

After data cleaning, a dataset of 4648 records was produced for Run 1 (Table S1). Trap drying under the drought conditions experienced during this run was notably more prevalent in standard pitfalls, with the majority containing little to no preservation fluid. Weather conditions were much more favourable during Run 2 and the trap preservation fluid did not evaporate. After data cleaning, a dataset comprising 1703 records was produced; less than half of the abundance seen in Run 1 (Table S1).

Carabid occurrence by treatment

For pooled carabid abundance, none of the factors in the LMM were found to be significant in Run 1. For species richness, only trap type was found to be significant, with greater numbers of species caught in subterranean traps, with a predicted mean of 4.42 while standard pitfalls had a predicted mean of 3.27 ($F_{1,66} = 13.36$, $P < 0.001$, LSD 0.6347). Since Fishers alpha relies on the combination of abundance and species richness, the unidentified damaged specimens and latent catch of eaten specimens rendered diversity analysis of this run unreliable.

For Run 2, we found crop ($F_{2,11} = 62.8$, $P < 0.001$), trap type ($F_{1,63} = 5.92$, $P = 0.018$), and their interaction ($F_{2,63} = 5.11$, $P = 0.009$) to be significant factors in the variation of pooled abundance. For barley under-sown with grass/clover, abundance was significantly greater in subterranean traps. In wheat and grass, trap types were comparable with lower abundance in grass compared to wheat and barley (Fig. 3). No significant effect of crop, trap, or tillage was detected for species richness and diversity.
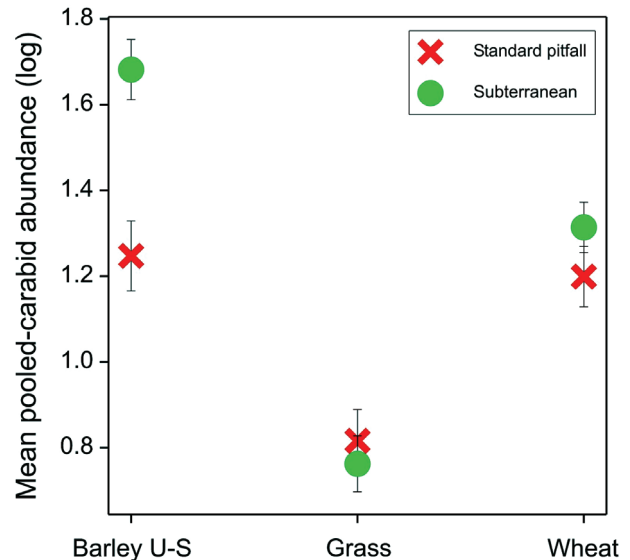

Figure 3 Run 2 fitted linear mixed model predictions for pooled-carabid abundance, predicted means with effective standard error bars. LSD for trap type 0.1215; LSD for crop type 0.1342. [Colour figure can be viewed at wileyonlinelibrary.com].

Assemblage differences

Crop, tillage, and above-/below-ground movements. The primary axis of the RDA for Run 1 was determined by the contrast between the carabid communities caught either in the pitfall or subterranean traps with the second axis resulting from differences between winter wheat and spring barley. For most
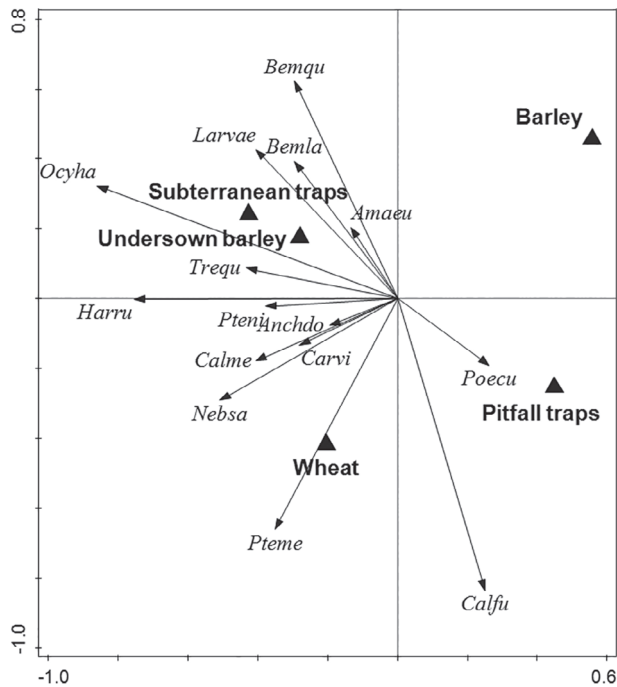
Figure 4 Redundancy analysis ordination of carabid species in run 1: with constrained axes of crop and trap type. Species names adult carabids: Bemqu = *Bembidion quadrimaculatum*; Bemla = *Bembidion lampros*; Ocyha = *Ocys harpaloides*; Amaeu = *Amara eurynota*; Trequ = *Trechus quadristriatus*; Harru = *Harpalus rufipes*; Pteni = *Pterostichus niger*; Anchdo = *Anchomenus dorsalis*; Calme = *Calathus melanocephalus*; Carvi = *Carabus violaceus*; Nebsa = *Nebria salina*; Poecu = *Poecilius cupreus*; Calfu = *Calathus fuscipes*; Pteme = *Pterostichus melanarius*. Larvae pooled.

Figure 5 Redundancy analysis ordination of carabid species in run 2: with constrained axes of crop and trap type. Species names adult carabids: Trequ = *Trechus quadristriatus*; Pteni = *Pterostichus niger*; Tacmi = *Tachys micros*; Harruf = *Harpalus rufipes*; Carvi = *Carabus violaceus*; Nebsa = *Nebria salina*; Bemla = *Bembidion lampros*; Calme = *Calathus melanocephalus*; Calfu = *Calathus fuscipes*; Pteme = *Pterostichus melanarius*. Larvae divided between predatory/omnivorous (Predlarv) and granvory (Granlarv).

species, relative abundance was higher in barley under-sown with grass and in subterranean traps (compared to pitfalls) (Fig. 4). Notably, all larvae were associated with subterranean traps, along with the two *Bembidion* species. *Pterostichus melanarius* (Illiger, 1798) and *Calathus fuscipes* (Goeze, 1777) showed association with wheat crops, and *Poecilus cupreus* (Linnaeus, 1758) solely showed an association with standard pitfalls. No species showed an association with (non-under-sown) barley.

Tillage did not explain any variance in carabid community composition in Run 1; including crop type and trap type accounted for 12.5% of the total variance in the RDA, with crop accounting for 5.9% and trap type 6.3% (pseudo-$F = 4.7$, $P = 0.001$, Fig. 4). While the community data from Run 1 provides useful supporting evidence of the effects of trap type and crop, the low variance explained may be partly due to the drought during the trapping period and individual species responses were, therefore, not analysed for this run.

For Run 2, the variation explained by RDAs was much greater. Crop accounted for 23.7% of variance, and trap type accounted for 13.1% of variance. Tillage was, again, found to be nonsignificant.

The final constrained ordination with explanatory variable terms crop and trap type accounted for 37.4% (pseudo-$F = 15.8$, $P = 0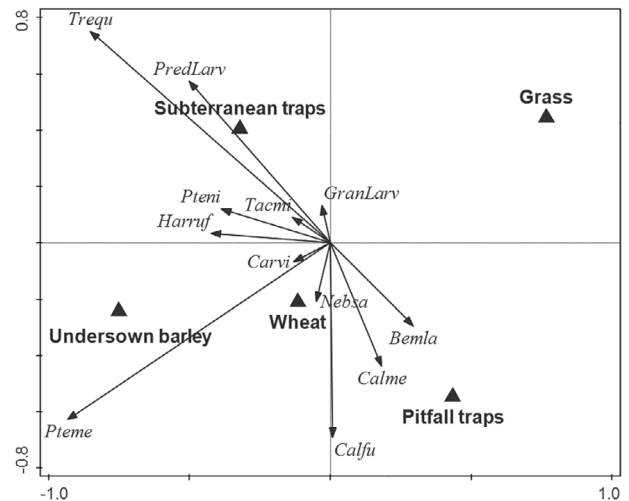.001$, Fig. 5). The inclusion of grass crops resulted in the primary RDA axis being determined by the contrast between communities in the perennial grass and annual cereals with trap type driving the second axis.

Species associations with management for Run 2 were stronger than in the Run 1 ordination (Fig. 5) but with some consistent effects. Predatory larvae and *Trechus quadristriatus* (Schrank, 1781) again showed a strong association with subterranean traps. *Calathus melanocephalus* (Linnaeus, 1758), *C. fuscipes* and, notably, *Bembidion lampros* (Herbst, 1784) showed an association with standard pitfall traps. *P. melanarius* showed a general association with cereal crops, and none between trap type. No carabid species showed an association with the grass crop.

Because of the stronger effects of crop and trap type observed in Run 2, additional univariate analyses were done on the abundance measures at the species level. The LMM predictions supported the association of *P. melanarius* with cereal crops in the ordination. There was also a significant interaction of trap type and crop (Table S2; Fig. 6a): in under-sown Barley, abundance was much higher in subterranean traps. *Trechus quadristriatus* showed a similar interaction to *P. melanarius* (Table S2; Fig. 6b), yet the abundance was consistently lower in standard pitfall traps across crop types. The abundance of *Harpalus rufipes* showed a significant response to crop, with the greatest abundances in barley under-sown, followed by grass, then wheat (Table S2; Fig. 6c). *Pterostichus niger* (Schaller, 1783) showed the same pattern of interaction as *P. melanarius*, yet with a lesser general abundance in standard pitfalls, apart from in the wheat crop (Table S2; Fig. 6d). In the fitted model for *Calathus fuscipes*, predictions showed higher abundances in pitfall traps (Table S2; Fig. 6e). In the fitted model for the abundance of *B. lampros*, tillage was shown to be significant along with trap type, whereby abundances were greater in
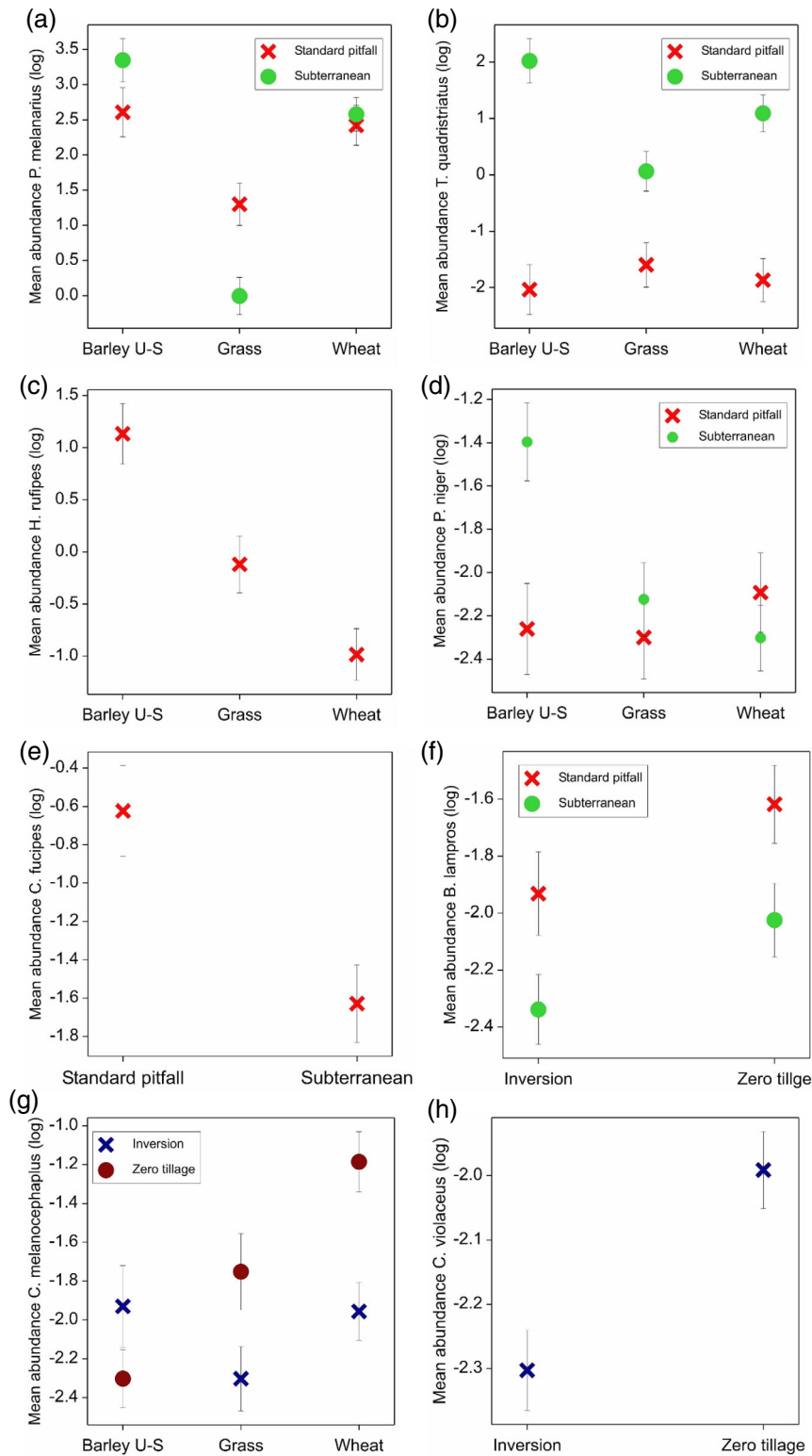
Figure 6 Linear mixed fitted model prediction means plots with effective standard error bars, for log abundance of adult carabids (a) *Pterostichus melanarius* LSD for trap type 0.4873; LSD for crop type 0.6769; (b) *Trechus quadristriatus* LSD for trap type 0.5450; LSD for crop type 0.9705; (c) *Harpalus rufipes*; LSD for crop type 0.8763; (d) *Pterostichus niger* LSD for trap type 0.3190; LSD for crop type 0.3821; (e) *Calathus fuscipes*; LSD for trap type 0.6636; (f) *Bembidion lampros* LSD for trap type 0.3599; LSD for tillage 0.3062; (g) *Calathus melanocephalus* LSD for crop type 0.4274; LSD for till 0.3273; and (h) *Carabus violaceus*; LSD for till 0.1916. [Colour figure can be viewed at wileyonlinelibrary.com].
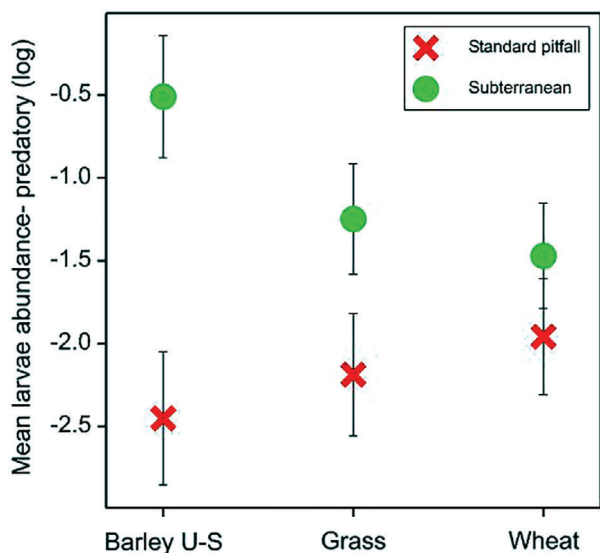
Figure 7 Linear mixed model fitted model prediction means plots with effective standard error bars, for predatory carabid larvae abundance by trap type in Run 2. LSD for trap type 0.4255; LSD for crop type 0.953. [Colour figure can be viewed at wileyonlinelibrary.com].

standard pitfalls, and in zero till (Table S2; Fig. 6f). Tillage was also retained as a significant effect in the model for *Calathus melanocephalus* abundance; however, in an interaction with crop type (Table S2; Fig. 6g). Tillage alone was significant in the fitted model for *Carabus violaceus* (Linnaeus, 1758), with higher abundances in zero tillage (Table S2; Fig. 6h).

Larvae occurrence. The larvae catch during Run 1 was very low, however, all larvae were found in subterranean pitfall traps (Table S1). This may have been due to the dry conditions reducing the movement of larvae at the soil surface. We were unable to analyse these low numbers statistically in LMMs. In the RDA analysis, larvae were strongly associated with subterranean traps in under-sown barley (Fig. 4).

Larvae were much more abundant in Run 2 (Table S1); therefore, statistical analysis of a division into granivorous and predatory species was possible. In the RDA analysis, granivorous larvae showed a weak association with subterranean traps, and predatory/omnivorous larvae showed a strong association with subterranean traps in under-sown barley (Fig. 5). The LMM for granivorous larvae failed to retain any significant terms. The fitted model for predatory/omnivorous larvae showed an interaction of crop and trap type ($F_{2,58} = 4.00$, $P = 0.024$) whereby abundances were higher in subterranean traps in all crops, yet highest in subterranean traps in barley under-sown, and lowest in pitfall traps in barley under-sown (Fig. 7).

Discussion

The infield factors influencing carabid abundance, species richness and diversity

Crop type and tillage were anticipated to have an effect on total species abundance. The results for Run 2 broadly conformed

with the literature on crop effects with relatively high catches in cereals compared with lower catches in grass (Eyre *et al.*, 2013). Variation was seen in abundance according to crop type, with an interaction with trap type. Notably higher abundance in subterranean traps in under-sown barley demonstrated the effects of above-ground structure, which is cited in the literature as crucial to the distribution of carabids (Thiele, 1977; Holland, 2002; Kotze *et al.*, 2011). It is likely this also holds true for the mirrored below-ground environment. Increased structure and resources afforded by shallower grass and nitrogen fixing clover roots in among the longer barley cereal roots supports a richer micro and macrofauna environment, including altering soil structure and microclimatic properties (Clapperton, 2003; Scopel *et al.*, 2013; Wezel *et al.*, 2014). Our results suggest this supports increased abundance of carabids and their potential for predation in this below-ground crop area and indicate under-sowing cereals may enhance this ecosystem service.

The absence of significant tillage effects in pooled analyses was surprising. Inversion tillage changes the soil structure, inverting the soil surface to a lower level and burying organic matter in the form of previous crop chaff remaining on the soil surface. This constitutes a drastic change in microclimate and resources at the level of soil macrofauna, and also a physical disturbance potentially killing adults and larvae at the time of treatment (Baguette & Hance, 1997; Holland & Luff, 2000). Although we sampled several months after the soil had been cultivated (potentially reducing the observed effect), other studies (Hatten *et al.*, 2007; Shearin *et al.*, 2014) that included multiple sample points across crop rotations with contrasting tillage found all species to be affected by tillage, with species richness and diversity higher in zero tillage.

However, neither crop type nor tillage significantly explained any of the observed variation for Run 1. These results were biased by the drought conditions and should be interpreted with caution. The effect of trap type on species richness is likely due to a combination of in-trap predation and the traps changing from passive to active, as the trapping fluid evaporated, attracting other invertebrates to previously caught specimens (Kotze *et al.*, 2011). The higher abundance and species richness observed in the desiccated standard pitfall traps is likely an artefact of these events.

The greater abundance observed in traps for Run 1 compared with Run 2 can be partially explained by the traps shifting from passive to active, altering trapping dynamics. However, it is more likely to be a measure of activity-density, which is largely influenced by species phenology, but is compounded here under drought conditions: carabids will move from an unsuitable habitat to find the resources they require. Consequently, the abundance in traps could have measured increased movement activity in searching behaviour (Chiverton, 1984; Wheater *et al.*, 2011).

Carabid species and community composition between treatments

Species responded differently to crop type. In Run 1, though it must be interpreted with caution because of the effect of the drought, the higher number of individual carabid species associated with under-sown barley than standard barley supports

the argument that the more complex structure (two canopy layers of vegetation) of this crop is beneficial for carabids as opposed to the fact that it was spring sown.

In Run 2, we saw less crop associations than Run 1 at species level, for example, *P. melanarius* abundances were associated with both cereal crops. However, the relatively low catches within the grass crop are surprising, given the recommendations in the literature that grass margins play an important role in survivorship and landscape level population dynamics. Though studies have found this to be beneficial to carabid abundance and survivorship (French & Elliott, 1999; Thomas *et al.*, 2002; Saska *et al.*, 2007; Holland *et al.*, 2009), this could be attributed to the nature of the habitat as a structural resource in refuge area and food resources of noncrop vegetation. As opposed to the attribute of grass as a plant harbouring resources in attendant pests and producing pollen and seeds as food. Sample timing may, therefore, be important in understanding the role of this habitat. Grass margins and adjacent habitat may only be used at certain times by carabid beetles which needs to be considered when designing farm habitats to optimise ecosystem services. Eyre *et al.*, (2013) also found no species to be strongly associated with grass crops in a study of a nine-crop rotation over 5 years, yet differences in community associations between organic and conventional cereal crops were noted.

The main split in community composition was by trap type. By examining the species captured moving in the top 30 cm of soil, we may draw conclusions about species not commonly trapped as surface active. Furthermore, subterranean traps may better reflect a species preference for a crop habitat, as below-ground movements suggest the area has ample resources. Surface measures of activity-density may give a false impression of abundance, for example Chiverton (1984), found increased catches in pitfall traps of insecticide treated plots were in fact of individuals that had low gut content. The author concluded that higher activity-density was a result of foraging behaviour in invertebrate denuded plots, and inferences should not be drawn from pitfall trapping alone. Juran *et al.* (2013) found that organic management supported greater abundance of carabids than conventional and integrated systems, with their subterranean sampling reflecting multiple management influences. Subterranean traps are therefore expected to provide a better indication of a species preference and assemblage within a given area, and the detrimental effects of such management as foliar insecticide applications would be dampened or removed. This is particularly important in obtaining an accurate and unbiased account of a species assemblage. For example, *P. niger* is a key predator of molluscs (Luff, 1998; Symondson, 2004), accurate estimation of hypogean movements of this species, especially in root crops for instance, could be implemented into management planning for crop pest problems.

Bembidion lampros showed an association with subterranean traps in the first run, but a converse link to pitfalls in Run 2. This could be attributed to climatic effects or phenological stage, but the LMM for this species suggests that it is more likely that in-trap predation is responsible for the disparity. Most likely due its smaller size, it was subject to higher predation by larger carabids, obscuring the observations. The predictions for *P. melanarius* show that species movements (surface and subterreanean) were significantly different only in under-sown

barley. Since the abundances, denoted by activity-density at the surface as measured by pitfalls, are equal in wheat and barley, this should not be an attribute of niche spill-over through sheer abundance. Increased below-ground catch was also observed in the data for *T. quadristriatus* and *P. niger*, although their overall crop preference patterns in wheat and barley vary from *P. melanarius*. *Trechus quadristriatus* was also noted to be abundant in a study of below-ground carabid assemblages in oilseed rape (Drmić *et al.*, 2016). It is evident that under-sown crop confers some advantage for carabid resources, yet this is not universal. Our previous work (Jowett *et al.*, 2019) concluded that species preferences, even in the reportedly omni-preferential Carabidae family, resulted in quite specific actualised niches, potentially being obscured in pooled measure analysis. This work supports and extends this for the species highlighted above.

At the species level, tillage effects were shown for *B. lampros*, *C. melanocephalus* and *C. violaceus*. Kinnunen and Tiainen (1999) found community composition to be different between green set-aside and tilled fields, relating this to the colonisation of tilled fields in early spring by spring breeders, while set-aside supported a higher proportion of autumn breeders. The only spring breeder modelled separately in our study was *B. lampros*. This species had higher abundance in zero till and no effect of crop type. Armstrong and McKinlay (1997) found a range of carabid responses to four under-sowing treatments, relating this to species preferences to plant cover, noting a temporal aspect with the spring abundance of *B. lampros* connected with spring plant cover. Thus, the abundance of this species in our study is likely due to weed cover in zero-till. While *C. violaceus* is predominantly nocturnal, its predatory behaviour on molluscs may drive association with weedier crops and shelter in surface chaff (Luff, 1998). *Calathus melanocephalus* is defined as mainly nocturnal but varies from the other species trapped in its noted xerophilic (dry tolerance) and preference for light soils. This is interesting in the respect of the interaction with crop. In grass and wheat, the effect of tillage may have made the soil structure more water retentive, negatively affecting this xerophilic species (Breland, 1996).

The literature is divided on the species specifics of tolerance to tillage – Baguette and Hance (1997) found *P. melanarius* to increase in abundance with increasing frequency of tillage treatments, while Shearin *et al.* (2014) highlights *P. melanarius* to be reduced by all tillage treatments – more so than weed seed specialists. This may indicate in relation to our results, that complex interactions play on species differentially within the singular treatment of tillage.

Differential response of carabid larvae to infield factors

We found significant patterns of larvae distributions in both runs. The strong associations of carabid larvae with the under-sown barley is likely to be due to the benefits of the microbiome of a dual vegetative structure, and its associated resources (Theunissen, 1994; Theunissen & Schelling, 2000; Hance, 2002; Ratnadass *et al.*, 2006). This is contrary to our expectation that larvae and adults would be most abundant in the same crop. We conclude that the resources and structure allow for the differential needs of both life stages.

The lack of effects observed from tillage treatments could be due to the short establishment period in respect of generational time and population processes as outlined above. However, Blubaugh and Kaplan (2015) used 1-year established similarly small plots to examine weed seed predatory adult and larval *Harpalus* spp. The authors found that both adults and larvae were substantially reduced in frequently tilled plots, but effects between no-till and strip till cover crops were insignificant. While we cannot conclude from our results that annual tillage events constitute a disturbance that is catastrophic to carabid populations, it will be valuable to monitor carabids in future years on the experiment following consecutive tillage events to study any long-term impacts.

The association of carabid larvae with subterranean traps is unsurprising given their inclusion primarily to reveal the distribution of larval life stages in this study. The clear dominance of the subterranean catch highlights the advantage of below-ground trapping to robustly assess the contribution of larvae to ecosystems services. Blubaugh and Kaplan (2015) used standard pitfall traps to assess the granivorous larvae of *Harpalus* spp., extending this to weed seed predation. This study was able to elucidate the movements of predatory species that are less surface active. Particularly, under the drought conditions of the first run, larvae were active in lower soil layers and present solely in subterranean traps. If the assessment of larval predation was merely on the pitfall traps as predictions showed, the barley under-sown would be assumed to have low abundances of predatory larvae and subsequently the pest regulation capacity would be underestimated.

Conclusions

Carabid distributions constitute a complex picture. We found that the above and below-ground assessments using standard and subterranean traps in tandem provided a more comprehensive and accurate understanding of carabid distributions. Our study saw that pitfall traps alone were insufficient to fully account for the contribution of carabids to sustainable pest control, particularly the vital contribution of carabid larvae. Specifically, the beneficial effects of under-sown barley would not have been apparent if only standard pitfall traps had been used without subterranean sampling. This may impact on the recommendation of appropriate management to boost service provision above- and below-ground. Future work should incorporate the accuracy of multiple trap types, along with estimates of predation for different life-stages and carabid species to accurately quantify the level of ecosystem services in farm habitats.

Acknowledgements

Authors' contributions

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

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Experimental plan for Large Scale Rotation Experiment at Brooms Barn in harvest year 2018. Rotation A: 1. winter wheat, 2. oilseed rape, 3. winter wheat; Rotation B: 1. winter wheat, 2. field beans, 3. winter wheat, 4. spring barley, 5. oilseed rape; Rotation C: 1. winter wheat, 2. spring barley under-sown with grass / clover, 3. grass / clover, 4. grass / clover, 5. winter wheat, 6. sugar beet, 7. soybean. Each phase of every rotation is part of both a zero till and a ploughed system, replicated twice. Three extra plots are included in the design (in italics) in 'Zero till Rotation C' but replacing sugar beet with linseed as it is not possible to completely avoid soil disturbance in a rotation that includes sugar beet. Each plot is 24 x 24 m and divided into two sub-plots; in future years, organic amendments are added to one sub-plot. Shaded plots were included in the invertebrate trapping Run 1 and plots with a solid border in Run 2.

Table S1. Run 1 and Run 2 trap species totals. S-T = subterranean, Pitfall = Standard pitfall traps. Damaged unidentifiable carabids were grouped by size; small 2-4 mm; small-med 4-9 mm, medium 9-14 mm.

Table S2. Individual species LMM outputs for Run 2 species with significant terms *Pterostichus melanarius*, *Trechus quadristriatus*, *Harpalus rufipes Pterostichus niger*, *Calathus fuscipes*, *Bembidion lampros*, *Calathus melanocephalus*, and *Carabus violaceus*.

References

Armstrong, G. & McKinlay, R.G. (1997) The effect of undersowing cabbages with clover on the activity of carabid beetles. *Biological Agriculture & Horticulture*, **15**, 269–277.

Baguette, M. & Hance, T.H. (1997) Carabid beetles and agricultural practices: influence of soil ploughing. *Biological Agriculture & Horticulture*, **15**, 185–190.

Beck, J. & Schwanghart, W. (2010) Comparing measures of species diversity from incomplete inventories: an update. *Methods in Ecology and Evolution*, **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. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1715–1727.

Blubaugh, C.K. & Kaplan, I. (2015) Tillage compromises weed seed predator activity across developmental stages. *Biological Control*, **81**, 76–82.

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. *Journal of Applied Ecology*, **56**, 10–20.

Bommarco, R., Vico, G. & Hallin, S. (2018) Exploiting ecosystem services in agriculture for increased food security. *Global Food Security*, **17**, 57–63.

Breland, T.A. (1996) Green manuring with clover and ryegrass catch crops undersown in small grains: effects on soil mineral nitrogen in field and laboratory experiments. *Acta Agriculturae Scandinavica B-Plant Soil Sciences*, **46**, 178–185.

Brooks, D.R., Bohan, D.A., Champion, G.T. *et al.* (2003) Invertebrate responses to the management of genetically modified herbicide–tolerant and conventional spring crops. I. Soil-surface-active invertebrates. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **358**, 1847–1862.

Brooks, D.R., Perry, J.N., Clark, S.J. *et al.* (2008) National-scale metacommunity dynamics of carabid beetles in UK farmland. *Journal of Animal Ecology*, **77**, 265–274.

Chiverton, P.A. (1984) Pitfall-trap catches of the carabid beetle *Pterostichus melanarius*, in relation to gut contents and prey densities, in insecticide treated and untreated spring barley. *Entomologia Experimentalis et Applicata*, **36**, 23–30.

Clapperton, M.J. (2003) Increasing soil biodiversity through conservation agriculture: managing the soil as a habitat. *Proceedings of Second World Congress on Conservation Agriculture: Producing in Harmony with Nature, Iguassu Falls, Parana-Brazil*, pp. 11–15.

Drmić, Z., Čačija, M., Gašparić, H.V., Lemić, D. & Bažok, R. (2016) Endogaeic ground beetles fauna in oilseed rape field in Croatia. *Journal of Central European Agriculture*, **17**(3), 675–684.

Eisenhauer, N., Schielzeth, H., Barnes, A.D. *et al.* (2019) A multi-trophic perspective on biodiversity–ecosystem functioning research. *Advances in Ecological Research*, **61**, 1–54.

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 and Environment*, **165**, 60–67.

French, B.W. & Elliott, N.C. (1999) Temporal and spatial distribution of ground beetle (Coleoptera: Carabidae) assemblages in grasslands and adjacent wheat fields. *Pedobiologia*, **43**, 73–84.

Hance, T. (2002) Impact of cultivation and crop husbandry practices. *The Agroecology of Carabid Beetles* (ed. by J. M. Holland), pp. 231–249. UK: Intercept Limited.

Hatten, T.D., Bosque-Pérez, N.A., Labonte, J.R., Guy, S.O. & Eigenbrode, S.D. (2007) Effects of tillage on the activity density and biological diversity of carabid beetles in spring and winter crops. *Environmental Entomology*, **36**, 356–368.

Holland, J.M. (2002) *The Agroecology of Carabid Beetles*. UK: Intercept Limited.

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**, 19–33. https://doi.org/10.1007/s10526-008-9152-2.

Holland, J.M. & Luff, M.L. (2000) The effects of agricultural practices on Carabidae in temperate agroecosystems. *Integrated Pest Management Reviews*, **5**, 109–129.

Hyvarinen, E., Kouki, J. & Martikainen, P. (2006) A comparison of three trapping methods used to survey forest-dwelling Coleoptera. *European Jounal of Entomology*, **103**, 397–407.

Jowett, K., Milne, A.E., Metcalfe, H., Hassall, K.L., Potts, S.G., Senapathi, D. & Storkey, J. (2019) Species matter when considering landscape effects on carabid distributions. *Agriculture, Ecosystems and Environment*, **285**, 106–131.

Juran, I., Gotlin Čuljak, T., Bűchs, W., Grubišić, D. & Sivčev, I. (2013) Impact of various oilseed rape productions on biological potential of endogaeic active ground beetles (Coleoptera: Carabidae). *Proceedings of the 14th Meeting of the IOBC/Wprs Working Group "Insect Pathogens and Entomoparasitic Nematodes" 16–20 June 2013*, Vol. **90** (ed. by J. A. Jehle, R. Bažok, N. Crickmore, M. López-Ferber, I. Glazer, E. Quesada-Moraga and M. Traugott), p. 351. IOBC/wprs Bulletin, Zagreb.

Kinnunen, H. & Tiainen, J. (1999) Carabid distribution in a farmland mosaic: the effect of patch type and location. *Annales Zoologici Fennici*, 36, pp. 149–158. Finnish Zoological and Botanical Publishing Board.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947–969.

Kotze, D.J., Brandmayr, P., Casale, A. *et al.* (2011) Forty years of carabid beetle research in Europe–from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys*, **100**, 55–148.

Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems & Environment*, **74**, 187–228.

Lami, F., Boscutti, F., Masin, R., Sigura, M. & Marini, L. (2020) Seed predation intensity and stability in agro-ecosystems: role of predator diversity and soil disturbance. *Agriculture, Ecosystems and Environment*, **288**, 106.

Luff, M.L. (1997) The Carabidae (Ground beetles) of Britain and Ireland. *Handbooks for the Identification of British Insects. Vol. 4 Part 2*, 2nd edn. UK: Royal Entomological Society.

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

Luff, M.L. & Larsson, S.G. (1993) *The Carabidae (Coleoptera) Larvae of of Fennoscandia and Denmark*, Vol. **27**. Leiden, Netherlands: Brill.

Magurran, A.E. (2013) *Measuring Biological Diversity*. Oxford, UK: John Wiley & Sons.

Marrec, R., Badenhausser, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N. & Gauffre, B. (2015) Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape. *Agriculture, Ecosystems and Environment*, **199**, 282–289.

McGavin, G. (1997) *Expedition Field Techniques. Insects: And Other Terrestrial Arthropods*. Royal Geographical Society, London.

Moreau, C.S., Wray, B.D., Czekanski-Moir, J.E. & Rubin, B.E. (2013) DNA preservation: a test of commonly used preservatives for insects. *Invertebrate Systematics*, **27**, 81–86.

New, T.R. (1998) *Invertebrate Surveys for Conservation*. Oxford University Press, Oxford.

Owen, J.A. (1995) A pitfall trap for repetitive sampling of hypogean arthropod faunas. *Entomologist's record and journal of variation*, **107**, 225–228.

Payne, R. W. (ed.) (1993) *Genstat 5 Release 3 Reference Manual*. Oxford, UK: Oxford University Press.

Petit, S., Bohan, D.A. & Dijon, A. (2018a) The use of insects in integrated weed management. *Integrated Weed Management for Sustainable Agriculture*, 42, pp. 453–468. Cambridge, UK: Burleigh Dodds Science Publishing. https://doi.org/10.19103/AS.2017.0025.23.

Petit, S., Cordeau, S., Chauvel, B., Bohan, D., Guillemin, J.P. & Steinberg, C. (2018b) Biodiversity-based options for arable weed management. A review. *Agronomy for Sustainable Development*, **38**, 48.

Ratnadass, A., Michellon, R., Randriamanantsoa, R. & Séguy, L. (2006) Effects of soil and plant management on crop pests and diseases. *Biological Approaches to Sustainable Soil Systems*, **41**, 589–602.

Redlich, S., Martin, E.A. & Steffan-Dewenter, I. (2018) Landscape-level crop diversity benefits biological pest control. *Journal of Applied Ecology*, **55**, 2419–2428.

Sasakawa, K., Ikeda, H. & Kubota, T. (2010) Feeding ecology of granivorous carabid larvae: a stable isotope analysis. *Journal of Applied Entomology*, **134**, 116–122.

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. *Agriculture, Ecosystems and Environment*, **122**, 427–434.

Schmidt, M.H., Clough, Y., Schulz, W., Westphalen, A. & Tscharntke, T. (2006) Capture efficiency and preservation attributes of different fluids in pitfall traps. *Journal of Arachnology*, **34**, 159–162.

Scopel, E., Triomphe, B., Affholder, F. *et al.* (2013) Conservation agriculture cropping systems in temperate and tropical conditions, performances and impacts. A review. *Agronomy for Sustainable Development*, **33**, 113–130.

Shearin, A.F., Reberg-Horton, S.C. & Gallandt, E.R. (2014) Direct effects of tillage on the activity density of ground beetle (Coleoptera: Carabidae) weed seed predators. *Environmental Entomology*, **36**, 1140–1146.

Sims, I. & Cole, J. (2016) Hypogean pitfall trapping: a novel technique for assessing soil biodiversity in agroecosystems. *British Journal 0f Entomology and Natural History*, **29**, 2016.

Sims, I. & Cole, J. (2017) *Baeus seminulum* (hymenoptera:scelionidae) new to Berkshire and a review of records from the British Isles. *British Journal of Entomology and Natural History*, **30**, 2017.

Smilauer, P. & Leps, J. (2014) *Multivariate Analysis of Ecological Data using Canoco 5*. Cambridge, UK: Cambridge University Press.

Smith, J., Potts, S. & Eggleton, P. (2008) Evaluating the efficiency of sampling methods in assessing soil macrofauna communities in arable systems. *European Journal of Soil Biology*, **44**, 271–276.

Suenaga, H. & Hamamura, T. (1998) Laboratory evaluation of carabid beetles (Coleoptera: Carabidae) as predators of diamondback moth (Lepidoptera: Plutellidae) larvae. *Environmental Entomology*, **27**, 767–772.

Symondson, W.O.C. (2004, 2004) Coleoptera (Carabidae, Drilidae, Lampyridae and Staphylinidae) as predators of terrestrial gastropods. *Natural Enemies of Terrestrial Molluscs* (ed. by G. M. Barker), pp. 37–84. CAB International, Oxford.

Telfer, M. (2017) *Subterranean Pitfall Traps for Beetles* [online blog] URL http://www.markgtelfer.co.uk/beetles/techniques-for-studying-beetles/subterranean-pitfall-traps-for-beetles/ [accessed on 20 November 2017]

Theunissen, J. (1994) Intercropping in field vegetable crops: pest management by agrosystem diversification—an overview. *Pesticide Science*, **42**, 65–68.

Theunissen, J. & Schelling, G. (2000) Undersowing carrots with clover: suppression of carrot rust fly (*Psila rosae*) and cavity spot (Pythium spp.) infestation. *Biological Agriculture & Horticulture*, **18**, 67–76.

Thiele, H.U. (1977) *Carabid Beetles in their Environments: A Study on Habitat Selection by Adaptations in Physiology and Behaviour*, Vol. **10**. Berlin: Springer Science & Business Media.

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

Thomas, R.S., Harwood, J.D., Glen, D.M. & Symondson, W.O.C. (2009) Tracking predator density dependence and subterranean predation by carabid larvae on slugs using monoclonal antibodies. *Ecological Entomology*, **34**, 569–579.

Traugott, M. (1998) Larval and adult species composition, phenology and life cycles of carabid beetles (Coleoptera: Carabidae) in an organic potato field. *European Journal of Soil Biology*, **34**, 189–197.

Tscharntke, T., Tylianakis, J.M., Wade, M.R., Wratter, S.D., Bengtsson, J. & Kleijn, D. (2007) Insect conservation in agricultural landscapes. *Insect Conservation Biology. Proceedings of the Royal Entomological Societies 23rd Symposium* (ed. by A. J. A. Stewart, T. R. New and O. T. Lewis), pp. 383–404. CABI, Oxford.

Tylianakis, J.M. & Romo, C.M. (2010) Natural enemy diversity and biological control: making sense of the context-dependency. *Basic Applied Ecology*, **11**, 657–668. https://doi.org/10.1016/j.baae.2010.08.005.

Wezel, A., Casagrande, M., Celette, F., Vian, J.F., Ferrer, A. & Peigné, J. (2014) Agroecological practices for sustainable agriculture. A review. *Agronomy for Sustainable Development*, **34**, 1–20.

Wheater, C.P., Bell, J.R. & Cook, P.A. (2011) *Practical Field Ecology: A Project Guide*. UK: John Wiley & Sons.

Woodcock, B.A., Harrower, C., Redhead, J. *et al.* (2014) National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key ukarable crops. *Journal of Applied Ecology*, **51**, 142–151.

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. *Ecological Entomology*, **32**, 302–311.