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

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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 actual abundances to be highest in this crop.
7. Comprehensive estimation of ecosystem services should incorporate both above- and below ground community appraisal, towards appropriate management.
   * *Keywords*

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

# Introduction

## Carabid service provision in agroecosystems

Carabid beetles, as ubiquitous 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; Petit et al 2018; Tscharntke et al., 2007). Furthermore, there is a general consensus that a diverse carabid community will provide more stable and increased natural pest regulation contributions to agricultural production (Bianchi, Booij, and Tscharntke, 2006; Bommarco, Vico, and Hallin, 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, Holland, and Brown, 2002). This may vary 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 (Jowett et al 2019; Kleijn and Sutherland 2003; Petit, Bohan, and Dijon, 2018).

There are around 350 species of carabid in the UK. They vary according to diet, phenology, dispersal, and environmental tolerances (such as moisture levels and recovery from disturbances) (Thielle 1977). Not all provide natural pest regulation services useful for farmers: species may be present that do not feed on particular crop pests when outbreaks occur, or the species may not be in the right place or active at the right time. Though much data exists on the most prevalent 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 (Kotze et al 2011; Kromp 1999; Redlich, Martin, and Steffan‐Dewenter, 2018; Tscharntke et al 2007). 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 and biological interactions — the resultant assemblage therefore can vary tremendously, following on to the type of services they provide spatially and temporally (Eisenhauer et al 2019; Tylianakis and Romo 2010).

Carabids may be generalised broadly into autumn (hibernating as larvae) or spring breeders (hibernating as adults), though much variation exists on a spectrum through this categorisation and even within it due to variability in climate and resources. Carabids of agro-ecosystems largely lay their eggs in the soil, and larvae are predominantly carnivorous, therefore assumed active in crop areas where soil arthropods are plentiful. Larvae, being morphologically vulnerable, less tolerant to extremes of environmental conditions, and subject to intense resource need for growth, exhibit high mortality rates. Thus, this is a crucial life-stage to consider for any intervention aiming to boost populations (Lovei and Sunderland 1996; Thielle 1977; Kotze et al 2011).

Carabid larvae are principally soil-dwelling, especially those species inhabiting agro-ecosystems (Luff and Larsson, 1993). Though some species may move metres down into the soil, most live near the surface (top 50cm) feeding on the biota of the top soil horizons. Larvae are predominantly carnivorous, even when the adults are herbivorous (Sasakawa Ikeda and Kubota 2010); and have even been observed climbing up crop plants to feed on invertebrate pests (Suenaga and Hamamura 1998). Some species such as *Harpalus rufipes* however, specialise in weed seed predation, collecting seeds in burrows for consumption (Traugott 1998).

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 and 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 and occurrence of carabids at all life stages.

The infield factors having the greatest influence on carabid communities across all life stages concern the structure and resources in the habitat, both above- and below-ground. 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). Of particular interest, is the increasingly common practice of under-cropping. Under-sowing describes the practice of sowing a second crop beneath the main crop, usually simultaneously- to allow the under crop to establish (for example cereals under-sown with grass). This method of continuous cropping is thought to improve soil structure and function. Under-sowing may also potentially benefit carabids by providing a greater variety of canopy structures and resources, and associated reductions in pesticides and disturbance (Clapperton and Clapperton, 2003; Scopel et al 2013). Cropping of grass is also of interest as it is suggested that tussocky grass margins and adjacent grass habitats can boost carabid populations (Boetzl et al 2018; Holland 2003; Woodcock et al 2007). For below-ground structure and resources, crop is still crucial in vegetative structure and associated resources, but added to this is cultivation timings- and crucially tillage. Constituting a major disturbance event below-ground, and a reconfiguration of the upper soil level structure and resources, tillage has a great effect on carabid abundance- particularly to larvae (Baguette, and Hance, 1997; Hatten et al 2007; Lami et al 2020). Cultivation timings of winter and spring cereals constitute probably the largest management effect upon carabids- due to the impacts on population processes between autumn and spring breeding (Marrec et al., 2015; Holland and Luff, 2000). Though the literature on carabids variously 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, Bell and Cook 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 2003). Pitfall traps do capture carabid larvae; but the numbers caught are relatively small compared to adults, typically less than 1% of the catch (Hyvarinen, Kouki, and Martikainen 2006; McGavin 1997; New 1998).

Soil cores are the standard approach for collecting soil-active invertebrates (Wheater, Bell and Cook 2011). Soil cores are dug out, and the invertebrates in that delimited area at that time are counted: either by sifting through by hand, or by drying techniques forcing out invertebrates into collection pots. Studies have used various sizes of soil core, and different sorting techniques, (Smith, Potts and Eggleton 2008) yet this method may be inefficient for surveying carabid larvae (Bell, pers. Comm), 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 (for example ethanol), 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; Telfer 2017; Simms and Cole 2016; 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 experiment to assess the effect of crop type and cultivation method on carabid communities at both larval and adult life stages. We hypothesised that carabid abundance, species richness and diversity would vary by crop type and extent of tillage. Based on our previous findings (Jowett et al., 2019) we also expected that there would be a difference in response to these factors according to species and growth stage (larvae vs. adults). We hypothesise that:

H1- Carabid abundance, species richness and diversity will vary by crop type and extent of tillage

H2- Carabid species will respond differentially to crop type and extent of tillage, therefore community composition will vary between treatments

H3- Carabid larvae will respond differently to adults.

# Methods

## Brooms barn LSRE

We used a new field-scale experimental platform established on the Rothamsted Research farm at Brooms Barn (Suffolk, UK) that has been set up to quantify the impact of alternative cropping systems on a range of agronomic and environmental variables. The LSRE (Large Scale Rotation Experiment) (LSRE) has 60 24 x 24m plots; the main treatments are crop rotation (three, five or seven) and cultivation (zero tillage vs. mouldboard ploughing). Each phase of every rotation is sown every year in both a zero till or ploughed plot and replicated twice. 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 but the sub-sample plot structure was used to inform the positioning of the traps.

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 replicates even if they were from different rotation treatments as they all had oats as the preceding crop. Multiple replications allowed the separation of factors in crop type, and extent of tillage (potentially crucial to larvae) whilst controlling for distance to the margin which literature identifies as important to carabids)by avoiding plots in the centre of the experiment.

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 spring barley, and spring barley under-sown with grass, winter wheat and grass (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 inversion. For the barley and barley under-sown plots there were only two replicates of each crop by tillage treatment.. To control for distance, plots were chosen for each set of treatment replicates at different distances close to the experiment edge.

Table 1- near here

Each 12m x 24m subplot was stratified into three 8m x 12m grids and one pitfall trap placed at random in each stratum. A subterranean trap was subsequently located randomly in each stratum, but at distance of at least a 5m from any other trap. This made a total of 60 traps of each type across the experiment. These were installed on the 04/05/2018. With a two-month settling in period (Sims and Cole, 2017) traps were run from 4/07/18. A pilot trap was undertaken on the 20/06/18 in two plots. Trap runs were carried out in 14-day timings. Farm operations necessitated plots being run differentially on the two trap occasions. Run 1 ran from 16th to the 30th July, grass plots were excluded due to plot harvesting. Run 2 ran from on the 30th August to the 13th September. Grass plots were included in this second run but B4 treatment (Spring barley) was dropped due to harvest.

## Trap design and layout

The standard pitfall equipment used was 7.5 diameter 10cm depth cups, set in space holding pipes, with lids raised 4cm when set (Fig 1a).

Figure 1 near here

The design of the subterranean trap was based on Owens (1995) (see also Sims and Cole 2016; 2017; Telfer 2017). The design is based on a 34cm x 7cm pipe with 3 cut-out sections 20 x 4cm, bordered by wire mesh of 1.2cm 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, whilst allowing access to empty (Fig 1b). When unset, stiff plastic film sits, blocking 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; ethanol (70:30 with water) was chosen because it will preserve samples for possible later DNA analysis (Athey Chapman and Harwood 2017; Moraeu et al 2013; Schmidt et al 2006).

## Statistical analysis

### Pooled-carabid abundance, species richness, and diversity

Carabid adults were identified to species level. Due to the intractability of species level larvae identification by ID keys, larvae were classified by size, and predatory morphology to definite seed-eaters or predatory/omnivorous. During Run 1, drought conditions and particularly high temperatures caused pitfall trap fluid to dry out in nearly all standard pitfall traps, in some cases causing in-trap predation (i.e. carabids ate one another); therefore we analysed the two runs separately.

Some traps (~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. For each trap occasion we calculated, what we refer to as, the ‘pooled-carabid abundance’ (), i.e. the total number of carabids of any species, and species richness (), i.e. the number of different species. We fitted the log series model (Equation 1) to the data by maximum likelihood to give estimates of Fisher’s log-series alpha (, a robust and widely used diversity metric (Beck and Schwanghart, 2010; Magurran, 2004) that accounts for the effect of total numbers of individuals in a sample on diversity estimates.

(eqn 1)

We fitted Linear Mixed Models (LMMs) using the Genstat statistical software package (Payne, 1993) to determine the effect of environmental factors on pooled-carabid abundance (N), richness (S), species diversity (quantified as α ̂), carabid larvae (pooled) and certain individual species. 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 site, trap. We log transformed the pooled-abundance and alpha so that residuals conformed better to normality. We selected terms using backwards 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≤0.05) when dropped from the model.

The effect of crop type and cultivation on carabid community composition was analysed using multivariate methods in Canoco (Smilauer & Leps 2014) for each run separately. 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. Redundancy Analysis (RDA) was used including trap type, crop and cultivation as explanatory variables. All variables were analysed singly before being included in a combined analysis.

# Results

### Summary of data

After data cleaning, a dataset of 4,648 carabids was produced for Run 1 (Table 2). 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 1,703 carabids was produced; less than half of the abundance seen in Run 1 (Table 2).

Table 2- near here

## Carabid occurrence by treatment

For pooled carabid abundance, none of the factors 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 (d.f. 1, F=13.36, p<0.001 Fig 2). Since Fishers alpha relies on abundance and species richness, the unidentified damaged specimens and latent catch of eaten specimens rendered diversity analysis of this run untenable.

Figure 2 Near here

The fitted model for pooled-carabid abundance in Run 2 retained both crop (d.f. 2, F=62.8, p,0.001), and trap type (d.f. 1, F=5.92, p=0.018), and an interaction of the two (d.f. 2, F=5.11, p=0.009). For barley under-sown, 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- near here

## Assemblage differences

### Crop, tillage and hypogeal/epigeal movements

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 with crop accounting for 5.9 % and trap type 6.3% ( pseudo-F=4.7, P=0.001, Fig 4). This low level of explained variance was deemed intractable for further analysis of run 1 data by individual LMM at species level, where the lesser abundances would constitute less statistical power to draw conclusions.

Figure 4 -near here

The primary axis of the RDA 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 species, relative abundance was higher in barley under-sown with grass and in subterranean traps (compared to pifalls) (Fig 5). Notably, all larvae were associated with subterranean traps, along with the two *Bembidion* species. *Pterostichus* *melanarius* and *Calathus fuscipes* showed association with wheat crops, and *Poecilius cupreus* soley showed an association with standard pitfalls. No species showed an association with (non-under-sown) barley.

For run 2, the variation explained by PCAs 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 insignificant.

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.

Figure 5- near here

Species associations with management for run 2 were stronger than in the run 1 ordination (Fig 6). Predatory larvae and *Trechus quadristriatus* showed a strong association with subterranean traps. *Calathus* *melanocephalus*, *C. fuscipes* and, notably, *Bembidion lampros* showed association with standard pitfall traps. *P. melanarius* showed a general association with cereal crops, and none between trap type. No carabid species showed association with the grass crop.

Because of the stronger effects of crop and trap crop observed in Run 2, additional univariate analyses were done 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 3; Fig 6a): in under sown Barley, abundance was much higher in subterranean traps. *Trechus quadristriatus* showed a similar interaction (Table 3; Fig 6b), yet the abundance was consistently lower in standard pitfall traps across crop types. *Harpalus rufipes* showed a significant response to crop, with highest abundances in barley under-sown, followed by grass, then wheat (Table 3; Fig 6c). *Pterostichus niger* 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 3; Fig 6d). In the fitted model for *Calathus fuscipes* predictions showed higher abundances in pitfall traps (Table 3; Fig 6e). In the fitted model for *B. lampros* tillage was shown to be significant along with trap type, whereby abundances were higher in standard pitfalls, and in zero till (Table 3; Fig 6f). *Calathus melanocephalus* also retained tillage in the fitted model, however in an interaction with crop type (Table 3; fig. 6g). Tillage alone was significant in the fitted model for *Carabus violaceus*, with higher abundances in zero tillage (Table 3; Fig 6h).

Table 3- near here

Figure 6- near here

### Larvae occurrence

The larvae catch during Run 1 was very low, however, all larvae were found in subterranean pitfall traps (Table 2). This is likely to be 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 7).

Larvae were much more abundant in Run 2 (Table 2), therefore statistical analysis under 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. 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 (dd.f. 58.5, F=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).

Figure 7- near here

# Discussion

Hypothesis 1: **Carabid abundance, species richness and diversity will vary by crop and tillage**

The results of Run 1 do not support hypothesis H1, however these results were biased by the drought conditions, and so should be interpreted with caution. The singular retained term of trap type in the fitted model for species richness indicates the bias created by pitfall fluid drying. Subterranean traps were subject to much less fluid loss, whereas the standard pitfalls in many cases were subject to in-trap predation. Smaller species, less voracious species, and vulnerable or less environmentally tolerant individuals or life-stages (for example larvae, newly emerged adults and gravid females) may survive less stress or be less able to resist predation. Also, identification to species level is sometimes only possible from certain physical features, and so was not possible for those specimens that were damaged. Additionally, the olfactory effects of dead specimens with no preserving fluid altered the passive trapping pitfalls into active traps, potentially attracting carrion feeding species- extenuating predation and sample spoiling (Kotze, 2011; Thielle, 1977). As a result, desiccated traps were likely to have caught more individuals and species due to this potential state change (passive to active) than was evident from the samples. Due to the collection fluid not evaporating in the subterranean traps, this bias was not present and is a distinct advantage when trapping in areas of high exposure levels.

The greater abundance recorded in traps for Run 1 compared with Run 2 may be explained by actual higher abundance in crops, at a key time of feeding- as carabids have been shown to disperse and follow pest distributions and crop resources (Holland 2002; Kotze 2011). However, this is more likely (given that Run 2 directly followed Run 1) an attribute of the measure of activity-density under drought conditions: carabids will move from an unsuitable habitat to find the resources they require. As such the abundance in traps may actually measure increased movement activity in searching behaviour (Chiverton 1984; Wheater, Bell, and Cook 2011), and the traps shifted from passive to active or attractant traps, providing (perceived) shade by the covering hats.

The results for Run 2 conformed more with our expectations under H1. The significant variation in abundance according to crop type partially supports H1 **-** with an interesting interaction suggesting that hypogean abundance was higher in under-sown barley. Above-ground structure is cited in the literature as crucial to the distribution of carabids (Holland, 2002; Kotze, 2011; Thielle 1977), and this holds true for the mirrored below-ground environment. The increased structure and resources afforded by the shallower grass and nitrogen fixing clover roots in amongst the longer barley cereal roots supports a richer macro and microfauna, and has impacts on soil structure and microclimatic properties (Clapperton and 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 hypogean in crop area.

However, the lack of significance in modelling species richness and diversity somewhat disprove this first hypothesis. Furthermore, the absence of tillage effects are contrary to anticipated differences. 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 (Bagette and Hance 1997; Holland and Luff 2003). The establishment of the experiment with just one years’ tillage prior to the current studies’ use of plots may explain the lack of population level effects and cumulative soil structure and organic matter retention- yet the microclimate should still present differences at the level of carabid movements. Shearin, Reberg-Horton, and Gallandt (2014) found carabid activity densities reduced by over 50% directly following different tillage disturbances. Although we sampled several months after the soil had been cultivated (potentially reducing the observed effect),other studies (Hatten et al (2007)) that included multiple sample points across crop rotations with contrasting tillage found all species to be affected, with species richness and diversity higher in zero tillage. Further sampling is planned on the experiment in the future to determine whether tillage effects become more apparent beyond the first year of the experiment.

Hypothesis 2: C**arabid species will respond differentially to crop and tillage, therefore community composition will vary between treatments**

The ordination for Run 1, though it must be interpreted with caution because of the effect of the pitfalls drying out, through the specifics of species occurrence (rather than the noise created by pooled summary measures) shows that species respond differently to crop type, supporting hypothesis H2. The distinction in carabid presence between barley and under-sown barley lends credence to the beneficial structure (as in two canopies of vegetation) of this crop for carabid presence, especially considering that more species had higher catches in wheat than the standard barley.

The ordination for Run 2 showed less specific crop associations for example with *P. melanarius* abundances associated with both cereal crops. However, the relatively low catches of within the grass crop is interesting to relate to 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 and Elliot 1999; Holland, Birkett, and Southway 2009; Saska et al 2007; Thomas and Holland 2010) this could be attributed to the nature of the habitat as a structural resource in refuge area and food resources of non-crop vegetation, rather than the attribute of grass as a plant harbouring resources in attendant pests and producing pollen and seeds as food. The aspect of the sample timing is important to this appraisal- in that the refuge attributes are spatio-temporal with the respect to cultivation practices and biological cycles. Grass margins and adjacent habitat may only be used at certain times by carabid beetles- and this needs to be considered with the desired presence for predation in crops. Eyre, Luff and Leifert (2013) likewise found no species to be strongly associated with grass crops in a study of a nine-crop rotation over five years, yet they noted differences in community associations between organic and conventional cereal crops- this suggests that the singular temporal sample point in our study does reflect the wider trend. We suggest here that the presence of crop grass in rotation with cereal crops may not be beneficial to the carabids at this key time of activity- but may be important for providing offset resources at other times, and does indeed have the attribute that it does not ‘pull’ the carabids away from vital ecosystem service delivery in the cereal crops at that key pre-harvest pest occurrence interval.

The main split in community composition is along the axes of trap type. This denotes the spatial movements from a different perspective than many carabid studies. Examining the species captured moving in the top 30cm of soil, we may draw conclusions about species not commonly trapped as surface active, or those active in different traps at different times. Furthermore, subterranean traps may better reflect a species preference in inhabiting a crop area, as hypogean movements suggest the area has ample resources. 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 less full gut areas. The author concluded that higher activity density was due to behaviour of searching for food in invertebrate denuded plots, and therefore that inferences should not be drawn from pitfall trapping alone. It is likely that subterranean traps act on a finer scale in comparison with conventional pit fall trapping due to higher associated movement costs within the hypogean layer. Subterranean traps would therefore be expected to provide a better indication of a species preference and assemblage within a given area, and the detrimental effects to non-target arthropods associated within agriculture (such as foliar insecticide applications) would be dampened, if not removed. This is particularly important in relation to obtaining an accurate and unbiased account of a species assemblage, facilitating correct and informative management decisions. 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 feed into management planning for crop pest problems.

*Bembidion lampros* shows 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 on this day-active species, but the linear model for this species suggests that it is more likely that in-trap predation is responsible for the disparity, since there was no interaction with other variables. As a result, it was likely equally abundant in pitfalls in run 1, yet due its smaller size, was subject to higher predation by larger carabids, obscuring the finding. The predictions for *P. melanarius* we can see that species movements (epigeal and hypogeal) are differential 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. This distinction of markedly more hypogean movements is echoed in the predictions for *T. quadristriatus* and *P. niger*, which is remarkable given their overall crop preference patterns in wheat and barley vary from *P. melanarius*. Clearly the 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 genus, resulted in quite specific actualised niches- which may be missed in pooled measure analysis. This work supports and extends this. The distribution of *C. fuscipes, C. violaceus* and *B. lampros* is not significantly associated with the crop in which they were trapped.

Interestingly, at the species level, tillage effects may be seen in *B. lampros*, *C. melanocephalus* and *C. violaceus*. Kinnunen and Tiannen (1999) found community composition to be different between green set-asides and tilled fields, relating this to the colonisation of tilled fields in early spring by spring breeders, whilst set-asides supported a higher proportion of autumn breeders. The only spring breeder in our study was *B. lampros*. This species showed higher abundance in zero till, and no effect of crop. The day-active *B. lampros* may have greater abundances in zero tilled plots due to the relative shelter given by the retained surface chaff and/or weedier crop areas- as refuge from climatic conditions and predation. In concordance with this, 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. Whilst *C. violaceus* is strongly nocturnal, its predatory behaviour upon prey slugs and snails may drive association with weedier crops and shelter in surface chaff (Luff 1998). *Calathus melanocephalus* is defined as largely nocturnal, but varies from the other species trapped in its noted xerophilic (dry tolerance) and prefence 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, yet in barley the water stresses may be different due to essentially increased and structurally divergent water demand (Breland, 1996).

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, whilst Shearin et al (2014) highlights *P. melanarius* to be reduced by all tillage treatments- more so than weed seed specialists. Hatten et al (2007) incorporated crop interactions and related idiosyncratic responses to direct and indirect effects, variable by species. This may indicate in relation to our results, that complex interactions play on species differentially within the singular treatment of tillage. Responses to mechanical disturbance and structural and resource differences vary between species, drowning out impacts in the statistical noise of multifaceted effects.

Hypothesis 3: **Carabid larvae will respond differentially to adults, to crop and tillage**

Despite environmental variables limiting larval movements we were able to discern patterns of larvae distributions in both runs, with the subterranean traps. The strong associations of carabid larvae with the under-sown barley is a noteworthy result. This is likely due to the aforementioned soil structural benefits to the microbiome of a dual vegetative structure, and their associated resources. This disproves hypothesis H3**,** in that larvae and adults were both most abundant in the same crop. We must conclude that the resources and structure allow for the differential needs of both life-stages. It is also pertinent to highlight that adult and larval abundances are not mutually exclusive. Authors have explored the possibility of intra-specific competition of carabids, but no evidence has been found for adult species- this likely extends to the niche differentiation of larvae inter-specifically (Holland 2002; Thielle 1977). Therefore, the practice of under-sown crops would seem to be promising for abundant, comprehensive (in niche overlap of pest and weed predation), and persistent (in time overlap of species and life-stages and associated survivorship) pest control (Scopel et al, 2013; Theunissen, 1994; Theunissen and Schelling, 2000).

The lack of effects seen from tillage treatments may be due to the short establishment period in respect of generational time and population processes as outlined above. However, Blubaugh and Kaplan (2015) used one-year established similarly small plots to examine weed seed predatory adult and larval *Harpalus* sp. 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. We may then postulate that annual tillage events do not constitute disturbance catastrophic to carabid populations- or, as in the analysis of adults, may be species specific- particularly in spring versus autumn breeders, intractable in this study.

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. However, the clear dominance of the hypogean catch highlights the necessity to more fully and robustly assess the contribution of larvae to ecosystems services. Blubaugh and Kaplan (2015) used standard pitfall traps to assess the granivorous larvae of *Harpalus* sp. extending this to weed seed predation. This study was able to elucidate the movements of predatory species that are reportedly, and as we experimentally prove, less surface active. 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- which would be an entirely spurious finding, and subsequently the pest regulation capacity would be erroneous.

## Conclusions

Due to the variable environmental tolerances and traits of carabid adults, the pooled measures revealed little meaningful data for application to farm habitat management for carabid mediated pest control. The analysis of communities and species, however, amply disproved the null hypothesis. Under-sown barley was shown to be beneficial in boosting in crop abundance of both adults and larvae, developing a strong argument for under-sown cropping for comprehensive natural enemy pest control. Annual inversion tillage was shown to have an insignificant effect on the majority of trapped carabid species- a conclusion that we caution requires more species-specific examination and time series sampling before recommendations are warranted. Particular future work of value may be examining larval responses at a species level.

Carabid distributions constitute a complex picture, we found that the above and below-ground spatial assessment afforded by standard and subterranean traps in tandem provided a more comprehensive and accurate understanding of carabid distributions. This is important to a full accounting of the contribution of carabids to sustainable pest control, and the implementation of appropriate management to boost service provision above- and below-ground.

* 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.

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# Tables

Table 1- LSRE treatments and runs in which treatments were included

|  |  |  |
| --- | --- | --- |
| Treatment codes | Crop | Included in: |
| WHEAT B1, B3, C5 | Winter wheat | Run 1, Run 2 |
| BARLEY B4 | Spring barley | Run 1 |
| BARLEY C2 | Spring barley under-sown grass clover mix | Run 1, Run 2 |
| GRASS C3, C4 | Grass | Run 2 |

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

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Run 1 | | | Run 2 | | |
|  | S-T | Pitfall | Total | S-T | Pitfall | Total |
| *Pterostichus melanarius* | 826 | 1151 | 1977 | 731 | 362 | 1093 |
| *Harpalus rufipes* | 1233 | 700 | 1933 | 133 | 59 | 192 |
| *Ocys harpaloides* | 72 | 2 | 74 | 0 | 0 | 0 |
| *Calathus fuscipes* | 19 | 52 | 71 | 21 | 42 | 63 |
| *Pterostichus niger* | 22 | 16 | 38 | 7 | 1 | 8 |
| *Poecilius cupreus* | 7 | 20 | 27 | 0 | 0 | 0 |
| *Trechus quadristriatus* | 25 | 0 | 25 | 235 | 9 | 244 |
| *Nebria salina* | 17 | 2 | 19 | 9 | 6 | 15 |
| *Carabus violaceus* | 10 | 8 | 18 | 3 | 2 | 5 |
| *Bembidion lampros* | 11 | 1 | 12 | 2 | 7 | 9 |
| *B. quadrimaculatum* | 6 | 0 | 6 | 0 | 0 | 0 |
| *Anchomenus dorsalis* | 3 | 2 | 5 | 1 | 0 | 1 |
| *Calathus melanocephalus* | 5 | 0 | 5 | 4 | 11 | 15 |
| *Amara eurynota* | 2 | 0 | 2 | 0 | 0 | 0 |
| *Bembidion tetracolum* | 2 | 0 | 2 | 3 | 0 | 3 |
| *Agonum muelleri* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Elaphorus parvulus* | 1 | 0 | 1 | 1 | 0 | 1 |
| *Notiophilus biggutatus* | 1 | 0 | 1 | 0 | 1 | 1 |
| *Tachys micros* | 0 | 0 | 0 | 4 | 0 | 4 |
| *Bembidion tetracolum* | 0 | 0 | 0 | 0 | 0 | 0 |
| *Harpalus affinis* | 0 | 0 | 0 | 1 | 0 | 1 |
| *Brachinus crepitans* | 0 | 0 | 0 | 1 | 0 | 1 |
| *Demetrius atricaillus* | 0 | 0 | 0 | 1 | 0 | 1 |
| *Pterostichus madidus* | 0 | 0 | 0 | 1 | 0 | 1 |
| Carabid larvae granivores | - | - | - | 12 | 5 | 17 |
| Carabid larvae predators/omnivores- | | - | - | 27 | 1 | 28 |
| Carabid larvae total | 5 | 0 | 5 | 39 | 6 | 45 |
| Unidentified damaged small | 22 | 0 | 22 | 0 | 0 | 0 |
| Unidentified damaged small-medium | 6 | 13 | 19 | 0 | 0 | 0 |
| Unidentified damaged medium | 14 | 371 | 385 | 0 | 0 | 0 |
| Total Carabidae | 2309 | 2338 | 4647 | 1197 | 506 | 1703 |

Table 3- 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*

|  |  |  |  |
| --- | --- | --- | --- |
| ***Species***  Model terms retained | d.d.f | F | P |
| ***Pterostichus melanarius*** |  |  |  |
| Crop type | 9.0 | 41.78 | <0.001 |
| Trap type | 60.7 | 0.18 | 0.672 |
| Crop type.trap type | 60.6 | 5.22 | 0.008 |
| ***Trechus quadristriatus*** |  |  |  |
| Crop type | 11.6 | 2.39 | 0.135 |
| Trap type | 60 | 110.50 | <0.001 |
| Crop type.trap type | 60 | 6.04 | 0.004 |
| ***Harpalus rufipes*** |  |  |  |
| Crop type | 10.7 | 15.46 | <0.001 |
| ***Pterostichus niger*** |  |  |  |
| Crop type | 11.1 | 4.38 | 0.04 |
| Trap type | 63.7 | 1.96 | 0.167 |
| Crop type and trap type | 63.6 | 3.73 | 0.029 |
| ***Calathus fuscipes*** |  |  |  |
| Trap type | 66.4 | 9.15 | 0.004 |
| ***Bembidion lampros*** |  |  |  |
| Tillage | 11.4 | 6.02 | 0.031 |
| Trap type | 65.6 | 5.09 | 0.027 |
| ***Calathus melanocephalus*** |  |  |  |
| Crop type | 7.8 | 7.39 | 0.016 |
| Tillage | 8.3 | 7.26 | 0.026 |
| Trap type | 65.5 | 3.48 | 0.067 |
| Crop type and tillage | 6.48 | 8.5 | 0.019 |
| ***Carabus violaceus*** |  |  |  |
| Tillage | 10.6 | 12.89 | 0.004 |