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# National-scale regulation of the weed seedbank by carabid predators

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## Summary

1. Assuring future food productivity and security will require that better use is made of pest regulation provided by naturally occurring ecological services. However, empirical evidence of large-scale regulatory effects that might be employed in agriculture is still relatively scarce.
2. Using data from 257 conventionally managed arable fields at the UK national scale, we examine whether changes in the long-term store of weed seed in the seedbank are consistent with regulation by seed predatory carabid beetles.
3. We test three expectations of a simple conceptual model for carabid seed predation. The relationships we estimate are consistent with the model and suggest that carabid predation of weed seeds shed onto the soil surface changes the amount of seed returned to the seedbank bringing about seedbank change and regulation.
4. Granivorous and omnivorous carabids regulated seedbank abundance, with effects being observed on monocotyledon seedbank abundance, in all crops, and on total seedbank abundance, in spring maize and winter oilseed rape; effects that were robust across fields with differing pesticide management and between regions of the UK.
5. We found evidence of density dependence, with increasing amounts of seed rain leading to stronger regulation of the seedbank.
6. Our results also suggest that correlations between seed predators and seed rain abundance, which might be used to infer important effects of seed predators, do not provide sufficient evidence to indicate regulation of the weed seedbank.
7. *Synthesis and applications.* A major challenge for the future is to manage ecological, pest control services in place of current pesticides with little or no additional risk to productivity and food security. Our work shows that carabid seed predators have regulatory effects on the seedbank that appear general and robust across a range of current cropping and farm management situations at the national scale. Environmental Stewardship methods already exist across Europe to enhance carabid numbers in farmland. This means that carabid seed predators fit within a working framework that could be used to promote integrated pest management alongside or even in place of herbicides.

**Key-words:** carabid, Carabidae, ecosystem service, food security, granivore, omnivore, regulation, seed predation, seed rain, seedbank

## Introduction

There is a critical need to assure future food security, and increasing emphasis will be placed on greater crop productivity while reducing environmental impact and the reliance on chemical use in modern agriculture (OECD-FAO 2008; Royal

Society 2009). One way of achieving this aim will be to make farmland biodiversity 'work harder' by identifying ecological processes that may be managed to deliver robust ecosystem services. Recent studies have put emphasis on ecosystem services provided in agro-ecosystems (Moonen & Barberi 2008; Macfadyen *et al.* 2009). After several decades of intensive use of chemicals in agriculture and landscape simplification, a key question that has emerged is whether the extent of biodiversity loss that has occurred in agro-ecosystems (Benton, Vickery &

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Wilson 2003) still allows ecosystem services to be delivered in intensive agricultural landscapes (Loreau, Mouquet & Gonzalez 2003; Tschardt *et al.* 2005).

The regulation and control of pests that results from the activity of naturally present predators (natural enemies) is frequently cited as an important ecosystem service in arable agriculture (Losey & Vaughan 2006). To date, however, few natural enemy functions have been demonstrated to elicit regulation or apply with robustness and generality in real agro-ecosystems. Although mass release of natural enemies has been shown to work in closed systems, such as greenhouses, management of agro-ecosystems to enhance natural enemies rarely matches expectations (Gurr, Wratten & Altieri 2004).

Policy-driven changes in herbicide use may lead to increases in weed plant densities in arable fields, and reductions in crop productivity (Kim *et al.* 2002) and more generally the economic performance of agriculture. In the UK, in 2008 alone, 3 229 254 ha of cereal crops were treated with some 5 717 110 kg of herbicides (Garthwaite *et al.* 2010). The move away from chemical weed control will only be possible if ecological services are available and function well enough to substitute for these chemical inputs. For farmers to adopt these alternatives, it will be necessary to show that ecological processes could be employed to replace herbicides with little or no additional risk.

Carabid beetles have been studied as potential natural enemies of weeds, through predation of weed seeds by omnivorous and granivorous species (Tooley & Brust 2002; Westerman *et al.* 2003; Honek *et al.* 2007; Baraibar *et al.* 2009). It has been suggested that an annual seed loss of 25–50% may be enough to slow down weed population growth substantially (Firbank & Watkinson 1985), and predation rates observed in the field can exceed this level. Weed seed predation studies have shown that certain carabid species can aggregate to weed patches in the field (Holland, Perry & Winder 1999; Hough-Goldstein, VanGessel & Wilson 2004) and readily eat weed seeds under laboratory conditions (Honek, Martinkova & Jarosik 2003).

Although one might expect a positive relationship between seed predation rate and activity density of granivorous ground beetles in the field (Kromp 1999; Tooley & Brust 2002), field data are relatively scarce and the results are equivocal; some data show a relationship (Honek, Martinkova & Jarosik 2003; Honek, Martinkova & Saska 2005; Menalled *et al.* 2007), while other data sets indicate a lack of spatio-temporal correspondence (Mauchline *et al.* 2005; Saska *et al.* 2008). Ongoing, unpublished analyses of large-scale data sets suggest that the abundance of many granivorous and omnivorous carabid species are positively associated with weed seed abundance, while predominantly carnivorous species are not (D. R. Brooks, pers. comm.). It is not clear, however, whether these associations indicate that granivorous and omnivorous carabids can regulate weeds and represent an ecosystem service.

For seed predation by carabids to be considered an important ecosystem service, it would be necessary to show that the beetles are capable of regulating the long-term store of seed in the weed seedbank. It might be expected (Expectation 1) that regulation would be apparent as a negative relationship

between the change in the weed seedbank over 1 year and the abundance of carabids in that year, all other factors being equal. In our simple model, the seedbank changes as weed seed are shed as seed rain from plants and return to the soil. Some of this seed rain may be found (intercepted), at the soil surface, and eaten by seed predator carabids reducing the amount returned to the seedbank. If the interception rate is high and enough seeds are eaten, there will be a net decline in the seedbank over the year. This simple model suggests two subsidiary expectations that would be required for systematic changes in the weed seedbank to be attributable to regulation by carabid beetles; Expectation 2 that 'seedbank population density is positively related to seed rain abundance'; and Expectation 3 that, with successful interception, 'carabid abundance is positively related to seed rain'. Here, we test these three expectations for seedbank regulation using data on carabid, seedbank and seed rain counts collected in 257 fields of four crops located across regions of Great Britain (GB).

## Materials and methods

### EXPERIMENTAL DESIGN AND DATA

The count data for the weed seedbanks, seed rain and carabids comes from 66 spring-sown beet, 59 spring maize, 67 spring oilseed rape and 65 winter oilseed rape fields sampled as part of the farm scale evaluations (FSE) of genetically modified, herbicide-tolerant (GMHT) crops (Champion *et al.* 2003; Bohan *et al.* 2005). The fields were spread across the geographical regions (Fig. 1) and conditions under which these four crops are grown commercially across mainland UK and each field was sampled for one cropping year (Firbank *et al.* 2003) between 2000 and 2004. Fields ranged in size from 2.7 to 70.8 ha, with an average of 11 ha, 79.4% of which were assessed to have hedgerows. Only data from the conventionally managed treatments were used for the analyses presented in this study. Herbicide management was applied by the farmers at levels designed to achieve cost-effective weed control (Champion *et al.* 2003). Applications of herbicides varied between fields from 1 to 6 applications of either dicotyledon (broadleaved) or monocotyledon (grass) specific herbicides or broad-spectrum herbicides against all weeds. Fields also received up to five applications of insecticide (including seed treatments) that could directly affect the carabids.

The pitfall-trapping of soil-surface-active invertebrates employed the method described by Brooks *et al.* (2003). Six-centimetre-diameter pitfall traps were positioned at 2, 8 and 32 m from the crop edge along four transects. Trapping was conducted in the spring (April/May) and summer (June/July), and in the late summer (August) for the spring-sown crops and in the autumn (September/October), spring (April/May) and summer (June/July) for winter oilseed rape. Traps were opened for a 2-week period and then removed. The invertebrate taxa were identified and counted. Data were then pooled, by summation to give in each field a year-total estimate of the *pitfall count* of each carabid species, of total carabids and the carabid functional groups of Granivore and Omnivore (Luff 2002).

Seedbank samples were taken just prior to sowing in the experimental cropping year ( $t$ ) and just prior to sowing in the following cropping year ( $t + 1$ ), which hereafter are termed the 'initial' and 'follow-up' seedbanks, respectively. Seedbank abundance was estimated by taking soil cores (2 L at 15 cm depth) at 2 and 32 m sampling points along four transects running into the crop. Counting of



**Fig. 1.** Distribution of the 66 spring-sown beet, 59 spring maize, 67 spring oilseed rape and 65 winter oilseed rape fields sampled as part of the farm scale evaluations (FSE) of GMHT crops (Champion *et al.* 2003; Bohan *et al.* 2005). Field sites are marked by symbols (●) across four regions of GB (East, West, North and Scotland).

the germinated seeds in the seedbank sample was done at the species level for up to 18 weeks after sample preparation (Squire, Rodger & Wright 2000; Heard *et al.* 2003). The seedbank counts were then pooled, by summation, to give an estimate of the seedbank in each field (total weeds) as well as dicotyledon and monocotyledon counts to account for differential responses to herbicide management.

The return of weed seed to the seedbank (*seed rain*) was measured using four seed rain traps (0.1 m diameter) at two locations along four transects per field (Heard *et al.* 2003). The traps, which were designed to exclude carabid beetles and prevent seed predation within the trap, were emptied every 2 weeks between anthesis and crop harvest (Heard *et al.* 2003). All non-crop seeds were identified to species, and viable seeds were counted. Counts were then pooled, by summation,

to give a year-total estimate of the seed rain in each field (total weeds) as well as dicotyledon and monocotyledon counts.

Alongside the factor for the *crop* grown in each experimental field, the fields were assigned a factor, *year*, denoting the experimental year. Each site was also assigned a level of a factor (*zone*) for one of the six Environmental Zones of the ITE Land Classification of Great Britain (Bohan *et al.* 2005) to describe its fundamental environmental and geographical properties.

#### STATISTICAL ANALYSIS

Carabid species data were treated as follows. Where a particular carabid species had a zero count at 10 or fewer sites, these sites were retained and the carabid variable was transformed as  $\log_{10}(\text{pitfall count} + 0.5)$ . Conversely, where a particular species had zero counts at more than 10 sites, these zero count sites were removed from the analysis and the carabid variable was calculated as  $\log_{10}(\text{pitfall count})$ . Logarithms of the seedbank were calculated as  $\log_{10}(\text{follow up} + 0.5)$  and  $\log_{10}(\text{initial} + 0.5)$  for each of three seedbank change variables. Seed rain was transformed as  $\log_{10}(\text{seed rain} + 0.5)$  for each of three seedbank change variables.

The expectations were tested using multiple linear or simple linear regression in GenStat (2008). Initial analysis of the data showed that there was no consistent pattern of significance for the co-variables of *zone* and *year*, or their interaction terms, and these were therefore excluded from all analyses. For Expectation 1 and 2, multiple linear regressions were performed for the follow-up seedbank against the initial seedbank, seed rain and carabid variables and the crop factor, for each combination of variables in turn. We tested Expectation 1 either by a significant main effect of carabid or significant carabid interaction terms, with negative coefficients indicating seedbank regulation. To test Expectation 2, significant, positive seed rain main effects or seed rain interactions would indicate that the change in seedbanks was at least in part driven by the amount of seed rain. For Expectation 3, simple linear regression of the carabid variables on each of the seed rain variables was carried out to test for positive seed rain or interaction effects. Discrimination between models was by standard partial *F*-tests on one degree of freedom (Perry 1982). The goodness-of-fit of the models was scrutinized by checking the standardized residuals for conformity to normality and evidence of systematic variation. It should be noted that only the main and interaction effects required to test the expectations are presented here. The relationships between the follow-up and initial seedbanks are not given.

#### Results

Full details of the abundance and diversity of carabids, the weed seedbank and seed rain sampled in the FSEs were presented by Heard *et al.* (2003), Brooks *et al.* (2003) and Bohan *et al.* (2005); all primary FSE papers are freely available on The Royal Society Publishing website.

#### CARABID COUNTS IN PITFALL TRAPS

A total of 374638 individuals of 126 species were identified in the pitfall traps. These carabid counts were spread unevenly between the spring-sown beet (42.4%), spring maize (19.8%), spring oilseed rape (25.4%) and winter oilseed rape (12.3%) crops. A total of 194333 of the carabids were *Pterostichus melanarius*, representing some 51.8% of the carabid total,



followed by *Pterostichus niger* (15 353) and *Poecilus cupreus* (9040) among the omnivores and *Harpalus rufipes* (14 853), *Calathus* spp. (8582) and *Amara* spp. (5431) among the granivores. Omnivores in the pitfall traps outnumbered granivores approximately in the ratio of 4:1.

#### THE SEEDBANK

A total of 38 402 seeds were sampled in the initial and 52 662 seeds in the follow-up seedbanks, representing some 201 taxa. The distribution of seeds in the initial seedbank was relatively evenly spread between the spring-sown beet (24.8%), spring maize (28.2%), spring oilseed rape (25.7%) and winter oilseed rape (21.3%) crops, possibly reflecting the mixed arable background of the fields. The ratio of monocotyledon to dicotyledon seed across the seedbank samples was approximately 3:2.

#### SEED SHED INTO SEED RAIN TRAPS

A year total of 5 08 777 seeds were shed into seed rain traps, and 211 taxa identified. This rain was highly uneven across the crops with spring-sown beet (6.8%) and spring maize (4.5%) having relatively low amounts, through spring oilseed rape (33.3%) to winter oilseed rape (55.4%) with the greatest amount. There was also a large difference in the relative amount of monocotyledon to dicotyledon seed shed which was approximately in the ratio of 1:6.

#### EXPECTATION 1. SEEDBANK POPULATION DENSITY IS NEGATIVELY RELATED TO CARABID ABUNDANCE

A significant Crop.Carabid interaction was found for total carabid abundance with the total seedbank (Table 1). The coefficients for spring maize and winter oilseed rape were significant and negative (Fig. 2a), while in spring beet and oilseed rape, the coefficients were not significantly different from 0. A significant negative coefficient was found for the total carabids on monocotyledon weeds across all crops (Fig. 2b). No effects of total carabids were observed for the dicotyledon weeds.

The omnivore functional group was found to have a significant Crop.Carabid interaction with the total seedbank (Table 1). This effect was limited to spring maize, where a significant negative coefficient was found (Table 1). A significant negative coefficient was found for the omnivore group on the monocotyledon seedbank across all crops (Table 1, Fig. 2c). No effect of the omnivore functional group was found on the dicotyledon seedbanks (Table 1). The granivorous carabid functional group was found to regulate the monocotyledon seedbank across crops (Table 1, Fig. 2d). No relationships were found between dicotyledon and total seedbank change and the Granivore functional group (Table 1).

We found a significant Crop.Carabid interaction for the omnivore, *P. melanarius*, and the total and monocotyledon follow-up seedbanks (Table 1), but no effect for the dicotyledon seedbanks (Table 1). In the total seedbank, a significant positive coefficient was found in beet and a negative coefficient

in maize alone (Fig. 2e), but for the monocotyledon seedbank, a negative coefficient was found across all crops (Fig. 2f). For both the total and monocotyledon seedbanks, significant negative Seed rain.Carabid interactions were found (Table 1). These suggest density-dependent responses of *P. melanarius* to seed rain amount, with the regulatory effect of the carabid increasing with increasing amounts of seed rain.

A significant Crop.Carabid interaction was found for the omnivore, *P. cupreus*, on the dicotyledon follow-up seedbanks, with significant negative coefficients being limited to winter oilseed rape. A significant main effect of the granivore, *H. rufipes*, was found on the monocotyledon seedbank, but all estimated coefficients were not significantly different from 0. We found no significant effects for any other carabid species, from either the omnivore or granivore functional groups.

#### EXPECTATION 2. SEEDBANK POPULATION DENSITY IS POSITIVELY RELATED TO SEED RAIN ABUNDANCE

Seedbank change was found to be positively related to the amount of seed rain, explaining a significant amount of variation in the dicotyledon, monocotyledon and total seedbanks (Table 1). No seed rain interactions were found.

#### EXPECTATION 3. CARABID ABUNDANCE IS POSITIVELY RELATED TO SEED RAIN

The total number of carabids was estimated to be related to dicotyledon and total seed rain, but not monocotyledon seed rain abundance (Table 2).

The abundance of the omnivore functional group was estimated to be related to dicotyledon, monocotyledon and total seed rain abundance (Table 2). The granivores were found to be related only to the rain of dicotyledon seeds (Table 2).

Significant relationships were found between the omnivorous carabids, *P. cupreus*, *P. melanarius* and *P. niger*, and all the seed rain groups (Table 2). The abundance of the granivore, *H. rufipes*, was found to be related to dicotyledon and total weed seed rain, but not monocotyledon rain abundance (Table 2). The abundance of granivorous *Amara* spp. was negatively related to all the seed rain groups (Table 2). No relationship was found for the granivorous, *Calathus* spp. Scrutiny of the model fits did not suggest that there was any systematic change in the standardized residual values with seed rain count.

## Discussion

We find strong evidence for carabid seed predation regulating parts of the weed seedbank, and potentially providing an important ecosystem service in farmland. The change in the total weed seedbank, in spring maize and winter oilseed rape, and the monocotyledon seedbank, in all crops tested, was found to be negatively related to the abundance of carabids; responses were consistent with our expectations that carabids intercept and eat seeds that have fallen as seed rain onto the soil surface, and that seed surviving this predation returns to the

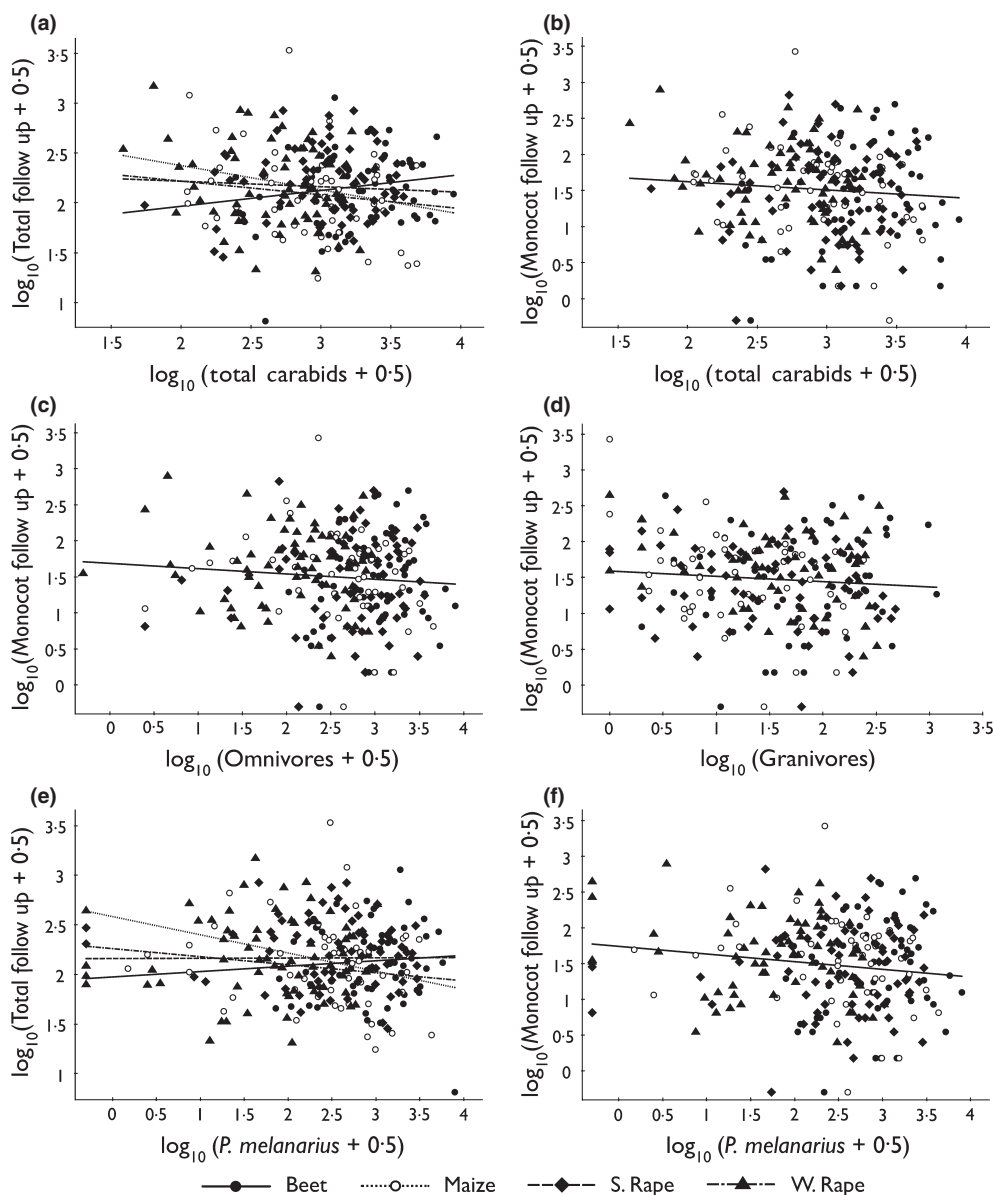
**Table 1.** Statistics of fit for the multiple linear regression relationships between the follow-up seedbank and initial seedbank, seed rain, crop and carabid count for Expectation 1 and 2. Here, the fit for the full model is presented, with the statistics and estimated coefficients for the seed rain and carabid main effects and interaction terms

Response variable (y)	Effects				
	Full model	Seed rain main effect (SE)	Carabid main effect (SE)	Interaction terms (SE)	$r^2_{(C)}$ %
Carabid explanatory variable (x)					$r^2_{(S)}$ %
Follow-up seedbank ( $\log_{10}(\text{follow-up} + 0.5)$ )					
Carabid counts					
Total					
$\log_{10}(\text{Total Carabids} + 0.5)$	$F_{9,225} = 21.37^{***}$ , $r^2 = 43.9\%$	$F_{1,225} = 54.46^{***}$ ; 0.171 (0.027)	ns	Cr:Ca $F_{3,225} = 2.96^*$ ; B 0.153 (0.101), M -0.399 (0.138), SR -0.211 (0.142), WR -0.290 (0.136)	13.04
$\log_{10}(\text{Omnivores} + 0.5)$	$F_{9,225} = 21.23^{***}$ , $r^2 = 43.8\%$	$F_{1,225} = 54.29^{***}$ ; 0.169 (0.027)	ns	Cr:Ca $F_{3,225} = 2.64^*$ ; B 0.090 (0.088), M -0.274 (0.114), SR -0.079 (0.106), WR -0.185 (0.102)	13.04
$\log_{10}(\text{Granivores})$	$F_{2,232} = 88.24^{***}$ , $r^2 = 42.7\%$	$F_{1,231} = 53.31^{***}$ ; 0.163 (0.022)	ns	ns	13.04
$\log_{10}(\text{Poecilus cupreus})$	$F_{2,232} = 88.24^{***}$ , $r^2 = 42.7\%$	$F_{1,231} = 53.31^{***}$ ; 0.163 (0.022)	ns	ns	13.04
$\log_{10}(\text{Pterostichus melanarius} + 0.5)$	$F_{10,224} = 19.86^{***}$ , $r^2 = 44.6\%$	$F_{1,224} = 55.14^{***}$ ; 0.316 (0.075)	ns	Sr:Ca $F_{1,224} = 3.90^*$ ; -0.066 (0.031) Cr:Ca $F_{3,224} = 2.64^*$ ; B 0.228 (0.105), M -0.234 (0.099), SR -0.053 (0.093), WR -0.136 (0.091)	13.04
$\log_{10}(\text{Pterostichus niger} + 0.5)$	$F_{2,232} = 88.24^{***}$ , $r^2 = 42.7\%$	$F_{1,231} = 53.31^{***}$ ; 0.163 (0.022)	ns	ns	13.04
$\log_{10}(\text{Amarra spp.})$	$F_{2,232} = 88.24^{***}$ , $r^2 = 42.7\%$	$F_{1,231} = 53.31^{***}$ ; 0.163 (0.022)	ns	ns	13.04
$\log_{10}(\text{Calathus spp.})$	$F_{2,232} = 88.24^{***}$ , $r^2 = 42.7\%$	$F_{1,231} = 53.31^{***}$ ; 0.163 (0.022)	ns	ns	13.04
$\log_{10}(\text{Harpalus rufipes})$	$F_{2,232} = 88.24^{***}$ , $r^2 = 42.7\%$	$F_{1,231} = 53.31^{***}$ ; 0.163 (0.022)	ns	ns	13.04
Dicot					
$\log_{10}(\text{Total Carabids} + 0.5)$	$F_{2,232} = 66.55^{***}$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56^{***}$ ; 0.190 (0.025)	ns	ns	15.77
$\log_{10}(\text{Omnivores} + 0.5)$	$F_{2,232} = 66.55^{***}$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56^{***}$ ; 0.190 (0.025)	ns	ns	15.77
$\log_{10}(\text{Granivores})$	$F_{2,232} = 66.55^{***}$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56^{***}$ ; 0.190 (0.025)	ns	ns	15.77
$\log_{10}(\text{P. cupreus})$	$F_{9,128} = 8.94^{***}$ , $r^2 = 34.3\%$	$F_{1,128} = 31.92^{***}$ ; 0.157 (0.040)	ns	Cr:Ca $F_{3,128} = 3.43^{**}$ ; B 0.041 (0.073), M -0.002 (0.122), SR 0.117 (0.114), WR -0.209 (0.098)	15.32
$\log_{10}(\text{P. melanarius} + 0.5)$	$F_{2,232} = 66.55^{***}$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56^{***}$ ; 0.190 (0.025)	ns	ns	15.77
$\log_{10}(\text{P. niger} + 0.5)$	$F_{2,232} = 66.55^{***}$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56^{***}$ ; 0.190 (0.025)	ns	ns	15.77

Table 1. Continued

Response variable (y)	Effects						
	Carabid explanatory variable (x)	Full model	Seed rain main effect (SE)	Carabid main effect (SE)	Interaction terms (SE)	$r^2_{(S)}$ %	$r^2_{(C)}$ %
$\log_{10}(\text{Amarra spp.})$	$F_{2,232} = 66.55$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56$ ***; 0.190 (0.025)	ns	ns	ns	15.77	–
	$F_{2,232} = 66.55$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56$ ***; 0.190 (0.025)	ns	ns	ns	15.77	–
	$F_{2,232} = 66.55$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56$ ***; 0.190 (0.025)	ns	ns	ns	15.77	–
	$F_{2,232} = 66.55$ , $r^2 = 35.9\%$	$F_{1,232} = 57.56$ ***; 0.190 (0.025)	ns	ns	ns	15.77	–
Monocot $\log_{10}(\text{Total Carabids} + 0.5)$	$F_{3,231} = 107.36$ ***, $r^2 = 57.7\%$	$F_{1,231} = 22.17$ ***; 0.113 (0.025)	$F_{1,231} = 4.37$ *; –0.123 (0.059)	ns	ns	4.00	0.79
	$F_{3,231} = 107.82$ ***, $r^2 = 57.8\%$	$F_{1,231} = 22.23$ ***; 0.116 (0.025)	$F_{1,231} = 4.96$ *; –0.084 (0.038)	ns	ns	4.00	0.89
	$F_{3,219} = 104.57$ ***, $r^2 = 58.3\%$	$F_{1,219} = 16.80$ ***; 0.101 (0.024)	$F_{1,219} = 4.44$ *; –0.079 (0.038)	ns	ns	3.15	0.83
	$F_{8,226} = 48.62$ ***, $r^2 = 61.9\%$	$F_{1,226} = 24.65$ ***; 0.096 (0.026)	ns	ns	ns	4.00	–
	$F_{10,224} = 41.65$ ***, $r^2 = 60.8\%$	$F_{1,224} = 25.68$ ***; 0.281 (0.072)	$F_{1,224} = 7.70$ **; –0.004 (0.044)	Sr.Ca $F_{1,224} = 6.83$ ***; –0.078 (0.030)	ns	4.00	2.27
	$F_{8,226} = 48.62$ ***, $r^2 = 61.9\%$	$F_{1,226} = 24.65$ ***; 0.096 (0.026)	ns	ns	ns	4.00	–
	$F_{8,226} = 48.62$ ***, $r^2 = 61.9\%$	$F_{1,226} = 24.65$ ***; 0.096 (0.026)	ns	ns	ns	4.00	–
	$F_{8,226} = 48.62$ ***, $r^2 = 61.9\%$	$F_{1,226} = 24.65$ ***; 0.096 (0.026)	ns	ns	ns	4.00	–
	$F_{9,183} = 40.57$ ***, $r^2 = 65.0\%$	$F_{1,183} = 9.25$ ***; 0.069 (0.028)	$F_{1,183} = 6.02$ *; –0.068 (0.038)	ns	ns	1.69	1.10

For the main effect of carabids, an  $F$ -value is presented with an associated probability value  $P$  (denoted ns  $P > 0.05$ , \*  $P \leq 0.05$ , \*\*  $P \leq 0.01$  and \*\*\*  $P \leq 0.001$ ); alongside the estimated regression coefficient. For the Interaction terms, an  $F$ -value is presented with an associated probability value alongside regression coefficients for spring beet (B) and the differences in value for maize (M), rape (SR) and winter oilseed rape (WR), if appropriate; we find significant Seed rain, Carabid (Sr.Ca) and Crop, Carabid (Cr.Ca) interactions. The percentage of total variation explained by the seed rain main effect ( $r^2_{(S)}$ ) and the carabid main effect and Interactions terms ( $r^2_{(C)}$ ) is also presented.



**Fig. 2.** Multiple linear regression model fits to test Expectation 1. The raw  $\log_{10}(\text{follow-up} + 0.5)$  seedbank is plotted against  $\log_{10}(\text{pitfall count} + 0.5)$  carabids in spring-sown beet (●), spring maize (○), spring oilseed rape (◆) and winter oilseed rape (△) for: (a) the total follow-up seedbank against total carabids; (b) the monocotyledon follow-up seedbank against total carabids; (c) the monocotyledon follow-up against omnivorous carabids; (d) the monocotyledon seedbank against granivorous carabids; (e) total follow-up seedbank and *Pterostichus melanarius*; and (f) monocotyledon follow-up seedbank and *P. melanarius*. The best models, shown for each relationship, were either four individual lines for spring-sown beet (solid line), spring maize (long dashed line), spring oilseed rape (medium dashed line) and winter oilseed rape (short dashed line) or a single line through all four crops (solid line). Sample data points removed during model checking and scrutiny are included in the figures.

seedbank and mediates seedbank change. As expected, we found both granivores and omnivores had a role in regulating the seedbank, although species within these two functional groups, most notably the omnivore *P. niger* and the granivorous *Amara* spp., did not have significant effect. Only the omnivore *P. melanarius* convincingly caused seedbank regulation. This signal of seedbank regulation was detectable against this noise in 257 fields, spread across much of the UK, suggesting that our results are valid for a range of agricultural situations. Seed predation only explained a small amount of seedbank variation (0.8–5%), but this is of comparable magnitude to the

contribution of the seed rain; the main source of seed entering the seedbank. Compounded over cropping years (see Bohan *et al.* 2011 for long-term effects on the seedbank), the effect would be much greater and we believe that the seed regulation effects of carabids could be employed alongside or even in place of herbicides in optimised integrated pest-management approaches. In other cropping systems where perturbations due to management are different, we would expect a greater apparent influence of seed predation on seedbank change.

Differences in crop traits and management mean that dicotyledon crops, such as spring-sown beet, spring oilseed rape and



**Table 2.** Statistics of fit for the simple linear regression relationships between carabid count and seed rain and crop for Expectation 3. Here, the fit for the full model is presented with the statistics and estimated coefficients for the seed rain main effect and interaction terms

Response variable (y)		Effect of seed rain	
Seed rain explanatory variable (x)	Full model	Main effect (SE)	Interaction terms (SE)
Carabid counts			
$\log_{10}(\text{seed rain} + 0.5)$			
$\log_{10}(\text{Total Carabids} + 0.5)$			
Total	$F_{4,246} = 16.00^{***}, r^2 = 19.4\%$	$F_{1,246} = 0.60$ ns; 0.068 (0.034)	ns
Dicot	$F_{4,248} = 15.55^{***}, r^2 = 18.8\%$	$F_{1,248} = 0.17$ ns; 0.066 (0.033)	ns
Monocot	$F_{3,251} = 19.93^{***}, r^2 = 18.3\%$	ns	ns
$\log_{10}(\text{Omnivores} + 0.5)$			
Total	$F_{4,239} = 23.33^{***}, r^2 = 26.9\%$	$F_{1,239} = 1.92$ ns; 0.117 (0.046)	ns
Dicot	$F_{4,243} = 23.63^{***}, r^2 = 26.8\%$	$F_{1,243} = 2.09$ ns; 0.091 (0.045)	ns
Monocot	$F_{4,237} = 23.07^{***}, r^2 = 26.8\%$	$F_{1,237} = 0.02$ ns; 0.076 (0.034)	ns
$\log_{10}(\text{Granivores})$			
Total	$F_{3,240} = 5.46^{***}, r^2 = 5.2\%$	ns	ns
Dicot	$F_{4,236} = 4.60^{***}, r^2 = 5.7\%$	$F_{1,236} = 4.25^*$ ; 0.093 (0.054)	ns
Monocot	$F_{3,237} = 5.11^{**}, r^2 = 4.9\%$	ns	ns
$\log_{10}(\text{Poecilus cupreus})$			
Total	$F_{4,140} = 6.97^{***}, r^2 = 14.2\%$	$F_{1,140} = 6.97^{***}$ ; -0.034 (0.086)	ns
Dicot	$F_{4,140} = 6.96^{***}, r^2 = 14.2\%$	$F_{1,140} = 6.78^{**}$ ; -0.028 (0.084)	ns
Monocot	$F_{4,140} = 6.97^{***}, r^2 = 14.2\%$	$F_{1,140} = 5.24^*$ ; 0.024 (0.059)	ns
$\log_{10}(\text{P. melanarius} + 0.5)$			
Total	$F_{4,236} = 24.88^{***}, r^2 = 28.5\%$	$F_{1,236} = 9.95^{***}$ ; 0.072 (0.050)	ns
Dicot	$F_{4,237} = 26.21^{***}, r^2 = 29.5\%$	$F_{1,237} = 6.55^{**}$ ; 0.081 (0.047)	ns
Monocot	$F_{4,234} = 26.00^{***}, r^2 = 29.6\%$	$F_{1,234} = 3.83^*$ ; 0.039 (0.037)	ns
$\log_{10}(\text{Pterostichus niger} + 0.5)$			
Total	$F_{4,247} = 27.02^{***}, r^2 = 29.3\%$	$F_{1,247} = 20.48^{***}$ ; 0.339 (0.070)	ns
Dicot	$F_{4,247} = 25.08^{***}, r^2 = 27.7\%$	$F_{1,247} = 16.82^{***}$ ; 0.287 (0.068)	ns
Monocot	$F_{7,245} = 19.55^{***}, r^2 = 34.0\%$	$F_{1,245} = 32.79^{***}$	Cr.Sr $F_{3,245} = 3.82^*$ ; B 0.410 (0.103), M -0.143 (0.148), SR 0.069 (0.141), WR -0.334 (0.134)
$\log_{10}(\text{Amara spp.})$			
Total	$F_{4,190} = 43.74^{***}, r^2 = 47.4\%$	$F_{1,190} = 26.99^{***}$ ; -0.028 (0.048)	ns
Dicot	$F_{4,186} = 43.89^{***}, r^2 = 47.4\%$	$F_{1,186} = 23.03^{***}$ ; -0.038 (0.047)	ns
Monocot	$F_{4,186} = 43.87^{***}, r^2 = 47.4\%$	$F_{1,186} = 12.43^{***}$ ; -0.028 (0.036)	ns
$\log_{10}(\text{Calathus spp.})$			
Total	$F_{3,140} = 6.07^{***}, r^2 = 9.6\%$	ns	ns
Dicot	$F_{3,140} = 6.07^{***}, r^2 = 9.6\%$	ns	ns
Monocot	$F_{3,137} = 6.58^{***}, r^2 = 10.9\%$	ns	ns
$\log_{10}(\text{Harpalus rufipes})$			
Total	$F_{4,205} = 15.53^{***}, r^2 = 21.8\%$	$F_{1,205} = 2.38$ ns; 0.204 (0.064)	ns
Dicot	$F_{4,205} = 15.67^{***}, r^2 = 21.9\%$	$F_{1,205} = 3.37$ ns; 0.205 (0.063)	ns
Monocot	$F_{3,208} = 16.52^{***}, r^2 = 18.1\%$	ns	ns

For the main effect of seed rain, an F-value is presented with an associated probability value  $P$  (denoted ns  $P > 0.05$ , \*  $P \leq 0.05$ , \*\*  $P \leq 0.01$  and \*\*\*  $P \leq 0.001$ ); alongside the estimated regression coefficient. For Crop.Seed rain interaction terms (Cr.Sr), an F-value is presented with an associated probability value alongside regression coefficients for spring beet (B), and the differences in value for maize (M), rape (SR) and winter oilseed rape (WR).

winter oilseed rape, tend to select for dicotyledon weeds and seed production, while monocotyledon crops like spring maize select for monocotyledon weeds (Heard *et al.* 2003; Bohan *et al.* 2005). This effect, coupled with high weed seed productivity in spring and winter oilseed rape, explains why the seed rain count was heavily dominated by dicotyledons. We estimated that dicotyledon seedbank change was positively related to the dicotyledon seed rain, suggesting that as the amount of dicotyledon seed rain increased the dicotyledon weed seedbank

grew. We also found that there were positive relationships between the counts of carabids and dicotyledon seed rain, suggesting that omnivorous and granivorous species respond to the dicotyledon weed seed. However, barring a result for *P. cupreus* in winter oilseed rape, no effect of carabids was found on dicotyledon seedbank change. There was much less monocotyledon seed rain present at the soil surface. Yet, we found carabids had a regulatory effect on the monocotyledon seedbank. Indeed, *P. melanarius* showed density-dependent

responses with monocotyledon seed rain. Seemingly, with increasing monocotyledon seed rain, the coefficient used to test for regulation became increasingly negative, indicating an increasing rate of regulation.

Tests of Expectation 3 suggest that a variety of carabid species intercepted dicotyledon and monocotyledon weed seed rain. It would appear, therefore, that the monocotyledons might have been eaten preferentially, despite the fact that monocotyledons were less abundant than dicotyledons (ratio of 1:6 in the seed rain). How such a difference in feeding rate could come about is not clear. It might be that monocotyledon seeds are simply easier to handle and devour. Alternatively, it might be that differences in the nutritional quality of the monocotyledon and dicotyledon seed (Wilson, Arroyo & Clark 1996) leads to seed-feeding preferences that increase individual predator fitness (Mayntz *et al.* 2005). Scrutiny of the model fits and standardized residuals, however, would not suggest that the apparent lack of effect of the carabids on the dicotyledon seedbank was because of the increasing abundance of dicotyledon seed rain 'swamping' the regulatory abilities of the carabids.

*Poecilus cupreus* and *Amara* spp. had unexpected, negative relationships with the seed rain. We believe that this may be because of interactions with other carabid species that both respond to the seed rain variates and are capable of intra-guild predation, such as *P. melanarius*. Predation interactions, removing individual *P. cupreus* and *Amara* spp., or predator avoidance behaviours by these seed predators (e.g. Armsworth *et al.* 2005) could lead to negative relationships. A recent study of carabid spatial and temporal patterns has shown that different carabid species have positive and negative co-occurrence patterns consistent with predation interactions (Bell *et al.* 2010).

Regulation of the total weed seedbank appears to be limited to the spring maize and winter oilseed rape. We do not believe that this result can be explained by variation in carabid activity brought about by systematic differences in cropping density and microclimate (Baker & Dunning 1975; Honek 1988) between the crops, because this would not account for why carabids are able to elicit control of monocotyledon weeds in all crops. An alternative explanation for crop-specific effects might be difference in the species compositions of crops. Smith *et al.* (2008) found that each of these crops had distinct weed and invertebrate species compositions. We also know that carabid seed predators show preferences for particular seed species when presented with a choice under laboratory conditions (Tooley & Froud-Williams 1999; Honek, Martinkova & Jarosik 2003; Honek, Saska & Martinkova 2006; White *et al.* 2007; Saska *et al.* 2008). The patterns of relationship we have observed here for broad weed classes will probably be determined by particular carabid species preying upon specific weed seeds within each class. Predation of monocotyledon weeds might also explain the effects on the total weed seedbank. Studies of these specific relationships, and in particular for economically important monocotyledon weed species, could be carried out with this data set. However, such analyses would be greatly strengthened by screening the guts of carabids for the DNA of

particular seeds using species-specific PCR primers, such as have been developed for invertebrate prey (Symondson, Sunderland & Greenstone 2002; King *et al.* 2010). Molecular analyses would directly test for predation which we only infer from tests of expectations for carabid seed predation interactions. This information would also allow us to evaluate the relative importance of the wide range of vertebrate and invertebrate species known to feed on weed seeds (Westerman *et al.* 2003, 2008; Holmes & Froud-Williams 2005; Franke *et al.* 2009), as well as intra-guild predation interactions and wider interactions with alternative prey.

Previous studies of carabid seed predation have typically considered predation of weed seed at the soil surface (Honek, Martinkova & Jarosik 2003; Honek, Martinkova & Saska 2005; Mauchline *et al.* 2005; Menalled *et al.* 2007; Saska *et al.* 2008). Relationships with seeds have been used to make statements about the value of carabid predation. This paper presents the first study that we are aware of that considers the effect of carabid predation on the soil seedbank, and consequently weed seed regulation, and it suggests that positive relationships between carabid and seed rain abundance are not evidence enough to indicate regulatory changes in the weeds. Particularly for the dicotyledon weeds, positive relationships between carabids and the seed rain do not translate into seedbank regulation.

Research on *P. melanarius* foraging for invertebrates has shown strong spatial and temporal scales of predation interaction (Bohan *et al.* 2000). Bohan *et al.* (2000) found spatial patterning on the scale of 9–10 m between *P. melanarius* and two species of slug prey. These patterns also changed from positive association, where the *P. melanarius* and slug distributions were similar, to negative, where if there were carabids there were no slugs, on a time-scale of about 1 month. A similar spatio-temporal scaling argument has been applied to carabid–seed interactions and can be used to explain why some studies have shown a relationship (Honek, Martinkova & Jarosik 2003; Honek, Martinkova & Saska 2005; Menalled *et al.* 2007), because the study was appropriate to this implicit scaling, while other data sets have not (Mauchline *et al.* 2005; Saska *et al.* 2008). Our study takes a more pragmatic approach. For a predation interaction to be a valuable ecosystem service, it should manifest at spatial and temporal scales that are appropriate to the management of the system being studied. Here, we show that seed-predation effects are apparent in the year total data from fields spread across the national scale; scales that are appropriate for policy for farmers to incorporate carabid seed predation within their management approaches.

## Conclusion

The needs of farming are undergoing revision. Current policy is directed toward conserving farmland biodiversity. The need to assure food security will place greater emphasis on increasing crop productivity and yield while reducing chemical inputs (Royal Society 2009). There will be real pressure

to better balance the often competing needs of biodiversity and crop productivity by maximising both and, where possible, utilizing biodiversity to support productivity (Foresight 2011).

We find that carabids can elicit regulatory effects on monocotyledon and total weed seedbanks sampled over a number of years and from fields undergoing management by farmers. Monocotyledon weeds have marked impact on arable system productivity, and there is great concern about the development and spread of herbicide-resistant varieties of pest grasses such as black-grass *Alopecurus myosuroides*. Non-herbicide control of monocotyledon weeds would be an important ecosystem service with the potential for considerable economic and societal impact. Moreover, much work on maintaining and managing carabids in farmland systems has already been carried out, in support of carabids as natural enemies of invertebrate pests (Kromp 1999). Policy tools have been developed for environmental stewardship that support the installation of beetle bank refuges for beetles and other approaches to maintain beetle numbers (Thomas, Goulson & Holland 2000). This means that carabids, as seed predators, already fit within a working framework in arable agriculture in Europe, and might be used to deliver an integrated pest management solution.

The priority for the future should be to establish the limits of seedbank regulation by carabids. Analysis of this, and other, data sets should indicate specific interactions between carabid and weed species that can be field-tested using molecular approaches. Tests should be conducted to examine whether carabid-driven changes in the soil seedbank lead to observable changes in the amount of standing weed flora. Herbicide manipulation experiments might then be used to determine whether carabids can be used alongside or even in place of herbicides in real-world situations.

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