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Arthropod abundance in agriculture

Quantifying abundance and activity of carabid beetles (Carabidae) in arable fields

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Abstract

Intensification of agriculture has been described as one of the main drivers of biodiversity loss in insects. To overcome this problem, an extensification of agriculture is desired, preferably without losses in production. One strategy is to rely more on natural processes rather than external outputs. Carabid beetles, for example, are generalist predators of crop harming organisms and weed seeds, and can therefore be a biological alternative to the use of pesticides, which has a tremendous contribution to the yearly losses seen in insect biomass. But little is known about how such an extensive system compares to the current intensively farmed systems, especially as we lack knowledge on the abundance of insects along farming intensity gradients. In this study, I explored the soil invertebrate communities living in arable fields in Eastern Groningen, with the main focus on carabid beetles. Sampling was done using pitfall traps. Pitfall traps are however not a perfect method to study invertebrate abundance as the number of caught individuals is a function of both abundance and activity. Therefore I also conducted an enclosure and a mark-recapture experiment, to investigate true densities and movement behaviour of the carabid beetle *Pterostichus melanarius* in Sugar Beet and Winter Wheat fields. Invertebrate communities of agricultural landscapes were dominated by the family Carabidae. Carabidae abundance differed between farms, crops and also varied over time. The results of the enclosure and mark-recapture experiments suggest that pitfall trapping is a valid method to estimate Carabidae abundance, and thus that differences found between farms and habitats presumably are genuine. We do not fully understand the driving factors behind Carabidae abundance as of yet, but the results from this study suggest that farming intensity and (semi-)natural habitat in the wider landscape might play an important role. Suggestions for future research are given.

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Introduction

The Green Revolution of agriculture is the period after the Second World War when crop yields increased by multiple magnitudes thanks to the development and mass production of pesticides and artificial fertilizers (Sanchez-Bayo, 2011). This, combined with improvements in irrigation, mechanization and the use of high-yielding crop varieties, greatly improved food production all around the world (Sanchez-Bayo, 2011). However, negative effects of agricultural intensification on the environment and biodiversity have not remained unnoticed (e.g. Butler, 1966; Igbedioh, 1991; McLaughlin and Mineau, 1995). We currently face a biodiversity crisis, with population declines in many unrelated taxa (e.g. Stuart et al., 2004; Ceballos and Ehrlich, 2002; Jackson et al., 2001; Gaston et al., 2003). Intensification of agriculture has been described as one of the main drivers of biodiversity losses (Sanchez-Bayo, 2019). Insects, which form around two thirds of all terrestrial species, seem to be highly affected, with larger population declines over time than birds or plants (Thomas et al., 2004). Since many animals directly or indirectly depend on insects, the quick loss of insects worldwide could have major cascading effects, ultimately even impacting humanity (Sanchez-Bayo, 2019).

Ecosystems can provide different services (Daily, 2003). Examples of these so-called ecosystem services for agriculture are crop pollination, improvement of soil quality and natural pest control (Zhang et al., 2007). Loss of biodiversity due to the intensification of agriculture results in the loss of ecosystem services, which implies a need for a further intensification of agriculture. For example, synthetic insecticides are a likely driver of insect biomass loss (Hallmann et al., 2017). Carabid beetles are predators of crop harming organisms such as slugs, aphids, herbivorous beetles and caterpillars, and the loss of generalist carabid beetles can significantly reduce natural pest control in agricultural fields (Symondson et al, 2002). So from a farmer's point of view, it would be beneficial to have a lot of these carabid beetles on their fields as this could potentially reduce the costs spent on pesticides. However, this would apply less intensive agriculture, in particular the reduction of the use of insecticides. The strategy to rely on natural processes rather than external outputs is called ecological intensification (Kleijn et al., 2019), but little is known about how such a system compares to the current intensively farmed systems, especially as we lack knowledge on the abundance of insects along farming intensity gradients (Kleijn et al., 2001).

In 2018 the University of Groningen started a monitoring program of insects in Eastern Groningen, a landscape dominated by intensive arable farming. Insects are sampled on farms that differ in management regimes, to ultimately work out what factors drive insect abundance in arable farming landscapes. One of the methods used to sample insects are pitfall traps, which capture surface dwelling insects, mainly carabid beetles. However, the number of beetles captured in pitfall traps is a function of both beetle abundance and locomotor activity (Thomas et al., 1998). Thus, differences in beetle abundance could be the result of a genuine difference in abundance, or caused by the beetles being more mobile in a certain crop type or area. A meta-analysis of studies on carabid dispersal revealed that the movement rate of carabid beetles was three times higher in farmland compared to forested land (Allema, 2014). Habitat type was the variable that explained most of the variation in movement in that study. Thus, it is likely that also differences in mobility and number of beetles captured could occur between different crop types. This complicates the interpretation of pitfall catches, and thus the research on the factors driving insect abundance in arable farming landscapes.

The aim of my study was to obtain insights in densities and movement behaviour of carabid beetles in different crop types at different farms in Eastern Groningen. More specifically, I wanted to quantify to what extend differences in pitfall captures could be explained by differences in abundance or beetle activity. To study this, I performed two different field experiments in different crops at different farms. First of all, I performed an enclosure experiment where all beetles within a fenced area were trapped to quantify true carabid beetle densities. Secondly, I performed a mark-recapture experiment to quantify movement rates.

The main subject of my study was the generalist carabid beetle species *Pterostichus melanarius*. Its diet consists of at least fourteen pest species, including Coleoptera, Diptera, Homoptera, Mullusca and Lepidoptera (Allema, 2014). *P. melanarius* is commonly found in Dutch arable farmland (Turin and Van Alebeek, 2007) including the study areas (pers. comm.). This species is specifically suited for this study as most adults are flightless due to their reduced wings or wing muscles (Aukema et al., 1996) – an important condition for the enclosure study, and it is large enough to be marked for the mark-recapture study.

In previous years, more *P. melanarius* beetles were captured in Sugar Beets compared to Winter Wheat, the two main crops in the study area (together with Potatoes which were not included in the current study). I hypothesize that this difference is mainly caused by the differences in activity as a result of differences in vegetation structure. Sugar Beets have a very open vegetation structure with a lot of bare ground, which makes it easy for the ground beetles to move around. Winter Wheat has a dense vegetation structure, which might hamper movement of the beetles. Thus, I expect similar densities in Sugar Beets and Winter Wheat in the enclosure experiment, but higher movement rates in Sugar Beets compared to Winter Wheat in the mark-recapture experiment. Furthermore, as crops are sown in straight lines, arable field are linear habitats, and I hypothesized whether this could influence beetle movement. Hence I also checked for directional preferences in the movements.

Results of this study will help to better understand the dynamics of carabid beetles in agricultural fields and it can provide methodological suggestions for future research on agricultural arthropods.

Materials and methods

This study consists of three different parts. (1) monitoring ground-dwelling arthropods at farms with different management regimes, (2) an enclosure experiment to quantify true densities, and (3) a mark-recapture experiment to quantify movement rates. These studies were, for practical reasons, partly conducted at different farms.

Monitoring invertebrates

For the study on the abundance of invertebrates in arable fields, four farms were selected in our main study area in Eastern Groningen, Netherlands. These farms have different management regimes resulting in a gradient of agricultural intensity. Farms differed in amounts of pesticide used, soil tillage management, number of crops grown and the presence of semi-natural habitats on and around the farm. Farm G (Geuko Ten Have) is farmed in a regular way, with standard fertilizer (slurry as well as synthetic fertilizer) and pesticide inputs. Soils are ploughed in the autumn. Crops grown in 2019 were Winter Wheat and Sugar

Beets. On the farm set-aside field edges, an agri-environment scheme, are present, but otherwise the farm is located in a landscape with almost no semi-natural habitat present. Farm G is the most intensively farmed area within my study. Farm MB (Midwolder Bouwten) is comparable to Farm G, with the exception that only farmyard manure was used instead of slurry. Furthermore, the area is located next to a nature reserve. On the farm, also set-aside field strips are present. Crops grown in 2019 were Summer Wheat and Oat. Thus, farming intensity is slightly lower compared to farm G. Farmer Peter Harry Mulder (farm PH) adopts a nature-inclusive way of farming. This implies less use of herbicides and fungicides, and no use of insecticides. In addition, the soil is fertilized using organic matter and farmyard manure, which reduces the use of synthetic fertilizer. Soil is not tilted (no-tillage farming). In addition, about 7% of the farm contains of non-farmed semi-natural habitats including set-aside field strips, ecologically managed road verges and patches of shrubs. In 2019, crops grown were Winter Wheat, Sugar Beets and Potatoes. Farming intensity is lower compared to farms G and MB. Area WE (Westeresch) is the least intensively farmed area of my study. Farming practices are organic, thus no pesticides or synthetic fertilizers are used. Farmyard manure and compost are used to fertilize the soil. In the area a larger number of crops is grown, including Fodder Beets, summer and winter cereals, Faba Beans and Buckwheat. Parcels are notably small, with a dense network of set-aside field edges. Moreover, the area is located within a nature reserve. In each area, I aimed sampling invertebrates in a cereal (preferably Winter Wheat), Sugar or Fodder Beets, Potatoes, set-aside field edges (flower strips), and a road verge. An overview of the different areas and the crops/habitats sampled within each area is provided in table 1.

To monitor soil-dwelling invertebrates, pitfall traps (diameter 85 mm, height 120 mm) were placed in each of the crops and habitats. Five pitfall traps were placed in a transect with ten meter between each pitfall trap. Pitfall traps were carefully leveled with the surrounding soil and filled up to around a third with an odorless soap solution. The pitfall traps remained in place for one week before collection. During the collection event, the content of the pitfall traps was poured over a fine sieve and all invertebrates were collected and stored in 95% bio-ethanol. Three data collection events took place between June and August 2019, although not all sampling events were successful. An overview of when which area was sampled is presented in table 2. Samples were analyzed in the lab and the organisms of interest were classified to the family or species level were possible with the help of field guides and online information. All organisms were at least classified up until the class level. All carabid beetles were identified to the species level based on Muilwijk et al. (2015). All organisms were counted and the average length of the different species was measured for the calculation of biomass.

Table 1: . An overview of the different study areas and the crops/habitats sampled within each area. ✓ = Crop was sampled at corresponding area.

Area	Crop							
	Sugar Beet	Fodder Beet	Winter Wheat	Summer Wheat	Oat	Potato	Flower strip	Road verge
G	✓		✓				✓	✓
PH	✓		✓			✓	✓	✓
MB				✓	✓		✓	
WE		✓	✓			✓	✓	✓

Table 2: An overview of the collection dates per Area. ✓ = Area was sampled on that date.

Area	Collection date		
	20-06-2019	11-07-2019	26-07-2019
G	✓	✓	✓
PH	✓	✓	✓
MB	✓	✓	✓
WE		✓	✓

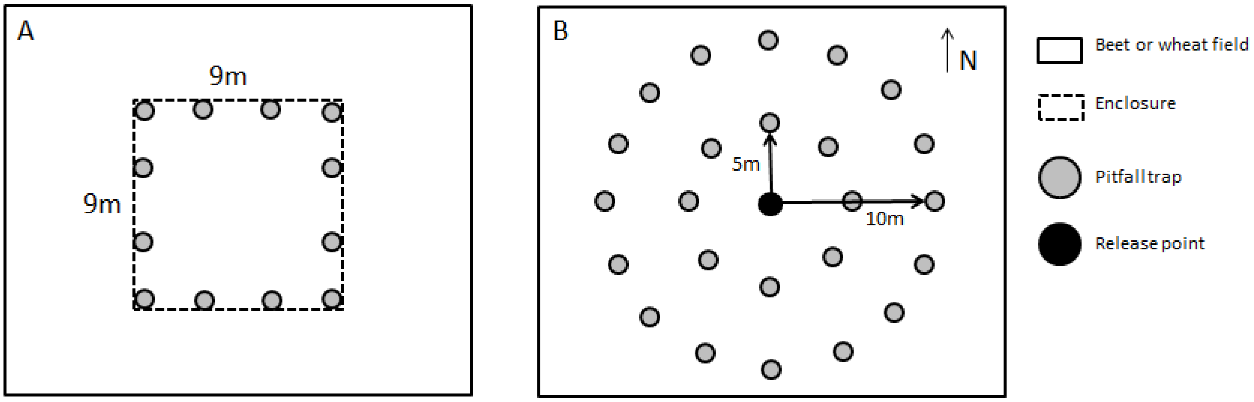
Enclosure and mark-recapture experiments

Experiments were performed at farms PH , G and E. Farm E is a regular farm with an intensive management (comparable to area G). These experiments were performed in Sugar Beet and Winter Wheat fields in three different weeks: week 26 (PH), week 28 (G) and week 30(E).

A 9 x 9m enclosure (81 m^2) was created using four 25 cm high and nine meter long plastic lawn edges (Mortene). Sheets were held upright by digging them into the soil and supporting them with sticks along the sides. Sheets were attached to one another by duct tape. Twelve pitfall traps were spread out evenly along the inside border of the enclosure (figure 1A). Pitfall traps were not filled with a soap solution in order to capture the beetles alive for the mark-recapture experiment. To prevent beetles from drying out, rocks and a bit of soil was added to provide shelter. Pitfall trap contents were collected and counted daily for the duration of four to seven days depending on observed catch trends and permission of the collaborating farmers. It was thought that this time period would be sufficient to catch most carabids within the enclosures, based on the estimated daily dispersal distances recorded for some of the expected species (Zhang et al., 1997; Allema, 2014).

Movement behaviour of *P. melanarius* was studied in a mark-recapture experiment, which was performed next to the enclosure experiment. One day before the start of the experiment 5 pitfall traps were placed in the field to obtain living beetles for the start of the experiment the next day. During subsequent days, living beetles were collected from the enclosure experiment, as well as all unmarked beetles in the mark-recapture experiment itself. *P. melanarius* beetles were marked with a dot of nail polish (HEMA, long lasting) on their backs. Beetles got marked with a different colour of nail polish every day of the experiment to differentiate between the time of release for recaptured beetles. After marking, the beetles were released in the center of a circular grid containing 24 pitfalls with 8 pitfalls evenly spread out over a circle with a radius of five meters and 16 pitfalls spread out over a circle with a radius of ten meters (figure 1B). A pile of grass placed in the center of the circular grid functioned as a release arena for the beetles where they could find shelter during the day (*P.melanarius* is nocturnal). Every day, the pitfall traps were checked for recaptures, and these were removed from the experiment. The mark-recapture experiments ran for four days.

Figure 1: Schematic overview of the field experiments studying: A) density and B) activity of carabid beetles.



Statistical analysis

Monitoring A linear model was used to examine the number of beetles caught in the pitfall traps. Explanatory variables of the models were: area, crop/habitat and date, with transect ID as a random term. Models with all the different combinations of explanatory values (fourty possible combinations, table 3) were ranked and model selection was based on the Akaike Information Criterion (AICc, Akaike, 1998). Models were deemed significantly better when $\Delta AIC_C < -2$. For the most parsimonious model with the lowest AICc a multiple comparison Tukey test was performed to test for significant differences between levels within factors. All data analyses were performed using R version 3.5.1 (R Core Team, 2018). Linear mixed models were ran using the package lme4 (Bates et al., 2014) and post-hoc comparisons were made using the emmeans function from the emmeans package (Lenth, 2019). Data were plotted using the ggplot2 package (Wickham, 2016).

Experiments To test for directional preference in beetles from the mark-recapture experiment, the function rayleigh.test of the package circular (Agostinelli and Lund, 2016) was used. Since the distribution of beetles in beet fields was expected to be a Von Mises distribution with the bimodal-modes mirrored, data was sometimes transformed *f*-fold before applying a Rayleigh test as suggested by Landler et al. (2018). The daily displacement of an individual beetle was calculated by dividing the distance between the release point and the pitfall trap in which it got captured by the amount of days between release and recapture.

Table 3: Overview of the mixed effect models compared in data analysis. y = abundance of group of interest. Fixed effects: Area, Crop and Date. Random effect: Transect ID.

Model number	Mixed Model
1	y ~ Area + (1|Transect ID)
2	y ~ Crop + (1|Transect ID)
3	y ~ Date + (1|Transect ID)
4	y ~ Area + Crop + (1|Transect ID)
5	y ~ Area : Crop + (1|Transect ID)
6	y ~ Area + Area : Crop + (1|Transect ID)
7	y ~ Area * Crop + (1|Transect ID)
8	y ~ Area : Crop + Crop + (1|Transect ID)
9	y ~ Area + Date + (1|Transect ID)
10	y ~ Area : Date + (1|Transect ID)
11	y ~ Area + Area : Date + (1|Transect ID)
12	y ~ Area * Date + (1|Transect ID)
13	y ~ Area : Date + Date + (1|Transect ID)
14	y ~ Crop + Date + (1|Transect ID)
15	y ~ Crop : Date + (1|Transect ID)
16	y ~ Crop + Crop : Date + (1|Transect ID)
17	y ~ Crop * Date + (1|Transect ID)
18	y ~ Crop : Date + Date + (1|Transect ID)
19	y ~ Area + Crop + Date + (1|Transect ID)
20	y ~ Area + Area : Crop + Date + (1|Transect ID)
21	y ~ Area : Crop + Date + (1|Transect ID)
22	y ~ Area + Crop + Crop : Date + (1|Transect ID)
23	y ~ Area : Crop + Crop : Date + (1|Transect ID)
24	y ~ Area : Date : Crop + (1|Transect ID)
25	y ~ Area * Date + Crop + (1|Transect ID)
26	y ~ Area + Crop * Date + (1|Transect ID)
27	y ~ Area * Date * Crop + (1|Transect ID)
28	y ~ Area + Area : Crop + Crop + Date + (1|Transect ID)
29	y ~ Area + Area : Crop + Crop + Crop : Date + (1|Transect ID)
30	y ~ Area * Crop + Crop * Date + (1|Transect ID)
31	y ~ Area + Area : Crop + Crop : Date + (1|Transect ID)
32	y ~ Area + Area : Crop + Crop : Date + Date + (1|Transect ID)
33	y ~ Area + Area : Date + Crop + (1|Transect ID)
34	y ~ Area * Date + Crop + (1|Transect ID)
35	y ~ Area + Crop : Date + (1|Transect ID)
36	y ~ Area : Crop + Crop + Crop : Area + (1|Transect ID)
37	y ~ Area : Crop + Crop * Date + (1|Transect ID)
38	y ~ Area : Date + Crop : Date + (1|Transect ID)
39	y ~ Area : Date + Crop + Crop : Date + (1|Transect ID)
40	y ~ Area : Date + Crop * Date + (1|Transect ID)

Results

General conditions

The summer of 2019 was exceptionally sunny, warm and dry. In the Netherlands, since 1901, only three summers have had a higher average temperature recorded than the 18.4° C measured in 2019 (KNMI, 2019). During the study period, there was one official heatwave recorded (week 30) and the country saw its highest temperature since recorded history (40.7° C) (KNMI, 2019).

Monitoring invertebrates

236 pitfall samples were analyzed containing a total of 46 770 organisms. Eight different invertebrate classes were identified (figure 2). Insecta was by far the most prevalent class making up ~81% of the total composition. Together with the second and third most abundant classes Arachnida and Collembola (~14 and 5%, respectively), Insecta comprised more than 99% of the total catch count. The remaining <1% was composed of the occasionally encountered Chilopoda (centipedes), Malacostraca (woodlouse), Clitellata (earthworms), Gastropoda (snails and slugs) and the vertebrate class Amfibia (frogs).

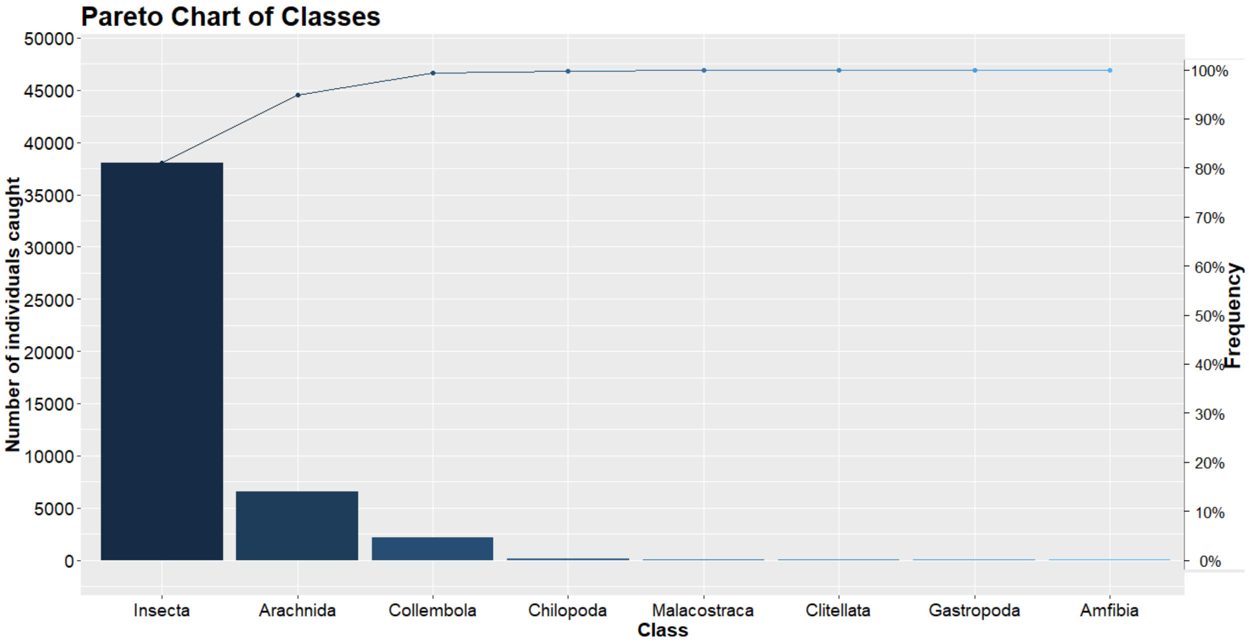


Figure 2: Pareto chart showing the composition of organisms caught in 236 pitfall traps spread out over 4 different agricultural areas during June and July 2019, grouped by class.

Insecta, which made up most of the caught organisms, mostly comprised of Coleoptera (82%) among eight other orders (Figure 3). The second largest order was Diptera at 12.8%. The remaining 5% contained Hymenoptera (2.6%), Hemiptera (1. 8%), Orthoptera (0.5%) and Lepidoptera (mostly caterpillars, 0.3%). Among the 37 896 insects caught, two Odonata and one Dermaptera was found (both <0.01%).

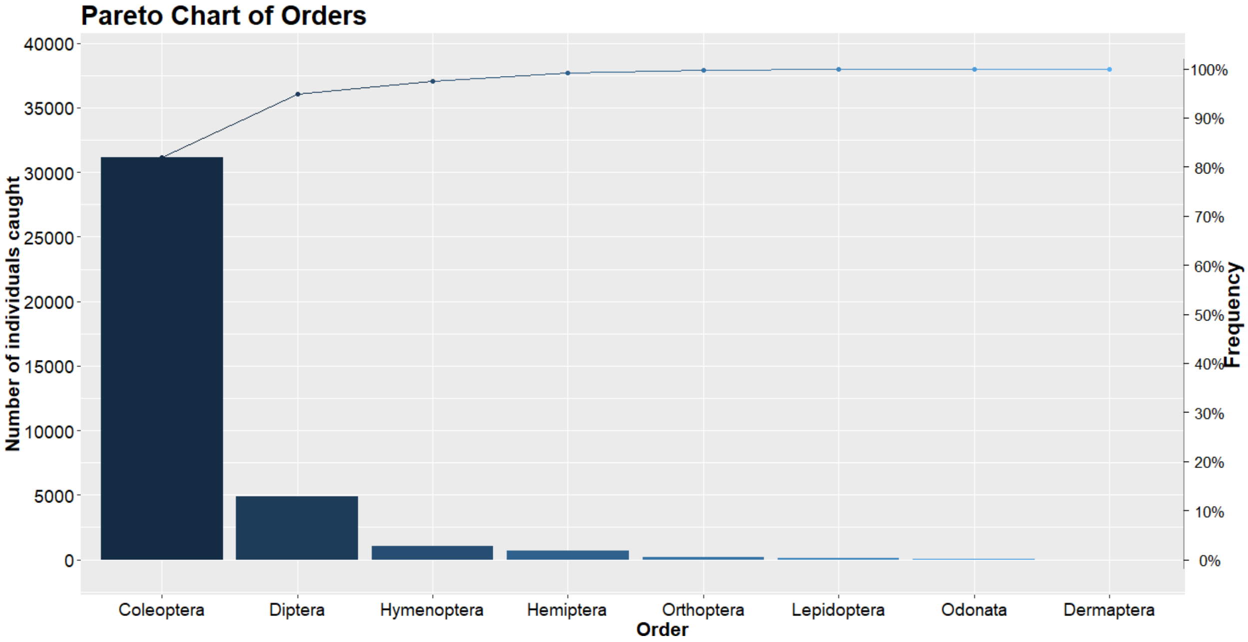


Figure 3: Pareto chart showing the composition of Insecta caught in 236 pitfall traps spread out over 4 different agricultural areas during June and July 2019, grouped by order.

The order Coleoptera (31 098 individuals caught) comprised of at least thirteen families: Carabidae (85.9%), Staphylinidae (3.6%), Silphidae (3.6%), Chrysomelidae (1.2%), Coccinellidae (0.8), Anthicidae (0.7), Hydrophilidae (0.4%), Elateridae (0.5%), Cantharidae (0.2%) and Curculionidae, Dermestidae, Geotrupidae and Scarabidae (all <0.1%). 3.1% of the Coleoptera could not be identified to the family level.

Family Carabidae (26 757 individuals caught) mostly consisted of four ground beetle species that together made up 86.7% of the catches: *Harpalus rufipes* (38.1%), *Poecilus cupreus* (19.6%), *Pterostichus melanarius* (19.5%) and *Acupalpus meridianus* (8.5%). In total 17 different species were identified. 7.3% of the carabid beetles could not be identified to the species level.

For Carabidae, the model best at explaining the data was the model containing the three fixed effects as well as a three-way interaction effect between area, crop and date (model 27, table 3). All effects were significant at p<2.2e-16. The three-way interaction indicates that the amount of caught Carabidae differed between the crop fields of different areas but that this difference varies over time. During the first collection week, Winter Wheat fields of area PH contained more carabid beetles than Winter Wheat fields of area G (p=0.0001). This difference was not found during the second collection week (p=0.2029) but it was found again in the third collection week (p=0.002). Also during the third collection week, Winter Wheat fields from area WE contained more carabid beetles than Winter Wheat fields from area G and PH (both p<0.0001). To compare Summer Wheat of area MB with the Winter Wheat of the other areas, the model was ran placing Winter Wheat and Summer Wheat under one crop variable "Wheat". This revealed that during all the weeks area MB's Wheat contained significantly more Carabidae than areas G, PH and WE in corresponding weeks. For flower strips, area MB contained more Carabidae than area G and PH during the second and third collection week (p=0.0256, 0.0184 and <0.0001, <0.0001, for the second and third collection week, respectively). During the third collection week, area MB's flower strip also contained more carabid beetles than area WE (p<0.0001) which contained more than area G and PH (both p<0.0001). Beet fields only differed in Carabidae abundance during the third week with area PH containing less than area G and WE (p=0.0018 and <0.0001, respectively). Also in this week, the road verge of area WE contained more carabid beetles than area G and PH (p<0.0001 and 0.0015). Finally, the potato fields of area WE contained more carabids than area PH (p<0.0001) during the third collection week. An overview of the Carabidae numbers found in the different area crop combinations is presented in figure 4. For the full overview of comparisons between area, crop and date combinations see Appendix, table 1.

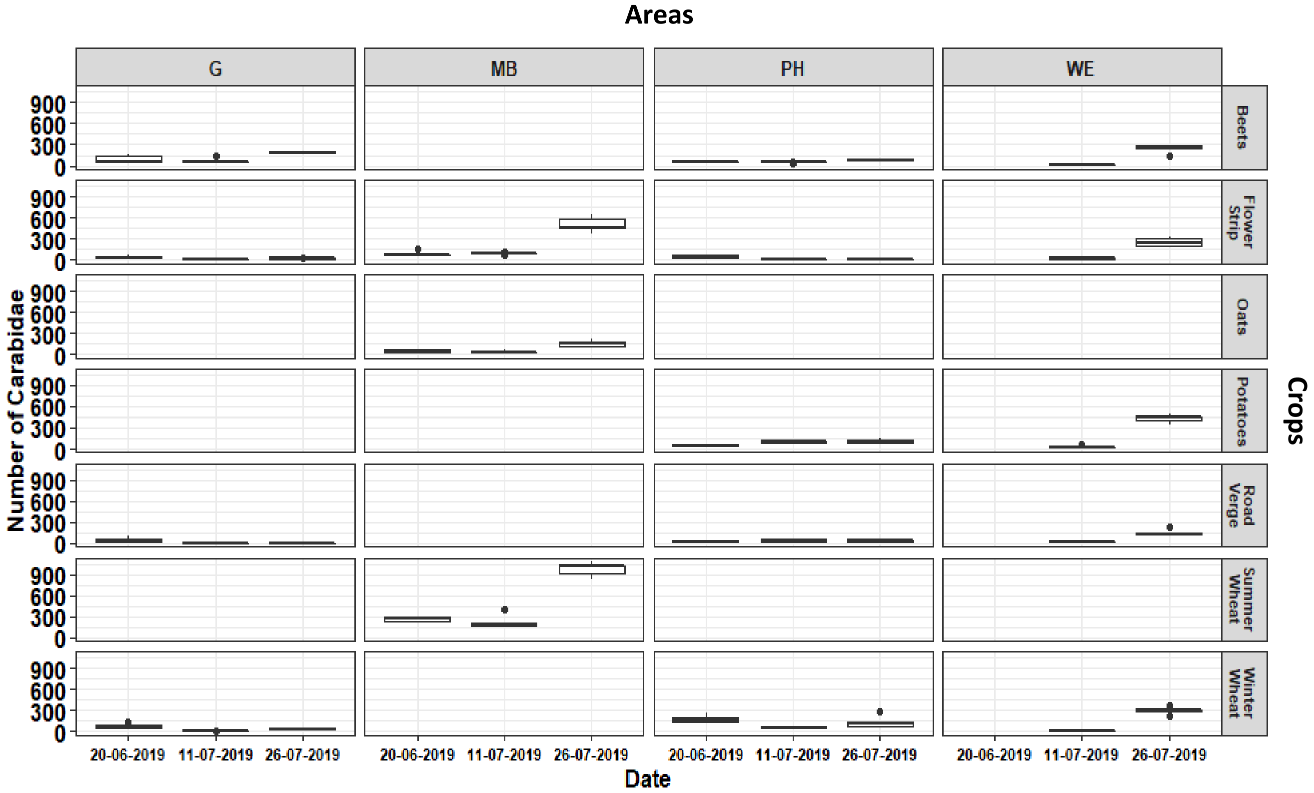


Figure 4: Boxplots of the total number of Carabidae found in pitfall traps placed in seven different crop types in four different agricultural areas in three different weeks.

Because the total dataset was quite unbalanced (figure 4), it was not possible to assess the relative contribution of the single fixed effects. To overcome this problem, a balanced dataset was made containing only the crop types Beets, Winter Wheat, road verge and flower strip of areas G, PH and WE from the second and third collection week (figure 5). Also for this dataset, the model best explaining the data was model 27 (table 3). Post-hoc analysis of the balanced dataset for carabid abundance showed that in general WE contained more carabidae than areas G and PH which did not differ between each other (estimated means: 124, 42 and 53). For crop types, most Carabidae were found in Beet and Winter Wheat fields followed by flower strip and road verge with estimated means of ± 109, 92, 53 and 40, respectively. Significantly more carabid beetles were caught during the third collection week in comparison to the second collection week (estimated means of 24 and 123). Table 4 provides an overview of the estimated effect sizes and contrasts. Carabidae abundances are highlighted here, but analyses of biomass and total invertebrate and insect (in-and excluding Carabidae) abundance can be found in the Appendix.

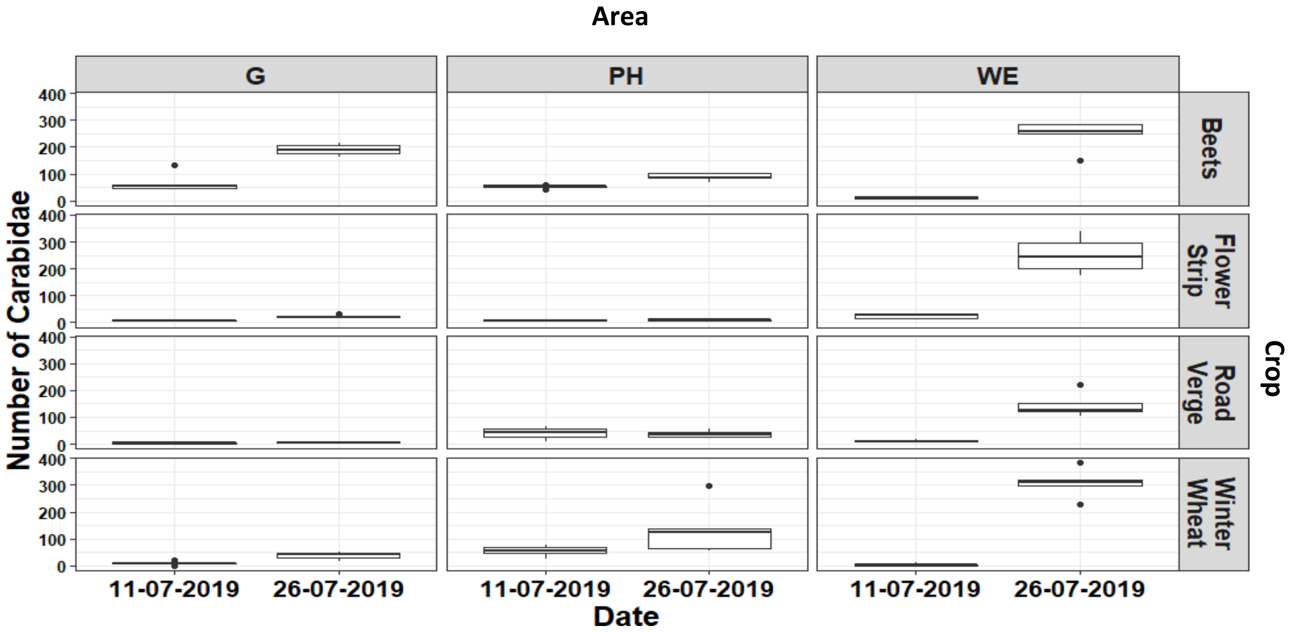


Figure 5: Boxplots of the total number of Carabidae found in pitfall traps placed in four different crop types in three different agricultural areas for two different weeks.

Table 4: Post-hoc analysis (Tukey's method) estimates of the best model describing the total number of Carabidae. SE = standard error. Significant P-values are highlighted in bold.

Fixed effect	Contrast	Estimate	SE	P-value
Area	G - PH	-10.7	7.39	0.3257
	G - WE	-82.3	7.33	**<.0001**
	PH - WE	-71.6	7.51	**<.0001**
Crop	Beets - Flower strip	56.1	8.83	**<.0001**
	Beets - Road Verge	68.8	8.69	**<.0001**
	Beets - Winter Wheat	17.4	8.10	0.1549
	Flower Strip - Road Verge	12.7	8.99	0.5003
	Flower Strip - Winter Wheat	-38.7	8.42	**0.0002**
	Road Verge - Winter Wheat	-51.4	8.28	**<.0001**
Date	11-07-2019 - 26-07-2019	-98.7	6.05	**<.0001**

Experiments

Enclosure experiment

The long drought experienced during the summer of 2019 had caused the clay soil of the wheat fields to become extremely hard. It was therefore not possible to place the plastic lawn edges in the wheat field of area PH, and thus this sampling point is missing from the analysis. However, I did manage to perform the enclosure study in the Sugar Beet fields at all three farms, and in the Winter Wheat fields of areas G and E. The experiment at farm E was terminated preliminarily because of the exceptionally early wheat harvest in 2019 (also caused by the dry and hot summer).

In total 1460 carabid beetles were caught within the enclosures translating to an average carabid density of 3.6 ± 3.0 beetles per square meter. Three species (*P. melanarius, H. rufipes, A. meridianus*) dominated the catches (table 5). I had expected the number of beetles caught to decline over time, with less individuals caught on each consecutive day. Clearly, the catches did not follow this pattern (figure 6), and I suspected that this was related to changes in weather. Hence, I downloaded the weather data from the nearby Nieuw-Beerta KNMI weather station (KNMI, 2019(2)), to find that the fluctuations in the number of beetles caught to coincide well with the amount of rainfall in the preceding 24 hours, especially in the Sugar Beets in area G (figure 6).

Densities of *P. melanarius* and *H. rufipes* differ between crops and areas (*A. meridianus* is not considered here as this is a species that can fly and thus unsuitable for this enclosure study) (figure 7A). There was however no significant difference found in densities between Sugar Beet and Winter Wheat fields (Welch Two Sample t-test, p=0.3742), but sample sizes were small. When comparing these catches with the catches of the monitoring program (from the same weeks, figure 7B), both the numbers and relative abundance of both species do not seem constant between the different methods.

Table 5: Densities for species of Carabidae in individuals m^{-2} as determined by 81 m^{2} enclosures placed in beet and wheat fields in different areas.

Area	Crop	Species	Density (m^{-2})
PH	Beet	P. melanarius	0.23
		H. rufipes	0.25
		A. meridianus	2.78
		Others	0.54
G	Beet	P. melanarius	2.37
		H. rufipes	5.59
		A. meridianus	0
		Others	0.75
	Wheat	P. melanarius	0.49
		H. rufipes	0.21
		A. meridianus	0
		Others	1.48
E	Beet	P. melanarius	0.59
		H. rufipes	0.56
		A. meridianus	0
		Others	0.12
	Wheat	P. melanarius	1.68
		H. rufipes	0.16
		A. meridianus	0.01
		Others	0.19

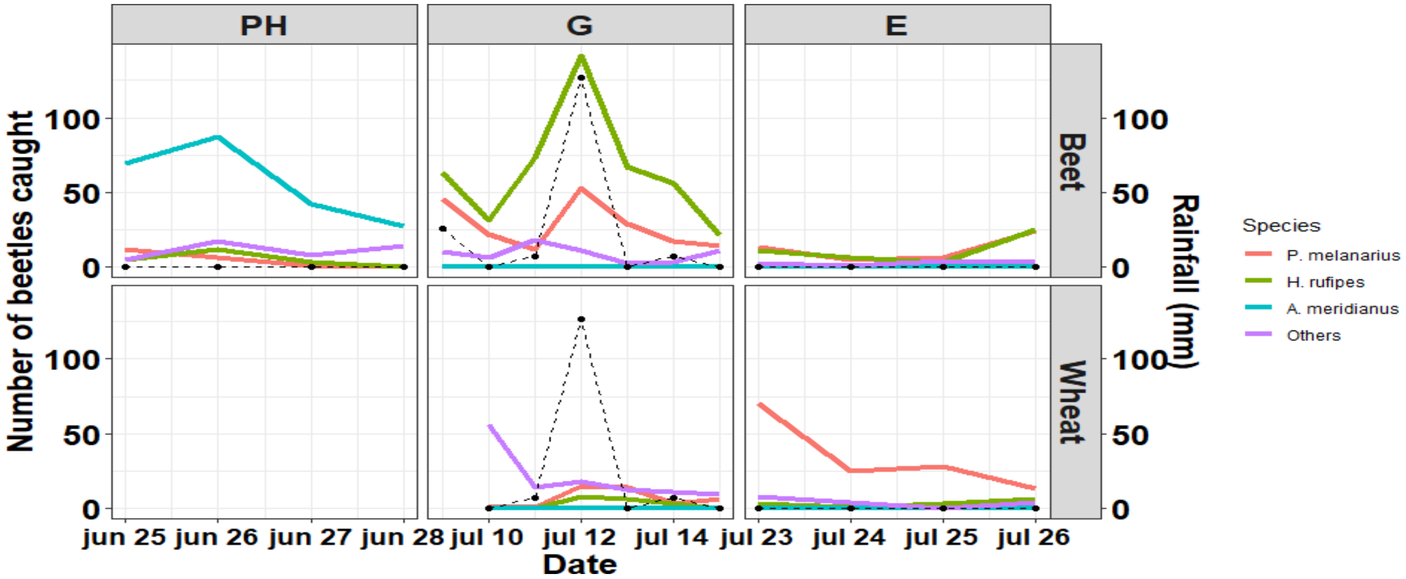


Figure 6: The number of beetles caught per day of the enclosure experiment for four species groups. The dotted black lines represent the amount of rainfall (mm) recorded in the 24 hours before collection of pitfall contents.

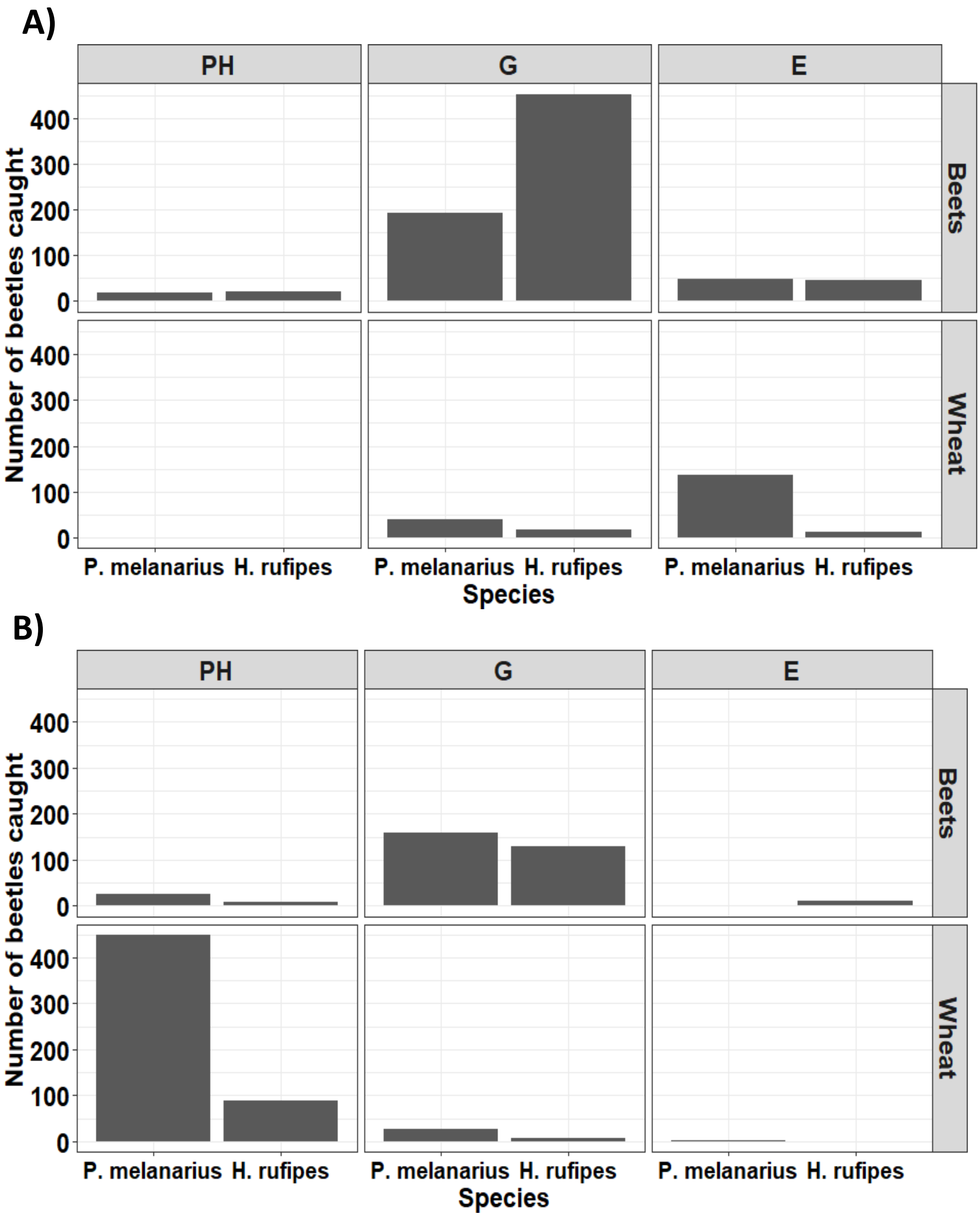


Figure 7: The number of beetles caught in the enclosures (A) and the number of beetles caught in the monitoring program during corresponding weeks (B). Grouped by area and crop.

Mark-recapture experiment

A total of 1321 *P. melanarius* beetles were marked and released. Only 88 beetles were recaptured, thus the overall recapture rate was 6.66%. Recapture rate was not dependent on crop type (X^2 = 1.0513, p=0.3052). The number of releases and recaptures per area is presented in table 6.

Table 6: The number of beetles released and recaptured in the mark-recapture experiment performed in Sugar Beet and Winter Wheat fields in area PH, G and E.

Area	Crop	Released	Recaptured	Recapture rate (%)
PH	Sugar Beet	278	16	5.76
PH	Winter Wheat	278	38	13.67
G	Sugar Beat	153	15	9.80
G	Winter Wheat	154	4	2.60
E	Sugar Beet	212	8	3.77
E	Winter Wheat	212	7	3.30

P. melanarius did not have a directional preference (figure 8). Rayleigh tests found no departures from uniformity in the circular distribution for any area-crop-distance combination (p-values ranging from 0.3275 to 1).

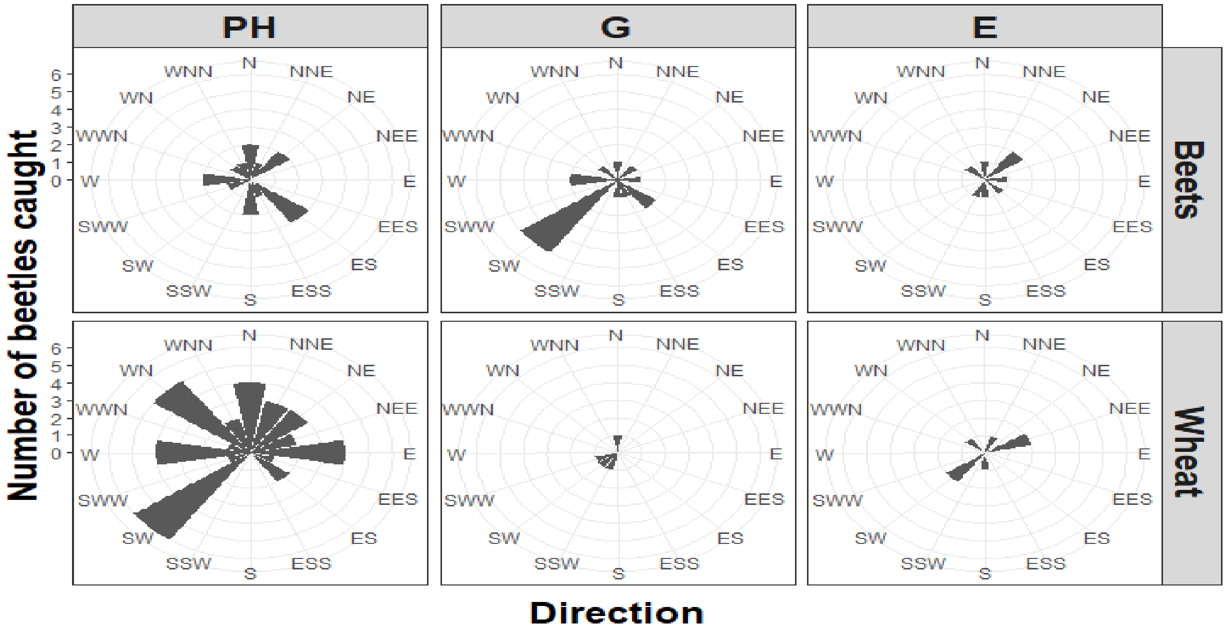


Figure 8: Number of recaptured *P. melanarius* grouped per direction relative to the point of release. Grouped by area and crop type.

Figure 9 depicts the amount of beetles caught per distance and the amount of days it took after release to be found at said distance. When the average daily displacement was calculated using all days and areas of the experiment (Figure 10), the difference in average speed was not significantly different between beetles released in Sugar Beet or Winter Wheat fields (means of 6.75 and 4.73 m day^{-1}, Welch Two Sample t-test, p=0.1844). Since area PH was the only area with quite a few recaptures (54 versus 19 and 15 for area G and E, respectively), An analysis was also made for only this dataset. The average daily displacement did also not differ between beetles released in Sugar Beet or Winter Wheat fields in this dataset with respective means of 7.33 and 6.86 m day^{-1} (p=0.7617).

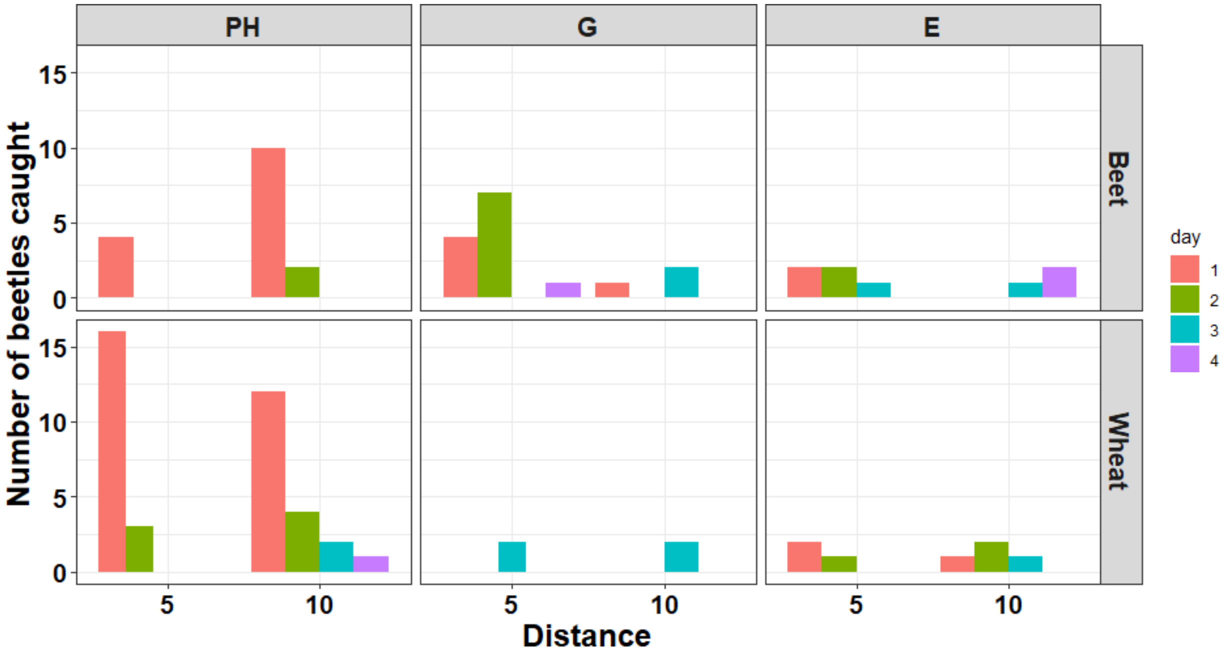


Figure 9: The number of recaptured beetles caught in pitfall traps located at 5 or 10 m from the point of release over the course of four days. The different colors represent the time after release (in days) the recaptures were made.

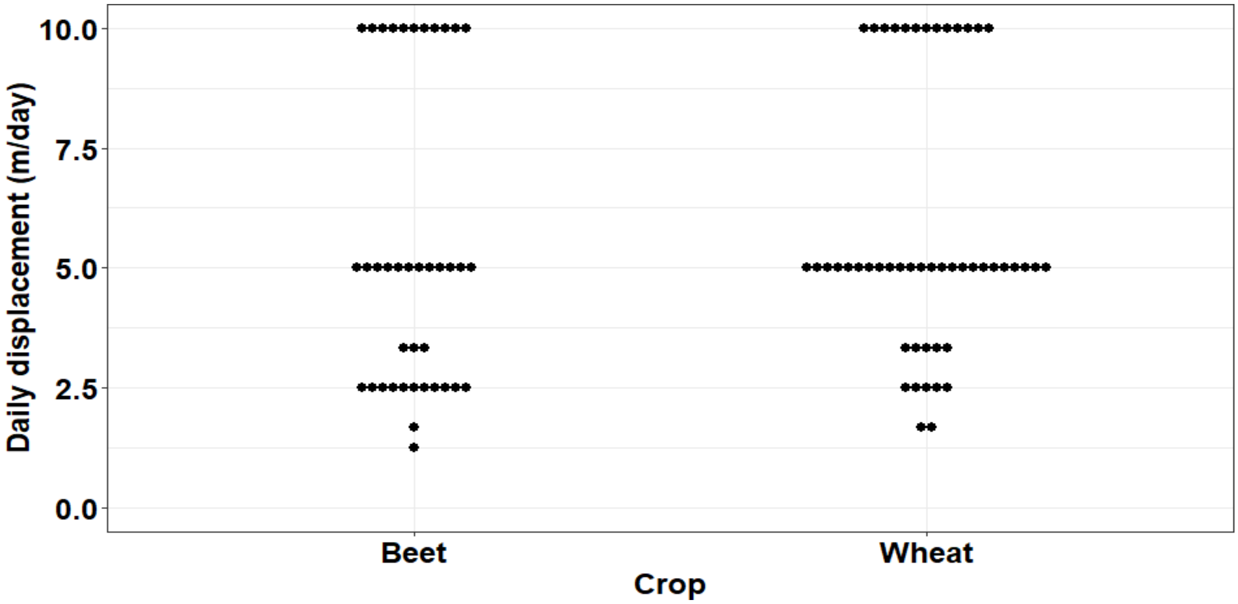


Figure 10: Visualization of the daily displacement (m/day) calculated for beetles caught in Sugar Beet and Winter Wheat fields in the mark-recapture experiments. Each dot represents an individual beetle.

Discussion

In this study, I explored the soil invertebrate communities living in arable fields in Eastern Groningen as sampled using pitfall traps. Pitfall traps are however not a perfect method to study invertebrate abundance as the number of caught individuals is a function of both abundance and activity (Halsall et al., 1988). Therefore I conducted an enclosure and a mark-recapture experiment, to investigate true densities and movement behaviour. Knowledge of these aspects helps me to interpret the results of the pitfall monitoring program.

Invertebrate abundance in different areas and crops

Pitfall traps were dominated by insects, and insects were dominated by Coleopteran beetles. These were in turn dominated by carabid beetles, thus the story about invertebrates in arable farming is mainly a story on the occurrence of ground beetles. Four ground beetle species made up almost ninety percent of all the carabid beetles found: *H. rufipes*, *P. cupreus*, *P. melanarius* and *A. meridianus*.

Analysis of the pitfall catches of ground beetles in different areas and crops revealed some general patterns. Higher numbers were consistently caught in area WE compared to PH and G. This might be related to the fact that WE is the farm with the least intensive agricultural management. However, if farming intensity would be the main driver of ground beetles abundance I would had expected to also find a difference in the number of beetles caught between area PH and areas G. This was not the case. Another factor that could explain the high number of beetles caught in WE is the fact that it is situated within a nature reserve. These nature reserves can act as sources for arthropods in crop fields (Öckinger et al., 2007). This idea is further strengthened by the relatively high numbers of Carabidae caught in area MB, which practices high intensity farming but is also surrounded by natural area. In order to entangle the relative contribution of farming intensity and amount of (semi-)natural habitats in the landscape on ground beetle abundance, a much larger number of farms should be sampled.

In addition, we found differences in the number of beetles caught between crops. Specifically, more ground beetles were captured in Sugar Beet and Winter Wheat fields compared to road verges and set-aside field edges (flower strips). This result is remarkable as road verges and set-aside field edges are semi-natural habitats that are believed to contain a higher biodiversity. A possible explanation could however be that it is much easier for beetles to move in the crops compared to the densely vegetated set-aside habitat. That movement is slower in set-aside field edges and flower strips compared to crop fields was already shown by Frampton et al. (1995) and Wratten et al. (2003). Interestingly, in 2019 no difference was found in the number of ground beetles caught in Sugar Beet and Winter Wheat fields. In previous years, this difference was very obvious, with many more beetles caught in Sugar Beets compared to Winter Wheat, and this result coined the current study on densities and movement behaviour in Sugar Beet and Winter Wheat fields. In 2019 it would had been more interesting to compare densities and movement behaviour between set-aside and either Sugar Beet or Winter Wheat.

Ground beetle activity and density

In order to be able to interpret the pitfall catches we need information on true densities and beetle movement behaviour in the different habitats. I studied this in Sugar Beets and Winter Wheat by conducting an enclosure and a mark-recapture experiment.

In the enclosure experiment I found an average density of 3.6 ground beetles per square meter. An average crop field spans around ten to twenty hectares meaning such fields contain over half a million ground beetles. The idea that agricultural fields contain very little insect life therefore seems to be a misconception. Few studies have reported beetle densities in arable fields. Andersen (1997) found a density of 8.3 ± 1.2 carabid beetles per square meter in cereal fields in Norway. This is about twice as high as the estimate from this study, which could be explained by differences in methods and the scale of sampling (Thomas et al., 1998). Densities of *P. melanarius* ranged from 0.23 to 2.37 beetles per square meter. This estimate is comparable to the densities found in other studies. Holland et al. (2004) and Thomas et al. (1998) found densities of respectively 0.30 and 0.26 m^{-2} in arable fields in the UK. In wheat fields in Sweden, Ericson (1977) estimated *P. melanarius* densities of 0.73 m^{-2}. Generally, *P. melanarius* densities in Eastern Groningen thus seem relatively high.

It was noticed that the pitfall catches in the enclosures did not follow the expected pattern of a decreasing catch for each consecutive day (figure 6). Even on the last day of the experiments still significant amounts of beetles were caught, which suggests that the densities we recorded are underestimates of the true ground beetle densities. Beforehand we believed that a midweek would be sufficient to deplete the enclosures. However, this was clearly not the case and future enclosure studies should thus run for a much longer time period. One possible reason why enclosures were not depleted after 4 days could be that the beetles were inactive due to the high temperatures. The dry and hot summer created deep cracks in the clayey soils, especially in the Winter Wheat fields. It is likely that the beetles mainly remained in the cracks when it was hot and dry, and thus were not captured by the pitfalls. This idea is supported by the observation that more carabid beetles were captured after a period of rainfall. Thomas et al. (1988) found similar results in cereal fields in England. They found that the onset of peaks in activity of *P. melanarius* seemed to correlate with periods of rainfall. These authors explained the lower activity of beetles during droughts by a lack of prey items on the surface, such as snails.

For the same fields, if we compare the densities estimated by the enclosures with the abundances recorded in the monitoring program, there actually seems to be a positive correlation (figure 11). Concluding from this, the impression arises that the pitfall trapping method adopted in the monitoring program actually provides a decent image of the underlying densities. This is however just a preliminary conclusion as there are only five datapoints, further stressing the need for more data.

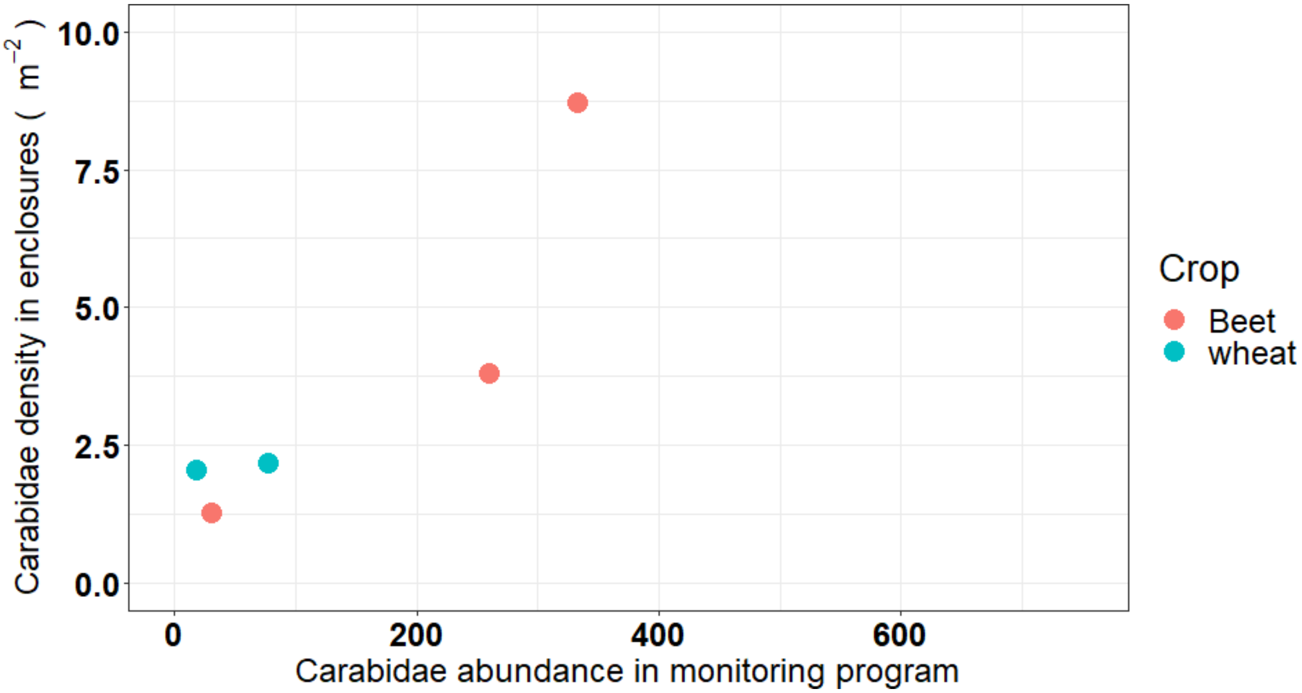


Figure 11: Comparison of the Carabidae abundances found in the monitoring program and the Carabidae densities found in the enclosures, for the same fields. Grouped by crop type.

No significant difference was found in daily displacement of *P. melanarius* beetles between Winter Wheat and Sugar Beet fields, although the estimate was slightly higher for Sugar Beet fields. Thus, differences in the number of beetles caught in Winter Wheat and Sugar Beet fields (which was not found this year) cannot be explained by differences in activity, but probably should be considered as genuine differences in abundance. However, due to the low recapture rate the sample size on which this conclusion builds is relatively small. A larger longer running study, preferably in a normal year without extreme droughts, is required. The mark-recapture study I performed only provides a snapshot of the movements of carabid beetles. I.e. we do not know what path the beetle followed between the release area and the pitfall where it was trapped, and moreover we do not know anything about the beetles that were not recaptured at all. A tracking study, if possible with these minute animals, would provide much more and better information on ground beetle movement.

The mark-recapture experiment revealed that *P. melanarius* did not have a directional preference when moving in Winter Wheat or Sugar Beet fields. It has been found that carabid beetle dispersal does not always follow a random walk (Wallin and Ekbom, 1988; Thomas et al., 1998) so it was thought that the linear structure if the crops might guide the beetles in their movements. This could be different for Potato fields as they are grown on high ridges.

I focused my study on the ground beetle *P. melanarius*, but it is interesting to make an comparison with the beetle *H. rufipes.* Interestingly, the ratios between *P. melanarius*/*H. rufipes* beetles is higher for monitoring transects than within the enclosures (figure 12). This result might reflect the differences in movement speed between these ground beetle species. Indeed, Frampton et al. (1995) and Thomas (1997) report higher movement rates for *P. melanarius* compared to *H. rufipes*. Thus, it would be very interesting to repeat the mark-recapture study also with *H. rufipes.*

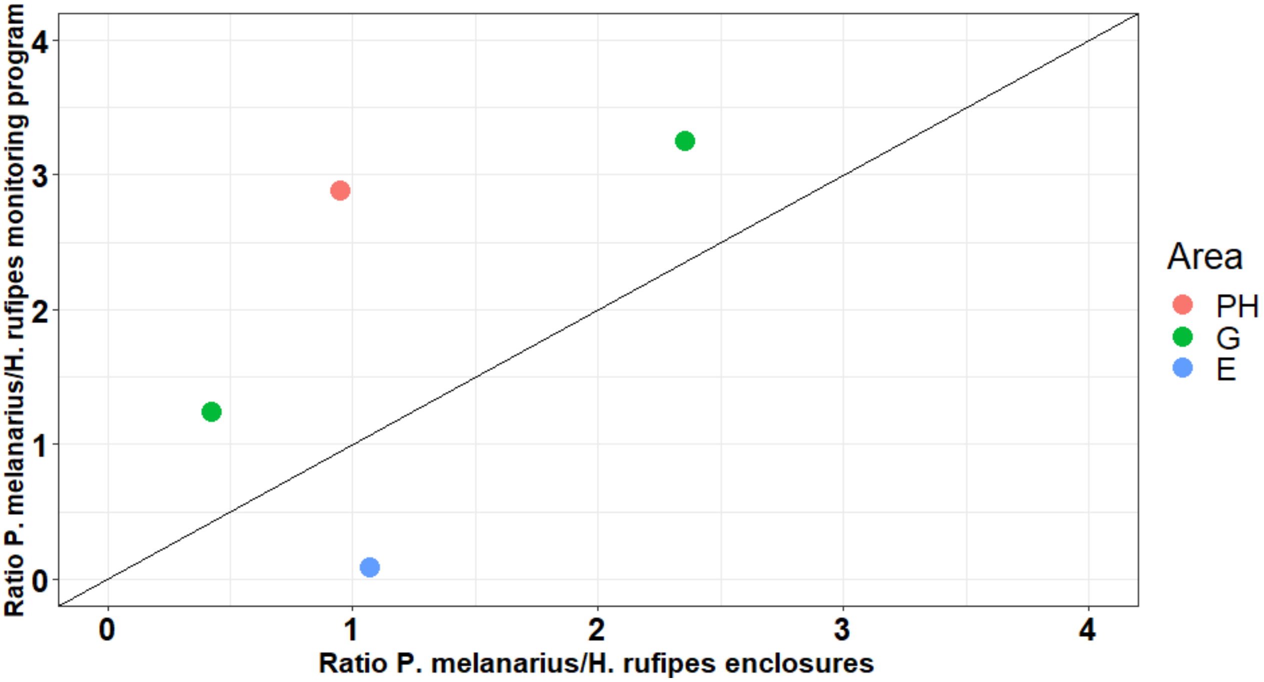


Figure 12: Plot showing the ratio of *P. melanarius* to *H. rufipes* from the enclosures versus those found in the monitoring program, for the same fields. Grouped by Area.

Conclusion

The experiments suggest (although preliminary as data is few) that pitfall trapping is a good method to estimate abundance, and thus that differences found between farms and habitats presumably are genuine. The experiments were however performed in Sugar Beet and Winter Wheat fields only, and other crops should be included in a follow-up study. For now this study validates the methods used for the monitoring of soil-dwelling arthropods in arable fields. Arthropods can fulfill many important ecosystem services in agriculture. By predating on weed seeds and crop harming organisms carabid beetles provide a form of natural pest-control beneficial to farmers. It is therefore important that we continue and expand the monitoring program to find out what specific factors drive Carabidae abundance in arable farming landscapes, and with that information how farmers can adopt these findings to restore the natural processes provided by these animals. We do not fully understand the driving factors as of yet, but the results from this study suggest that farming intensity and (semi-)natural habitat in the wider landscape might play an important role.

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Appendix

Table 1: Complete output of post-hoc Tukey's analysis (emmeans function) on total Carabidae abundance comparing the different crop-area-date combinations. Significant p-values are highlighted in bold.

$emmeans					
Crop = Beets, Date = 20-06-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	87.60	18.5	187	51.097	124.1
MB	nonEst	NA	NA	NA	NA
PH	52.00	18.5	187	15.497	88.5
WE	nonEst	NA	NA	NA	NA
Crop = Flower Strip, Date = 20-06-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	39.60	18.5	187	3.097	76.1
MB	87.00	18.5	187	50.497	123.5
PH	48.73	20.7	188	7.957	89.5
WE	nonEst	NA	NA	NA	NA
Crop = Oats, Date = 20-06-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA
MB	42.94	20.7	188	2.164	83.7
PH	nonEst	NA	NA	NA	NA
WE	nonEst	NA	NA	NA	NA
Crop = Potatoes, Date = 20-06-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA
MB	nonEst	NA	NA	NA	NA
PH	44.60	18.5	187	8.097	81.1
WE	nonEst	NA	NA	NA	NA
Crop = Roadside, Date = 20-06-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	38.00	18.5	187	1.497	74.5
MB	nonEst	NA	NA	NA	NA
PH	21.80	18.5	187	14.703	58.3

WE	nonEst	NA	NA	NA	NA
Crop = Summer Wheat, Date = 20-06-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA
MB	254.40	18.5	187	217.897	290.9
PH	nonEst	NA	NA	NA	NA
WE	nonEst	NA	NA	NA	NA
Crop = Winter Wheat, Date = 20-06-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	78.50	13.1	187	52.689	104.3
MB	nonEst	NA	NA	NA	NA
PH	179.00	18.5	187	142.497	215.5
WE	nonEst	NA	NA	NA	NA
Crop = Beets, Date = 11-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	66.60	18.5	187	30.097	103.1
MB	nonEst	NA	NA	NA	NA
PH	52.40	18.5	187	15.897	88.9
WE	12.20	18.5	187	24.303	48.7
Crop = Flower Strip, Date = 11-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	4.29	23.8	188	-42.758	51.3
MB	90.00	18.5	187	53.497	126.5
PH	8.02	20.7	188	-32.752	48.8
WE	23.40	18.5	187	13.103	59.9
Crop = Oats, Date = 11-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA
MB	29.40	18.5	187	7.103	65.9
PH	nonEst	NA	NA	NA	NA
WE	nonEst	NA	NA	NA	NA
Crop = Potatoes, Date = 11-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA

MB	nonEst	NA	NA	NA	NA
PH	96.60	18.5	187	60.097	133.1
WE	30.40	18.5	187	6.103	66.9
Crop = Roadside, Date = 11-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	4.80	18.5	187	-31.703	41.3
MB	nonEst	NA	NA	NA	NA
PH	40.03	20.7	187	-0.758	80.8
WE	10.00	18.5	187	26.503	46.5
Crop = Summer Wheat, Date = 11-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA
MB	221.80	18.5	187	185.297	258.3
PH	nonEst	NA	NA	NA	NA
WE	nonEst	NA	NA	NA	NA
Crop = Winter Wheat, Date = 11-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	8.65	13.8	187	-18.545	35.8
MB	nonEst	NA	NA	NA	NA
PH	54.00	18.5	187	17.497	90.5
WE	4.20	18.5	187	32.303	40.7
Crop = Beets, Date = 26-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	190.41	20.7	188	149.636	231.2
MB	nonEst	NA	NA	NA	NA
PH	88.60	18.5	187	52.097	125.1
WE	244.40	18.5	187	207.897	280.9
Crop = Flower Strip, Date = 26-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	21.40	18.5	187	15.103	538.3
MB	501.80	18.5	187	465.297	538.3
PH	9.00	18.5	187	27.503	45.5
WE	251.08	20.7	187	210.285	291.9
Crop = Oats, Date = 26-07-2019:					

Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA
MB	151.00	18.5	187	114.497	187.5
PH	nonEst	NA	NA	NA	NA
WE	nonEst	NA	NA	NA	NA
Crop = Potatoes, Date = 26-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA
MB	nonEst	NA	NA	NA	NA
PH	114.00	18.5	187	77.497	150.5
WE	425.60	18.5	187	389.097	462.1
Crop = Roadside, Date = 26-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	4.40	18.5	187	-32.103	40.9
MB	nonEst	NA	NA	NA	NA
PH	36.28	20.7	187	-4.508	77.1
WE	145.22	20.7	187	104.424	186.0
Crop = Summer Wheat, Date = 26-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	nonEst	NA	NA	NA	NA
MB	974.40	18.5	187	937.897	1010.9
PH	nonEst	NA	NA	NA	NA
WE	nonEst	NA	NA	NA	NA
Crop = Winter Wheat, Date = 26-07-2019:					
Area	emmean	SE	df	lower.CL	upper.CI
G	39.00	13.1	187	13.189	64.8
MB	nonEst	NA	NA	NA	NA
PH	136.60	18.5	187	100.097	173.1
WE	307.20	18.5	187	270.697	343.7
Degrees-of-freedom method: satterthwaite					
Confidence level used: 0.95					
$contrasts					
Crop = Beets, Date = 20-06-2019:					

Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	35.60	26.2	187	1187.360	0.5258
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Flower Strip, Date = 20-06-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	-47.40	26.2	187	-1.811	0.2712
G - PH	-9.13	27.7	187	-0.329	0.9876
G - WE	nonEst	NA	NA	NA	NA
MB -	38.27	27.7	187	1.379	0.5139
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Oats, Date = 20-06-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Potatoes, Date = 20-06-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Roadside, Date = 20-06-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	16.20	26.2	187	0.619	0.9259
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA

PH - WE	nonEst	NA	NA	NA	NA
Crop = Summer Wheat, Date = 20-06-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Winter Wheat, Date = 20-06-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	-100.50	22.7	187	-4.435	**0.0001**
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Beets, Date = 11-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	14.20	26.2	187	0.543	0.9484
G - WE	54.40	26.2	187	2.079	0.1638
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	40.20	26.2	187	1.536	0.4180
Crop = Flower Strip, Date = 11-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	-85.71	30.2	188	-2.840	**0.0256**
G - PH	-3.74	31.6	188	-0.118	0.9994
G - WE	-19.11	30.2	188	-0.633	0.9212
MB -	81.98	27.7	187	2.955	**0.0184**
MB - WE	66.60	26.2	187	2.545	0.0564
PH - WE	-15.38	27.7	187	-0.554	0.9453
Crop = Oats, Date = 11-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA

G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Potatoes, Date = 11-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	66.20	26.2	187	2.530	0.0586
Crop = Roadside, Date = 11-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	-35.23	27.7	187	-1.270	0.5833
G - WE	-5.20	26.2	187	-0.199	0.9972
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	30.03	27.7	187	1.082	0.7007
Crop = Summer Wheat, Date = 11-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Winter Wheat, Date = 11-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	-45.35	23.1	187	-1.965	0.2049
G - WE	.45	23.1	187	0.193	0.9974
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	49.80	26.2	187	1.903	0.2303

Crop = Beets, Date = 26-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	101.81	27.7	187	3.670	**0.0018**
G - WE	-53.99	27.7	187	-1.946	0.2125
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	-155.80	26.2	187	-5.954	**<.0001**
Crop = Flower Strip, Date = 26-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	-480.40	26.2	187	-18.358	**<.0001**
G - PH	12.40	26.2	187	0.474	0.9647
G - WE	-229.68	27.7	187	-8.277	**<.0001**
MB -	492.80	26.2	187	18.832	**<.0001**
MB - WE	250.72	27.7	187	9.036	**<.0001**
PH - WE	-242.08	27.7	187	-8.724	**<.0001**
Crop = Oats, Date = 26-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Potatoes, Date = 26-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	-311.60	26.2	187	-11.908	**<.0001**
Crop = Roadside, Date = 26-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	-31.88	27.7	187	-1.149	0.6596
G - WE	-140.82	27.7	187	-5.075	**<.0001**

MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	-108.93	29.2	187	-3.725	**0.0015**
Crop = Summer Wheat, Date = 26-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	nonEst	NA	NA	NA	NA
G - WE	nonEst	NA	NA	NA	NA
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	nonEst	NA	NA	NA	NA
Crop = Winter Wheat, Date = 26-07-2019:					
Contrast	Estimate	SE	df	t.ratio	p.value
G - MB	nonEst	NA	NA	NA	NA
G - PH	-97.60	22.7	187	-4.307	**0.0002**
G - WE	-268.20	22.7	187	-11.835	**<.0001**
MB -	nonEst	NA	NA	NA	NA
MB - WE	nonEst	NA	NA	NA	NA
PH - WE	-170.60	26.2	187	-6.519	**<.0001**
Degrees-of-freedom method: satterthwaite					
P value adjustment: tukey method for comparing a family of 4 estimates					

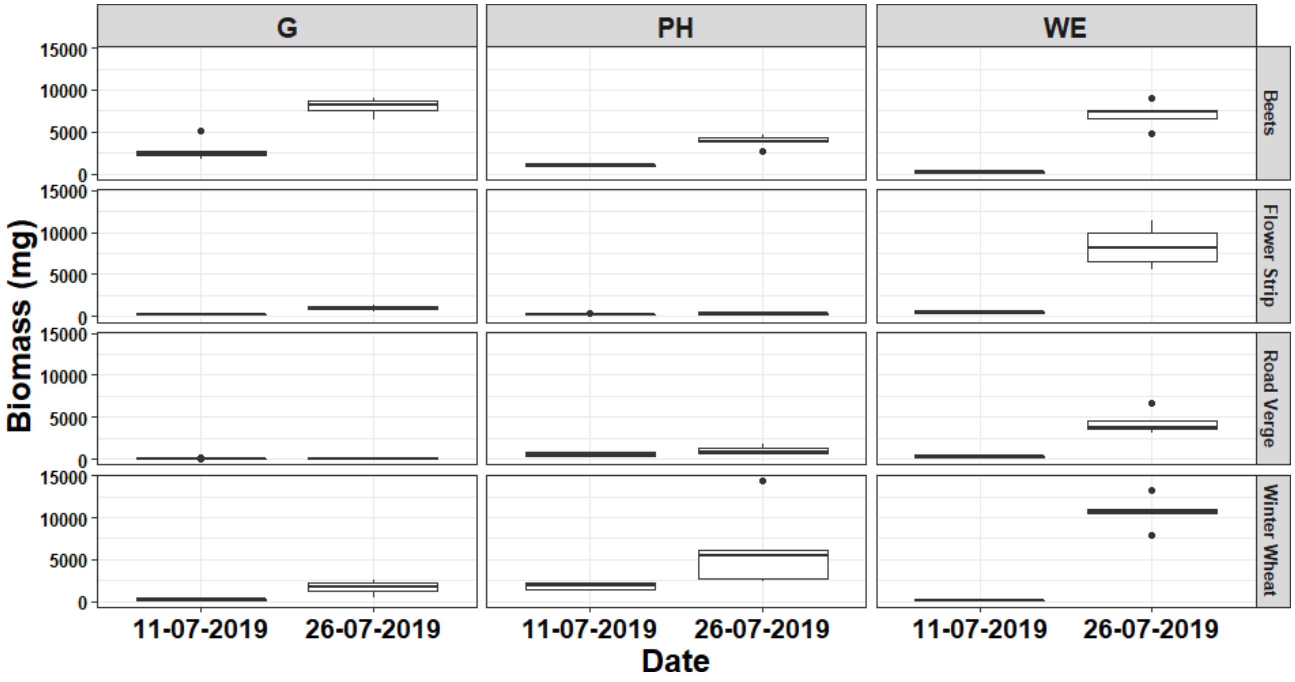

Figure 1: Boxplots of the Carabidae biomass (mg) estimated by pitfall traps placed in four different crop types in three different agricultural areas for two different weeks.

Table 2: Post-hoc analysis (Tukey's method) estimates of the best model (model 27, table 3 main text) describing amount of biomass. SE = standard error. Significant P-values are highlighted in bold.

Fixed effect	Contrast	Estimate	SE	P-value
Area	G - PH	-111	300	0.9269
	G - WE	-2162	298	**<.0001**
	PH - WE	-2051	305	**<.0001**
Crop	Beets - Flower strip	2063	358	**<.0001**
	Beets - Road Verge	2772	353	**<.0001**
	Beets - Winter Wheat	376	329	0.6634
	Flower Strip - Road Verge	710	365	0.2159
	Flower Strip - Winter Wheat	-1678	342	**<.0001**
	Road Verge - Winter Wheat	-2396	336	**<.0001**
Date	11-07-2019 - 26-07-2019	-3718	246	**<.0001**

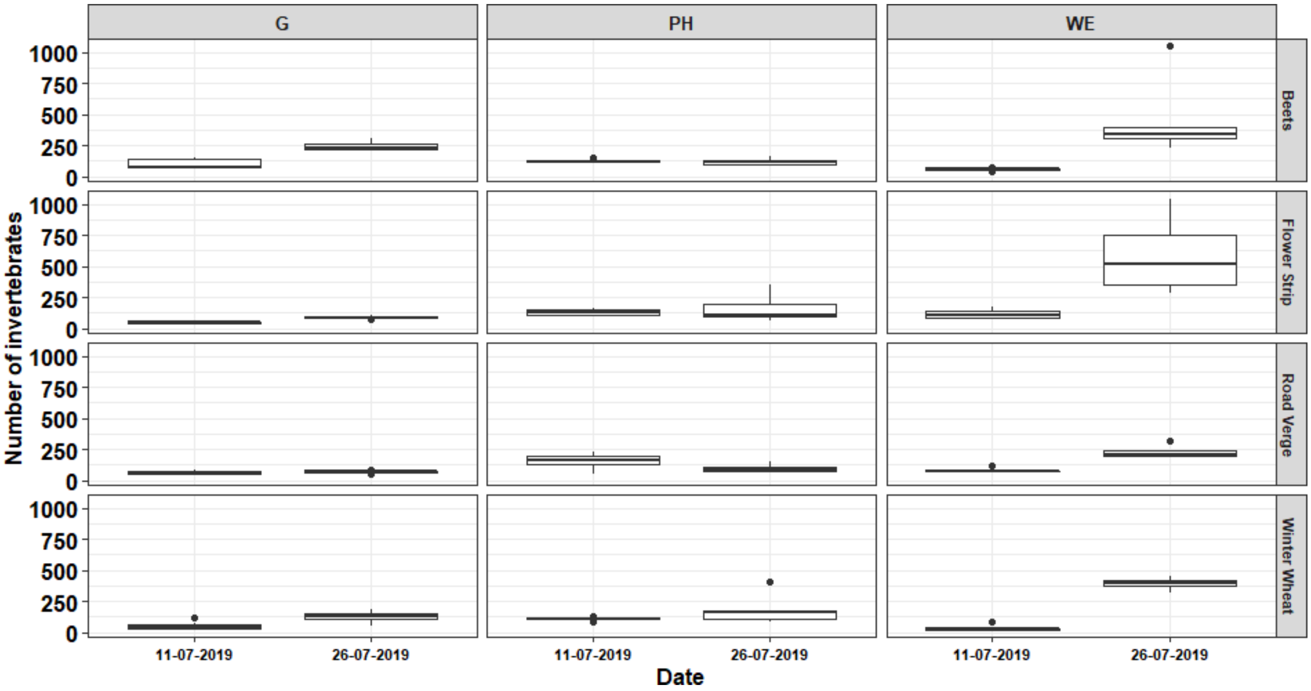

Figure 2: Boxplots of the total number of invertebrates found in pitfall traps placed in four different crop types in three different agricultural areas for two different weeks.

Table 3: Post-hoc analysis (Tukey's method) estimates of the best model (model 27, table 3) describing the total number of invertebrates. SE = standard error. Significant P-values are highlighted in bold.

Fixed effect	Contrast	Estimate	SE	P-value
Area	G - PH	-37.2	24.1	0.2806
	G - WE	-146.0	23.9	**<.0001**
	PH - WE	-108.8	24.6	**0.0001**
Crop	Beets - Flower strip	-1.03	28.8	**1.0000**
	Beets - Road Verge	72.66	28.5	0.0635
	Beets - Winter Wheat	37.57	26.5	0.4944
	Flower Strip - Road Verge	73.70	29.4	0.0694
	Flower Strip - Winter Wheat	38.61	27.5	0.5014
	Road Verge - Winter Wheat	-35.09	27.1	0.5700
Date	11-07-2019 - 26-07-2019	-142	18.1	**<.0001**

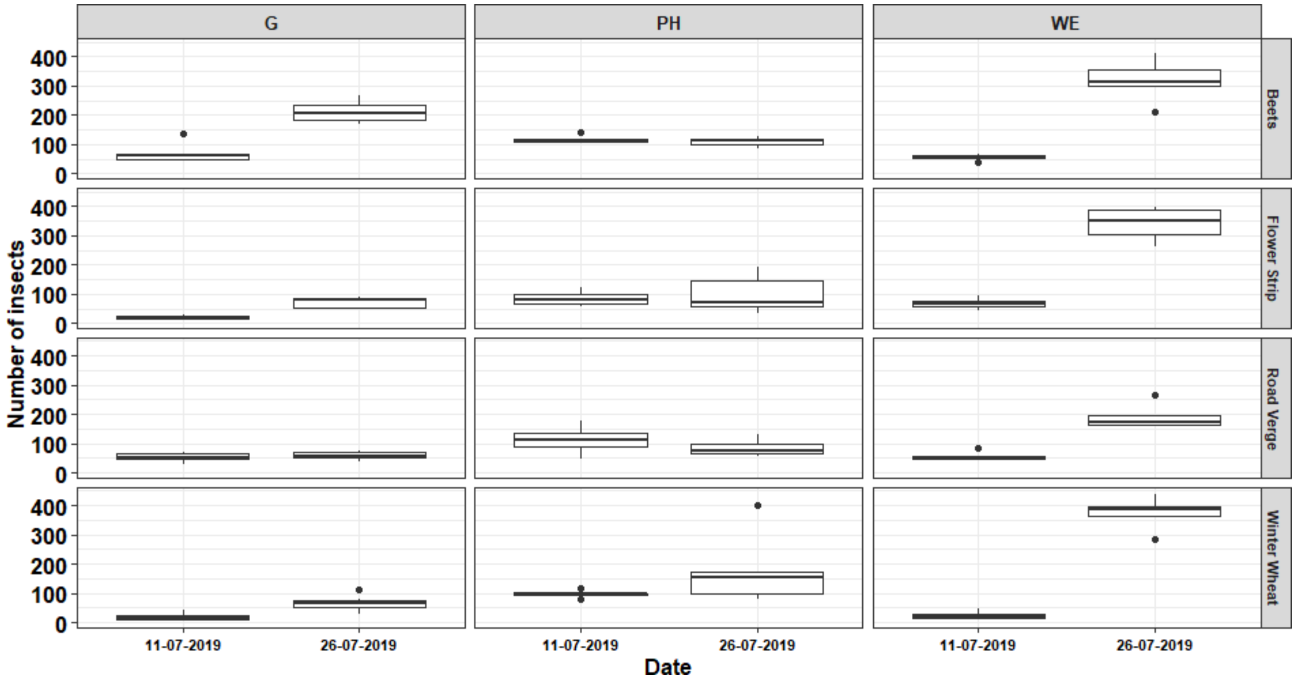

Figure 3: Boxplots of the total number of insects including Carabidae found in pitfall traps placed in four different crop types in three different agricultural areas for two different weeks.

Table 4: Post-hoc analysis (Tukey's method) estimates of the best model (model 27, table 3) describing the total number of insects. SE = standard error. Significant P-values are highlighted in bold.

Fixed effect	Contrast	Estimate	SE	P-value
Area	G - PH	-39.9	10.4	**0.0009**
	G - WE	-107.4	10.3	**<.0001**
	PH - WE	-67.5	10.6	**<.0001**
Crop	Beets - Flower strip	33.1	12.4	**0.0468**
	Beets - Road Verge	53.9	12.2	**0.0003**
	Beets - Winter Wheat	20.0	11.4	0.3045
	Flower Strip - Road Verge	20.8	12.6	0.3572
	Flower Strip - Winter Wheat	-13.1	11.8	0.6860
	Road Verge - Winter Wheat	-33.9	**11.6**	**0.0263**
Date	11-07-2019 - 26-07-2019	-110	7.5	**<.0001**

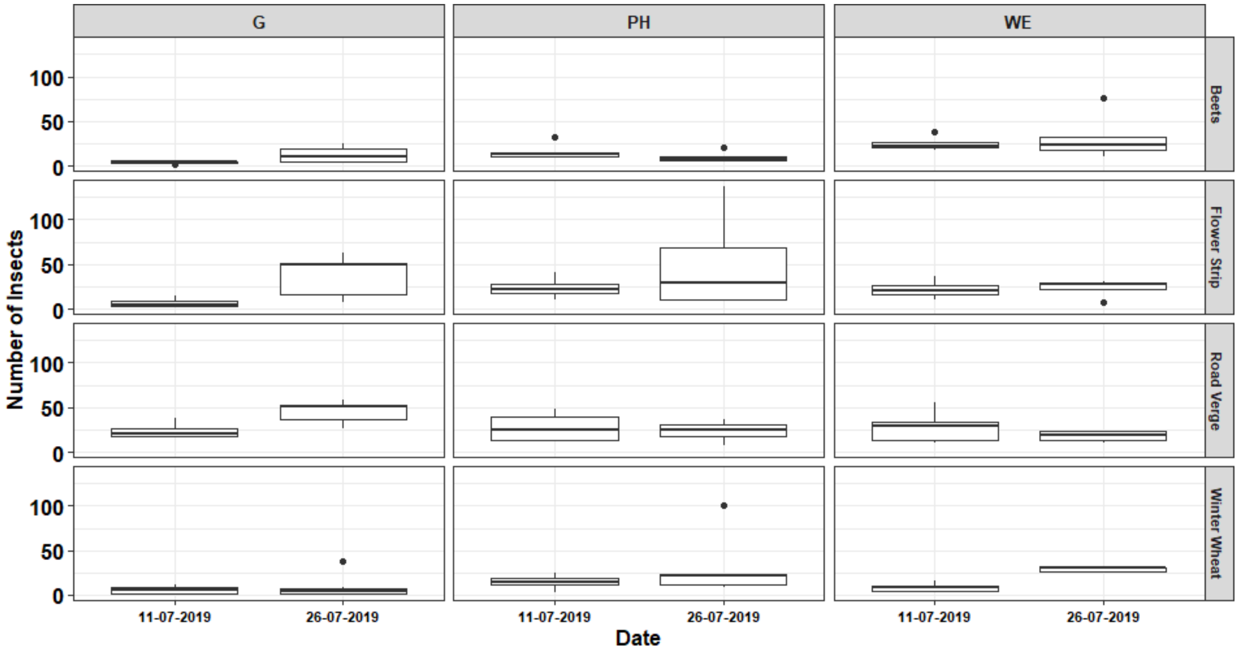

Figure 4: Boxplots of the total number of insects excluding Carabidae found in pitfall traps placed in four different crop types in three different agricultural areas for two different weeks.

Table 5: Post-hoc analysis (Tukey's method) estimates of the best model (model 27, table 3) describing the total number of insects excluding Carabidae. SE = standard error. Significant P-values are highlighted in bold.

Fixed effect	Contrast	Estimate	SE	P-value
Area	G - PH	-7.23	4.88	0.1846
	G - WE	-5.59	4.81	0.3551
	PH - WE	1.64	4.11	0.9164
Crop	Beets - Flower strip	-10.786	4.88	0.1279
	Beets - Road Verge	-10.908	4.81	0.1124
	Beets - Winter Wheat	0.390	4.49	0.9998
	Flower Strip - Road Verge	-0.122	4.93	1.0000
	Flower Strip - Winter Wheat	11.176	4.62	0.0798
	Road Verge - Winter Wheat	11.298	4.54	0.0678
Date	11-07-2019 - 26-07-2019	-110	7.5	<.0001