WEEDS DETERMINE THE COMPOSITION OF CARABID ASSEMBLAGE IN MAIZE AT A FINE SCALE*

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Weeds cause problems to farmers but on the other hand they contribute to the local biodiversity by providing food and shelter for many insect species and birds, many of which are dependent solely on weeds. In this paper we investigated how composition of weed assemblage in a small maize field (400 m^2) affects composition of assemblages of carabid beetles at the scale of metres. By using pitfall traps and sampling weeds around them, we were able to show that carabid beetles respond to composition of weed assemblage at this fine scale. Percentage cover of bare ground, *Viola arvensis*, *Lolium multiflorum*, *Persicaria maculosa*, and *Echinochloa crus-galli* significantly affected composition of carabid assemblages in the study field. Twenty-nine significant correlations were found between carabid activity density and percentage cover at the species level. We therefore conclude that a diverse weed community promotes carabid diversity in arable fields. This, besides being a value itself from the perspective of biodiversity conservation, fosters the ecosystem services including pest and seed predation by carabid beetles.

ground beetles; *Zea mays*; habitat association; pitfall traps; biodiversity in agroecosystems

INTRODUCTION

Traditionally weeds are regarded as troublesome for farmers because they compete with crop for water, nutrients, and light (Zimdahl, 2004), and from that perspective farmers tend to remove them from their fields by every tool that is currently available. Besides causing harm to crop, considerable value of weeds was recognized for preserving biodiversity in agroecosystems (Marshall et al., 2003; Storkey, 2006; Franke et al., 2009). Not only have many previously common species of weeds become rare and endangered as a result of intensive use of herbicides or other weed control tactics (Andreasen et al., 1996). Many weed species provide food source for various kinds of animals and in this way they form the basis of the trophic cascade in arable fields (Norris, Kogan, 2000; Marshall et al., 2003; Franke et al., 2009). Among herbivorous or granivorous insects, a number of species are specialized on weeds (Ward, Spalding, 1993; Campobasso et al.,

1999; Saska, 2008b), so the weed presence ensures that these insect species may survive in intensively managed agricultural landscape. At the higher levels of the food chain, many predatory insect species feed on herbivorous species and their larvae (Honěk, Jarošík, 2000; Birkhofer et al., 2008). It is also common that primarily carnivorous insects utilize plant material as a food source at some phase of their development (Norris, Kogan, 2000). Weed patches in crops thus may host very diverse arthropod assemblages composed both of herbivores and their predators. A number of bird species, including the game ones, are dependent on weed seeds and insects associated with them as the food source (Holland et al., 2006; 2012; Franke et al., 2009). Indeed, weed decline in the past years has been interpreted as the major cause of the farmland bird population reduction in the UK, for example (Moreby, Southway, 1999; Holland et al., 2006).

Insects and other arthropods may benefit from weed presence in the field in other ways than using

it as a direct food source. Besides providing shelter from vertebrate predators, weed cover substantially alters microclimate on the soil surface: it buffers daily fluctuation in temperature (N o r r i s , K o g a n , 2000; D i e h l et al., 2012) and increases humidity of air above ground and in soil (N o r r i s , K o g a n , 2000; B r a n t et al., 2006). This is especially important in row crops such as maize where typically large areas of bare soil occur when properly weeded, and as such they represent hostile environment for many epigeal arthropods (L ö v e i , 1984; P a v u k et al., 1997). By changing microclimate weeds make such environment suitable for insect living and reproduction, and in this way help promote biodiversity at the species and functional level.

Carabid beetles are well known predatory insects that have an important function in the agoecosystems and surrounding habitats, as they play the role of natural enemies of insect pests, such as aphids, dipteran eggs, and lepidopteran larvae (S u n d e r l a n d , 2002). Besides that, a number of species consume weed seeds (e.g. H o n ě k et al., 2007; S a s k a et al., 2008) and contribute to the reduction of soil seed bank within the fields (B o h a n et al., 2011). That carabids were attracted to the weedy sites had been periodically reported (e.g. S p e i g h t , L a w t o n , 1976; K o k t a , 1988; H o l l a n d et al., 1999). It has been shown previously that carabid assemblages differed between fields according to the degree of weediness, including manipulative studies where weeds were removed by herbicides (e.g. P o w e l l et al., 1985; K r o m p , 1990; H a w t h o r n e , H a s s a l l , 1995; P a v u k et al., 1997). It was also demonstrated using enclosures that some carabid beetles occur more often in patches of particular weed species (S a s k a , 2008a), and that these responses often correlate with the food preferences or requirements of the species (compare e.g. field data of S a s k a (2008a) with seed preference data of H o n ě k et al. (2007) and seed requirement data of S a s k a (2008b)). H o n ě k et al. (2005) furthermore demonstrated that dandelion specialist *Amara montivaga* Sturm aggregated in stands grown by *Taraxacum officinale*, while in stands only a few meters apart grown by other weeds, this carabid was scarce. Carabids were able to track patches with higher seed density in previous studies (H o n ě k , J a r o š í k , 2000; H o n ě k , M a r t i n k o v á , 2001; F r a n k et al., 2011). Data on specific carabid-weed associations from the field are, however, scarce and they usually originate from different fields or from non-crop environments.

In this paper we investigated how the composition of weed assemblage translates in the carabid assemblage composition at a fine scale. The novel approach of this study is that naturally established weed patches within one crop field of maize were investigated, looking at carabid-weed spatial associations at the scale of metres.

MATERIAL AND METHODS

The experiment was located in the Červený Újezd field station of the Czech University of Life Sciences Prague (cca 8 km west of Prague, 50°4´22″N, 14°10´16″E). We used a small patch of the maize crop sizing ca. 20 × 20 m in which high diversity of weed patches could be found. The experiment was conducted between July 20 and September 8, 2009. This period of the year was selected as no agrotechnical operations or agrochemical applications were employed in the crop. In this small patch of maize crop, 40 sampling sites of 1 m^2 were non-randomly selected in a way that all major species of weeds present in that particular maize patch were represented, and were ca. 3–5 m from each other. Phytocoenological samples were taken on each site, and the list of weed species and their relative cover at the ca. ground level was compiled. Plant species were identified according to K u b á t et al. (2002). Sample sites that contained only bare ground at the focal level were also included.

In the centre of each sample site, one pitfall trap was placed. The pitfall traps consisted of one plastic cup (0.33 l volume, orifice diameter 7.5 cm) which was set to 15 cm deep plastic tube dug vertically to the ground, so the orifice of the trap was at level with soil surface and the soil surface remained undisturbed each time the trap was emptied. The traps were half-filled with 30% ethylene-glycol water solution. Each trap was covered with aluminium roof (15 × 15 cm) that prevented from flooding by rainfall. The traps were emptied in weekly intervals on July 27, August 18, and September 8, 2009. Between the periods of collecting the traps were inactivated by pulling the plastic bag over the cup orifice. At the time of emptying, the trap content was poured through a fine sieve (mesh width 0.25 mm), and the trapped arthropods were transferred to 75% ethanol where they remained stored until identified, separately for each trap and date. The carabid beetles were identified according to H ů r k a (1996). The contaminated preservative solution was brought back from the field and disposed.

The data were analyzed using multivariate approach in the CANOCO (Version 4.5, 2002) statistical software for MS Windows. Counts of each carabid species and trap pooled across sample dates were used as response variables. Species that were collected in less than 10 individuals were excluded from the analysis. Relative cover of each weed species on the sample site was used as environmental variables. Four weed species were excluded prior to analysis as they occurred only once or twice. We started the analysis with DCA without including the environmental data, in order to investigate the data structure. As the length of the first gradient was close to 1, RDA was used in the next step (L e p š , Š m i l a u e r , 2003) with particular weed and bare ground cover (on relative scale) for each sample site as environmental variables. The

Table 1. List of species collected in the study site of the maize crop (Červený Újezd, summer 2009). Nomenclature after Hůrka (1996)

Species	Catch size				% catch size
	Total	July 27	Aug 18	Sept 8	
Pseudoophonus rufipes (DeGeer)	2836	604	1557	675	60.4
Pterostichus melanarius (Illiger)	844	380	271	193	18.0
Anchomenus dorsalis (Pontoppidan)	288	272	14	2	6.1
Dolichus halensis (Schaller)	123	33	74	16	2.6
Calathus fuscipes (Goeze)	103	20	48	35	2.2
Calathus ambiguus (Paykull)	79	5	25	49	1.7
Synuchus vivalis (Illiger)	58	21	27	10	1.2
Loricera pilicornis (Fabricius)	54	27	22	5	1.2
Harpalus affinis (Schrank)	39	17	13	9	0.8
Amara aulica (Panzer)	36	2	13	21	0.8
Trechus quadristriatus (Schrank)	33	7	18	8	0.7
Amara bifrons (Gyllenhal)	31	2	21	8	0.7
Poecilus cupreus (Linnaeus)	22	13	5	4	0.5
Bembidion lampros (Herbst)	18	16	2	0	0.4
Carabus granulatus (Linnaeus)	14	7	7	0	0.3
Harpalus atratus (Latreille)	13	3	7	3	0.3
Ophonus azureus (Fabricius)	12	2	4	6	0.3
Harpalus honestus (Duftschmid)	11	7	3	1	0.2
Amara plebeja (Gyllenhal)	10	10	0	0	0.2
Platynus assimilis (Paykull)	10	9	1	0	0.2
Pseudoophonus griseus (Panzer)	10	1	9	0	0.2
Calathus melanocephalus (Linnaeus)	7	6	1	0	0.1
Harpalus tardus (Panzer)	6	4	1	1	0.1
Stomis pumicatus (Panzer)	6	2	4	0	0.1
Brachinus crepitans (Linnaeus)	4	0	1	3	0.1
Amara apricaria (Paykull)	3	0	3	0	0.1
Amara ovata (Fabricius)	3	2	0	1	0.1
Bembidion obtusum Audinet-Serville	3	0	3	0	0.1
Bembidion quadrimaculatum (Linnaeus)	3	1	0	2	0.1
Harpalus distinguendus (Duftschmid)	3	1	2	0	0.1
Carabus nemoralis O.F. Müller	2	1	1	0	0.05
Ophonus (*Metophonus*) sp.	1	0	0	1	0
Agonum muelleri (Herbst)	1	1	0	0	0
Amara convexiscula (Marsham)	1	0	0	1	0
Amara similata (Gyllenhal)	1	0	1	0	0
Anisodactylus binotatus (Fabricius)	1	0	1	0	0
Harpalus signaticornis (Duftschmid)	1	1	0	0	0
Notiophilus palustris (Duftschmid)	1	0	1	0	0
Pterostichus niger (Schaller)	1	1	0	0	0
Total	4692	1478	2160	1054	

carabid catch was log+0.1 transformed to improve the carabid data distribution. Species scores were divided by standard deviance to reduce the influence of dominant species (Ter Braak, Šmilauer, 2002). To increase weight of species well responding to the environmental data, the species data were standardized by error variance (Lepš, Šmilauer, 2003). The significance of individual weed species for the carabid assemblage composition was tested using Monte-Carlo permutation tests (499 iterations) at $\alpha < 0.05$. The correlation of the occurrence of individual carabid species with particular weed species was tested

Table 2. Weed species recorded at the sample sites in maize (Červený Újezd, summer 2009). Nomenclature after Kubát et al. (2002)

Weed species	Number of sample sites where present	Mean cover (%) at sites where present
Veronica persica Poiret	22	35
Echinochloa crus-galli (L.) P.B.	11	37
Viola arvensis Murray	8	38
Fumaria officinalis L.	6	48
Lamium amplexicaule L.	6	30
Chenopodium album L.	5	38
Lolium multiflorum Lamk.	5	74
Persicaria maculosa S.F. Gray	3	30
Poa annua L.	3	27
Convolvulus arvensis L.	2	40
Amaranthus retroflexus L.	1	5
Bromus hordeaceus L.	1	20
Euphorbia helioscopia L.	1	5

Table 3. Environmental variables that significantly affected the carabid assemblage composition in maize, based on the Monte-Carlo permutation tests (Červený Újezd, summer 2009)

Environmental variable	% explained variance	F	P
Bare ground	6.99	2.89	0.002
Viola arvensis	6.25	2.66	0.004
Lolium multiflorum	6.48	2.90	0.006
Persicaria maculosa	5.85	2.75	0.002
Echinochloa crus-gali	3.96	1.91	0.042

Table 4. Associations of individual carabid species with particular species of weeds or bare ground in maize (Červený Újezd, summer 2009). Names of carabid beetles in bold indicate negative response of that species.

Environmental variable	Species with significant response
Chenopodium album	***Calathus ambiguus***
Echinochloa crus-galli	*Pseudoophonus rufipes, Dolichus halensis, Platynus assimilis*
Lamium amplexicaule	*Ophonus azureus, Harpalus honestus*
Lolium multiflorum	*Anchomenus dorsalis, Calathus fuscipes, Synuchus vivalis, Amara aulica*
Poa annua	*Anchomenus dorsalis,* ***Calathus ambiguus***
Persicaria maculosa	*Amara plebeja, Harpalus affinis, Carabus granulatus*
Veronica persica	*Ophonus azureus, Carabus granulatus, Harpalus honestus*
Viola arvensis	*Harpalus affinis, Poecilus cupreus, Harpalus atratus*
Bare ground	***Dolichus halensis**, **Harpalus affinis**, **Calathus fuscipes***

based on the correlation test (df = 38, critical level of r at α < 0.05 = 0.318) (Z a r, 1999).

RESULTS

Altogether 4692 individuals of 39 species were found, eight of which were found in only 1 individual (Table 1). Three species (*Pseudoophonus rufipes*, *Pterostichus melanarius,* and *Anchomenus dorsalis*) dominated the assemblage as each constituted more than 5% of the total catch (Table 1).

Thirteen weed species (plus bare ground) were documented on the study sites, among which *Veronica persica*, *Echinochloa crus-galli*, and *Viola arvensis* were the most frequently represented. The number of sites and the relative coverage for each of the weed species can be found in Table 2.

RDA proved that the composition of the weed assemblage around the trap influenced the carabid assemblage composition in the pitfall catch. The first two axes explained 20.9% of the variance in the species data and 49.7% of the variance in the fitted species data, and the first three axes altogether explained

27.5% of the variance in the species data and 65.3% of the variance in the fitted species data. We found that the relative cover of four species of weeds and relative proportion of bare ground on the sample sites significantly affected the carabid assemblage in the traps, based on the Monte-Carlo permutation tests (Table 3). Bare ground explained the biggest part of the variance in the data, followed by *V. arvense* and *L. multiflorum* (Table 3). Correlation analysis of the species-specific responses revealed numerous carabid associations with weeds cover and bare ground, both negative and positive (Table 4). More interestingly, associations of carabids and weeds were found also for weed species which did not show an overall significant effect (Table 4). The two-dimensional projection of placement of individual carabid species in the multidimensional space of environmental variables is visualized in Fig. 1 for the first two canonical axes and in Fig. 2 for axes 1 and 3. Displaying these two graphs better visualizes the observed associations of carabids and weeds reported in Table 4.

DISCUSSION

The sampled assemblage of carabid beetles was typical of Central European maize field (T h i e l e , 1977; L ö v e i , 1984; H o l l a n d , 2002), dominated only by a limited number of species. All species recorded are characteristic inhabitants of arable land and adjacent non-crop habitats, and are ranked as eurytopic or adaptable by H ů r k a et al. (1996). What may deserve attention is that the species number is relatively high for the sampled area of 400 m², but this may be due to rather high sampling effort combined with high diversity of microhabitats within the study site. This is indeed supportive for the fact that carabid beetles benefit from weed presence in the fields.

The foraging range of many species recorded in this study is much larger than the sampled area (T h i e l e 1977). Despite that we found that carabid beetles distribute themselves within a habitat such as a small arable field even at the scale of metres, and that the variation in species composition at microscale can be explained by the variation in weed assemblage composition and therefore cannot be viewed as the result of random foraging behaviour. This is the major discovery of this paper. In previous studies it was found for carabid beetles that species composition in a habitat can be predicted by the composition of plant community (S c h a f f e r s et al., 2008), or that
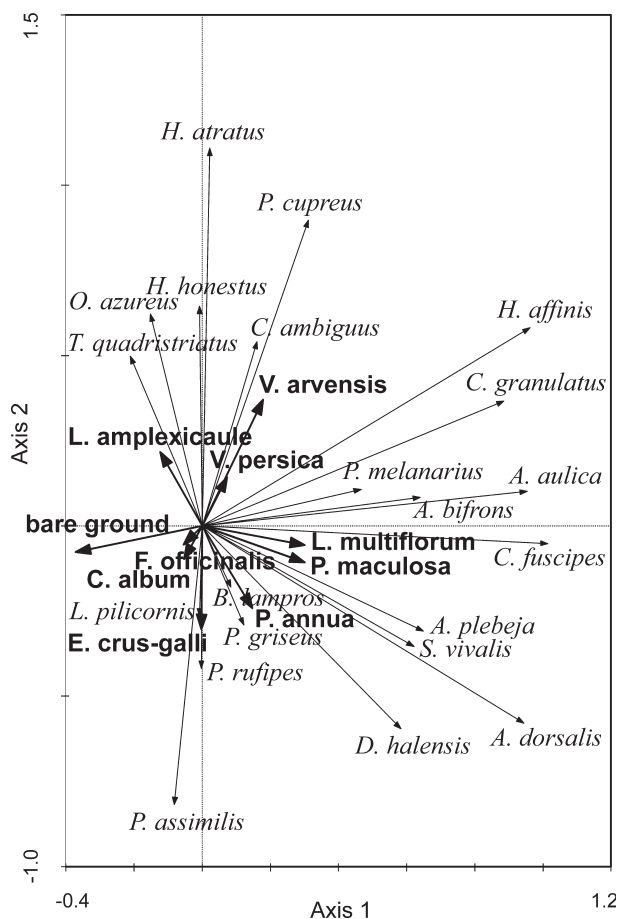

Fig. 1. RDA bi-plot (first and second canonical axes) of the effect of composition of weed assemblage on carabid species composition. Full names of carabids and plants can be found in Tables 1 and 2, respectively.
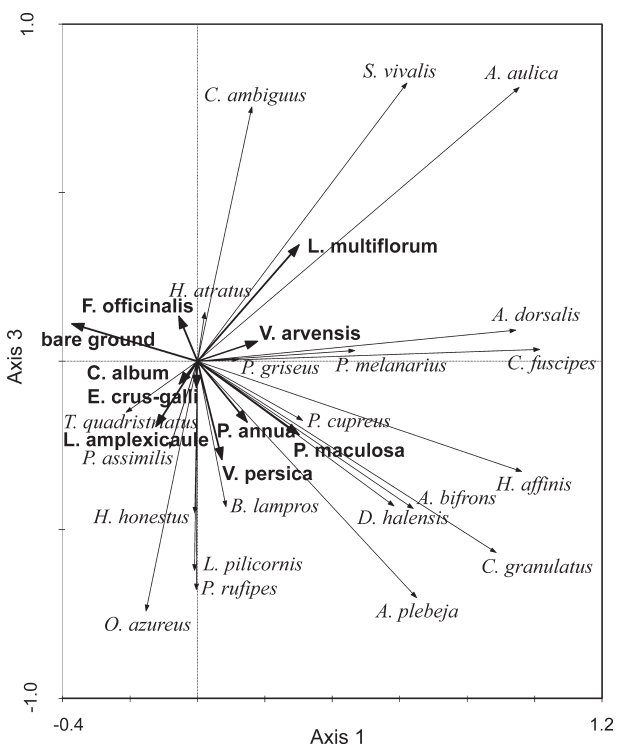

Fig. 2. RDA bi-plot (first and third canonical axes) of the effect of composition of weed assemblage on carabid species composition. Full names of carabids and plants can be found in Tables 1 and 2, respectively.

differences in weed cover composition affect carabid species composition among the fields (e.g. P a v u k et al., 1997; D i e h l et al., 2012). It was shown by S a s k a (2008a) that patches of particular weeds hosted a typical carabid assemblage, but the patches in that particular study were spatially unrelated and distant. The observed relationship between weed and carabid assemblages at the scale of metres within the same maize field is thus a new result.

In our study, some of the weed species were more decisive for the composition of carabid assemblages than others. This fully conforms to the previous observations that the diversity of associated herbivorous insects, including granivorous carabids, considerably varies among the species of weeds (W a r d, S p a l d i n g, 1993; C a m p o b a s s o et al., 1999; S a s k a, 2008a). Bare ground also significantly affected the carabid assemblages at the scale of our experiment, mostly negatively. This is not surprising as the negative response of carabid assemblages to the bare ground in agroecosystems has substantial literature support (e.g. P a v u k et al., 1997; H o n ě k, J a r o š í k, 2000; D i e h l et al., 2012). As clearly demonstrated by D i e h l et al. (2012), carabid beetles respond both to habitat structure and to habitat-mediated resources, such as food. However, each of the carabid species significantly associated with some of the microhabitats in our study will respond to different cues, based on its trophic specialization.

We identified 29 significant correlations of carabid catch size with relative coverage of particular weed species or bare ground, both positive and negative. Bare ground appeared to be clearly unsuitable environment for carabids in our study, as all significant associations with it were negative. Interestingly, significant associations of carabids with weeds were found also for species which have not been reported as granivores previously, such as *D. halensis* or *S. vivalis*. We assume that these species responded to more favourable microclimatic conditions under the weed plants. Alternatively, these species may include seeds in their diets, or profit from higher concentration of other arthropods which they feed on. We may only speculate on this as the trophic requirements of these species remain unknown. Having closer look at the nature of these associations may represent a new direction for research on ecology of these species. Undoubtedly several carabid-weed correlations are in line with known trophic associations between the carabid and the weed (e.g. *P. rufipes* with *E. crus-galli*, or *H. affinis* and *H. atratus* with *V. arvensis*), and have support in the literature (e.g. H a r t k e et al., 1998; H o n ě k et al., 2007). In other cases the associations of granivorous species with weeds may indicate new trophic relationships and deserve further investigations (e.g. *O. azureus* with *L. amplexicaule* and *V. versica*).

We admit that a caveat of this study was the timing in the middle of the summer, so only weed species that grow/produce seeds, and carabids that occur/reproduce in that period could be studied. This was caused by the fact that we had to wait with placing our traps for the period without any agricultural practices taking place in the study field. As the weed community and carabid assemblages change with season (T h i e l e, 1977; P a v u k et al., 1997; Z i m d a h l, 2004), we probably missed several important interactions among spring weed and carabid species as a consequence of this limitation.

CONCLUSION

In conclusion, we documented notable spatial differences in species composition of carabid assemblages within a small maize field, and these differences can be explained by the variable structure of weed community in this field. Such spatial segregation in diverse environment may increase resource partitioning, reduce intraguild predation (J a n s s e n et al., 2007), and consequently facilitate coexistence of more diverse carabid assemblages in arable fields. This, besides being a value itself from the perspective of biodiversity conservation, fosters the ecosystem services that carabid beetles provide to farmers (e.g. S u n d e r l a n d, 2002; B o h a n et al., 2011), including pest and seed predation.

REFERENCES

Andreasen C, Stryhn H, Streibig JC (1996): Decline of the flora in Danish arable fields. Journal of Applied Ecology, 33, 619–626. doi: 10.2307/2404990.

Birkhofer K, Fliessbach A, Wise DH, Scheu S (2008): Generalist predators in organically and conventionally managed grass-clover fields: implications for conservation biological control. Annals of Applied Biology, 153, 271–280. doi: 10.1111/j.1744-7348.2008.00257.x.

Bohan DA, Boursault A, Brooks DR, Petit S (2011): National-scale regulation of the weed seedbank by carabid predators. Journal of Applied Ecology, 48, 888–898. doi: 10.1111/j.1365-2664.2011.02008.x.

Brant V, Pivec J, Venclova V, Soukup J, Holec J (2006): The influence of different soil vegetation covers onto the volumetric water content in upper soil layers. Plant, Soil and Environment, 52, 275–281.

Campobasso C, Colonnelli E, Knutson L, Terragitti G, Cristofaro M (1999): Wild plants and their associated insects

in the Palearctic Region, Primarily Europe and the Middle East. U.S. Department of Agriculture, Agricultural Research Service, Washington.

Diehl E, Wolters V, Birkhofer K (2012): Arable weeds in organically managed wheat fields foster carabid beetles by resource- and structure-mediated effects. Arthropod–Plant Interactions, 6, 75–82. doi: 10.1007/s11829-011-9153-4.

Frank SD, Shrewsbury PM, Denno RF (2011): Plant versus prey resources: influence on omnivore behavior and herbivore suppression. Biological Control, 57, 229–235. doi: 10.1016/j.biocontrol.2011.03.004.

Franke AC, Lotz LAP, van der Burg WJ, van Overbeek L (2009): The role of arable weed seeds for agroecosystem functioning. Weed Research, 49, 131–141. doi: 10.1111/j.1365--3180.2009.00692.x.

Hartke A, Drummond FA, Liebman M (1998): Seed feeding, seed caching, and burrowing behaviors of *Harpalus rufipes* De Geer larvae (Coleoptera: Carabidae) in the Maine Potato Agroecosystems. Biological Control, 13, 91–100.

Hawthorne A, Hassall M (1995): The effect of cereal headland treatments on carabid communities. In: Toft S, Riedel W (eds): Arthropod natural enemies in arable land I. Density, spatial heterogeneity and dispersal. Acta Jutlandica, 70, 185–198.

Holland JM (2002): The agroecology of carabid beetles. 1st Ed. Intercept Ltd., Andover.

Holland JM, Perry JN, Winder L (1999): The within-field spatial and temporal distribution of arthropods in winter wheat. Bulletin of Entomological Research, 89, 499–513. doi: 10.1017/S0007485399000656.

Holland JM, Hutchison MAS, Smith B, Aebischer NJ (2006): A review of invertebrates and seed-bearing plants as food for farmland birds in Europe. Annals of Applied Biology, 148, 49–71. doi: 10.1111/j.1744-7348.2006.00039.x.

Holland JM, Smith BM, Birkett TC, Southway S (2012): Farmland bird invertebrate food provision in arable crops. Annals of Applied Biology, 160, 66–75. doi: 10.1111/j.1744--7348.2011.00521.x.

Honěk A, Jarošík V (2000): The role of crop density, seed and aphid presence in diversification of field communities of Carabidae (Coleoptera). European Journal of Entomology, 97, 517–525. doi: 10.14411/eje.2000.080.

Honěk A, Martinková Z (2001): Aggregation of ground beetles (Carabidae, Coleoptera) on winter rape seeds dispersed on the ground. Plant Protection Science, 37, 97–102.

Honěk A, Martinková Z, Saska P (2005): Post-dispersal predation of *Taraxacum officinale* (dandelion) seed. Journal of Ecology, 93, 345–352. doi: 10.1111/j.1365--2745.2005.00987.x.

Honěk A, Martinková Z, Saska P, Pekár S (2007): Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). Basic and Applied Ecology, 8, 343–353. doi: 10.1016/j.baae.2006.07.002.

Hůrka K (1996): Carabidae of the Czech and Slovak Republics. 1st Ed. Kabourek, Zlín. (in Czech)

Hůrka K, Veselý P, Farkač J (1996): The use of ground beetles (Coleoptera: Carabidae) as indicators of environmental quality. Klapalekiana, 32, 15–26. (in Czech)

Janssen A, Sabelis MW, Magalhaes S, Montserrat M, Van der Hammen T (2007): Habitat structure affects intraguild predation. Ecology, 88, 2713–2719. doi: 10.1890/06-1408.1.

Kokta C (1988): C. Bezeihungen zwischen der Verunkratung und Phytophagen Laufkäfern der Gattung *Amara*. Mitteilungen aus der Biologischen Bundesanstalt fur Land- und Forstwirtschaft Berlin-Dahlem, 247, 139–145.

Kromp B (1990): Carabid beetles (Coleoptera, Carabidae) as bioindicators in biological and conventional farming in Austrian potato fields. Biology and Fertility of Soils, 9, 182–187.

Kubát K, Hrouda L, Chrtek jun. J, Kaplan Z, Kirschner J, Štěpánek J (2002): The key to the flora of the Czech Republic. 1st Ed. Academia, Praha. (in Czech)

Lepš J, Šmilauer P (2003): Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.

Lövei GL (1984): Ground beetles (Coleoptera, Carabidae) in two types of maize fields in Hungary. Pedobiologia, 26, 57–64.

Marshall EJP, Brown VK, Boatman ND, Lutman PJW, Squire GR, Ward LK (2003): The role of weeds in supporting biological diversity within crop fields. Weed Research, 43, 77–89. doi: 10.1046/j.1365-3180.2003.00326.x.

Moreby SJ, Southway SE (1999): Influence of autumn applied herbicides on summer and autumn food available to birds in winter wheat fields in southern England. Agriculture Ecosystems and Environment, 72, 285–297. doi: 10.1016/S0167-8809(99)00007-9.

Norris RF, Kogan M (2000): Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems. Weed Science, 48, 94–158. doi: 10.1614/0043-1745(2000)048%5B0094:IBWAPA%5D2.0.CO;2

Pavuk DM, Purrington FF, Williams CE, Stinner BR (1997): Ground beetle (Coleoptera: Carabidae) activity density and community composition in vegetationally diverse corn agroecosystems. American Midland Naturalist, 138, 14–28. doi: 10.2307/2426650.

Powell W, Dean GJ, Dewar A (1985): The influence of weeds on polyphagous arthropod predators in winter wheat. Crop Protection, 4, 298–312. doi: 10.1016/0261-2194(85)90032-8.

Saska P (2008a): Composition of weed community determines carabid assemblage. Back to the roots or back to the future. In: Penev L, Erwin TL, Assmann T (eds): Towards a new synthesis amongst taxonomic, ecological and biogeographical approaches in carabidology. 1st Ed. Pensoft, Sofia, 339–351.

Saska P (2008b): Effect of diet on the fecundity of three carabid beetles. Physiological Entomology, 33, 188–192. doi: 10.1111/j.1365-3032.2008.00618.x.

Saska P, Van der Werf W, de Vries E, Westerman PR (2008): Spatial and temporal patterns of carabid activity-density in cereals do not explain levels of predation on weed seeds. Bulletin of Entomological Research, 98, 169–181. doi: 10.1017/S0007485307005512.

Schaffers AP, Raemakers IP, Sykora KV, Ter Braak CJF (2008): Arthropod assemblages are best predicted by plant species composition. Ecology, 89, 782–794. doi: 10.1890/07-0361.1.

Speight MR, Lawton JH (1976): The influence of weed cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. Oecologia, 23, 211–223. doi: 10.1007/BF00361237.

Storkey J (2006): A functional group approach to the management of UK arable weeds to support biological diversity. Weed Research, 46, 513–522. doi: 10.1111/j.1365-3180.2006.00528.x.

Sunderland KD (2002): Invertebrate pest control by carabids. In: Holland JM (ed.): The agroecology of carabid beetles. 1st Ed. Intercept, Andover, 165–214.

Ter Braak CJF, Šmilauer P (2002): CANOCO Reference Manual and CanoDraw for Windows User's Guide. Software for Canonical Community Ordination (Version 4.5). Biometris, Wageningen, Ceske Budejovice.

Thiele H-U (1977): Carabid beetles in their environments. 1st Ed. Springer-Verlag, Berlin.

Ward LK, Spalding DF (1993): Phytophagous British insects and mites and their food-plant families – total numbers and polyphagy. Biological Journal of the Linnean Society, 49, 257–276. doi: 10.1006/bijl.1993.1036.

Zar JH (1999): Biostatistical analysis. 4th Ed. Prentice-Hall, New Jersey.

Zimdahl RL (2004): Weed-crop competition. 2nd Ed. Blackwell Publishing, Oxford.

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