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Beneficial arthropods respond differentially to wildflower areas of different age

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We investigated the response of predatory spiders, carabids, staphylinids and heteropteran bugs to the age of wildflower areas at twenty 1- to 4-year-old wildflower sites and in wheat fields. Density, biomass and species richness of spiders, carabids and bugs increased with the age of wildflower sites, and were higher at older wildflower sites than in the wheat fields. In contrast, staphylinid density decreased significantly with the age of wildflower sites. Canonical correspondence analysis explained 42.4% and 46.7% of the total variance of spider and carabid assemblages, respectively. Spider and carabid assemblages were best explained by vegetation cover. Mean individual weights of spiders, carabids and staphylinids increased significantly with the age of wildflower sites. The positive response of these three groups of beneficials is of practical relevance because many farmers currently remove wildflower areas after two to three years of establishment. Thus, older stages of succession increase the numbers of most beneficials studied.

Introduction

To counteract the dramatic loss of species in cultivated landscapes and to prevent overproduction, set-aside programmes have been established in the European Union (Kleijn *et al.* 2001, Marshall & Moonen 2002, Bianchi *et al.* 2006, Olson & Wäckers 2007). Wildflower areas (a term synonymous with wildflower or weed strips) are one type of such semi-natural habitats designed to enhance both arthropod diversity and numbers of beneficials, i.e. predatory arthropods and insect parasitoids, in agroecosystems. Wildflower areas have been gradually introduced into the European agricultural landscape over the last decade (Nentwig 2000). They are sown with a mixture of wild, arable plant species. Typically, wildflower areas are sown either inside fields or along their edges and are maintained up to six years, thereby passing through the early stages of secondary succession.

There is a current debate involving farmers and decision makers on whether or not wildflower areas help enlarge populations of beneficial arthropods with increasing age. Therefore, one objective of the present study was to investigate the density, biomass and species richness of arthropod predators (Araneae, Carabidae, Staphylinidae, Heteroptera) at 1- to 4-year-old wildflower sites and in winter wheat fields representing the most widespread crop in Switzerland. These groups were examined because they are amongst the most abundant polyphagous predatory arthropods and are important natural control agents of agricultural pests (Duelli *et al.* 1999, Bohan *et al.* 2000, Thomas *et al.* 2001, Collins *et al.* 2002, Symondson *et al.* 2002, Schmidt *et al.* 2003, Holland *et al.* 2005). A further objective was to examine the influence of soil and environmental parameters on spider and carabid assemblages. Increasing vegetation cover and water content during early succession are expected to affect various epigeic species differently, and large soil pores can provide space for epigeic arthropods to hide and gain protection from desiccation or predation (e.g. Sotherton 1985, Kromp 1999). Landscape structure surrounding the fields can be a major factor determining diversity and density of epigeic predatory spiders and carabid beetles (Purtauf *et al.* 2005, Schmidt *et al.* 2005, Drapela *et al.* 2008), and there are contradictory observations regarding the impact of field size on epigeic spiders and carabids (Holland *et al.* 2005, Bolger *et al.* 2008, Galle 2008).

By offering a great variety of food resources, shelter and overwintering places, wildflower areas have been shown to increase the numbers of several beneficial predatory arthropod groups (Lys & Nentwig 1994, Lys *et al.* 1994, Zurbrügg & Frank 2006). In particular, the density of overwintering carabid and staphylinid beetles as well as the fitness and reproduction of common arable carabids were observed to increase with increasing age of wildflower areas (Barone & Frank 2003, Frank & Reichhart 2004, Frank *et al.* 2007), increasing the potential of biological control of agricultural pests. However, we know nothing about the density, biomass and species richness of predatory arthropods in response to the age of wildflower areas during summer months. Although there are contradictory findings on the responses of arthropods to succession (e.g. Siemann *et al.* 1999, Steffan-Dewenter & Tscharntke 2001, Krauss *et al.* 2009), overall arthropod diversity likely increases with succession (Corbet 1995). Accordingly, we expect that the density, biomass and species richness of predatory spiders and insects will increase with the age of wildflower areas due to advancing structural complexity of the vegetation (Günter 2000) and the absence of disturbance by farming activities, i.e. tillage, harvesting and pesticide application. The absence of disturbance by farming activities is expected to provide favourable conditions for development enabling arthropod predators to build up large populations over time. In particular, epigeic spider, and carabid and staphylinid beetle numbers may increase with time if there is no soil management and pesticide application (White & Hassall 1994, Hummel *et al.* 2002, Kotze & O'Hara 2003, Balog & Marko 2007), and heteropteran bugs inhabiting the vegetation layer may profit from advancing structural complexity of the vegetation and the lack of both cutting and pesticide application (Di Giulio *et al.* 2001, Albajes *et al.* 2003). Based on the theory of secondary succession, which states that species richness should increase and assemblage composition should change with successional age (Brown & Southwood 1987), it is hypothesized that (i) the density, biomass and species richness of predatory spiders, carabid beetles, staphylinid beetles and zoophagous heteropterans will increase with advancing age, and that these parameters will be higher in wildflower areas than in winter wheat fields, and (ii) individual spider and carabid species will respond differentially to the soil and environmental parameters measured.

Materials and methods

Study area and sites

The study was carried out from May to July 2001 at 20 study sites around Bern (Swiss plateau) and Solothurn (Bucheggberg). The study area was situated in an intensively used arable region in Switzerland of about 430 km^2, at an altitude of 480–655 m a.s.l. The study sites were in the same climatic zone, providing similar site conditions in terms of altitude, mean annual rainfall and temperature. The sites belonged to five habitat types (1-, 2-, 3-, 4-year-old wildflower sites, winter wheat fields) with four replicates each. Winter wheat (WW) is the most widespread crop in Switzerland and served as a control for a typical arthropod community in the agricultural landscape. It was managed following the guidelines for integrated production. None of the four winter wheat fields were sprayed with insecticides, and maize had been the previous crop on all of them. The studied wildflower sites were adjacent to crop fields and grew on land formerly cultivated with cereals. Wildflower sites were sown with a recommended mixture containing 25 native arable weeds, meadow and ruderal plants (Günter 2000), but not fertilized or treated with pesticides. The four 1-year-old wildflower sites (WA1) were sown in the first week of May 2001. These sites were, therefore, not one year old yet, but in their first year of establishment. The four 2-year-old wildflower sites (WA2) were sown in spring 2000. The four 3-year-old wildflower sites (WA3) were sown in spring 1999, and the 4-year-old sites (WA4) in spring 1998. We were unable to investigate wildflower sites older than four years because, from the fourth year onwards, grassy vegetation begins to dominate and farmers usually remove them. The wildflower sites of different age and the winter wheat fields were intermingled within the research area to avoid spatial autocorrelation. The five habitat types ranged from 0.2 ha to 2.7 ha in size, with a mean of 0.8 ha, and a minimum distance of 500 m between sites.

Sampling of epigeic predatory arthropods

For epigeic predators, the present work focused on estimating their density and biomass per m^2. Therefore, photo-eclectors were preferred over pitfall traps. The authors are aware that this method as compared with pitfall traps captures fewer species (Mosimann 2002). Three eclectors were used per study site; they were placed 20 m apart in the central part of each site. The eclectors were cone-shaped funnels made of fibre cement and inserted 2 cm into the soil to prevent arthropods from escaping or immigrating. Eclectors had a height of 46 cm and covered an area on the surface of 0.21 m^2 (diameter = 52 cm). One pitfall trap (68 mm diameter, 74 mm depth, filled with 4% formaldehyde plus 0.5% detergent) was installed in the centre of each eclector. A round transparent plastic box filled with 4% formaldehyde plus 0.5% detergent was placed on the top of each eclector to catch animals flying and crawling towards the light. The eclectors were deployed for an initial run of one month, then replaced for a second one-month period. Accordingly, spiders and carabid and staphylinid beetles were collected from mid-May to mid-July 2001. This time span was determined by the date of establishment of the 1-year-old wildflower sites (first week of May) and the harvest of the wheat fields, which was conducted after the end of the sampling period (mid-July). Arthropods captured in the plastic boxes and pitfall traps were stored in 70% ethanol. The carabids and spiders of each eclector were counted and determined to species level; staphylinids were only counted. For biomass determinations, arthropods were removed from the ethanol, dried on blotting paper at room temperature and weighed. The total number of species found per site and the means for individuals and biomass per m^2 were used in the statistical analyses.

Sampling of predatory heteropterans inhabiting the vegetation layer

Zoophagous heteropteran bugs (i.e. predators including phyto-zoophagous) were sampled four times between mid-May and mid-July 2001 using a standardised sweep-net method (Otto 1996). The sampling order of the sites varied between sampling dates. Sampling was restricted to periods favourable for insect activity, i.e.

between 10:00 and 17:30 when the minimum air temperature was 15 °C, it was sunny and not windy, and the vegetation was dry. The sweep-net had a diameter of 40 cm and was fitted with a heavy cloth net suitable for use in coarse vegetation. For each of the four samples per study site, 100 sweeps were drawn through the vegetation at a constant pace along a transect of 80 m. The insects were killed immediately in the field with diethylether ($C_4H_{10}O$). The minimum distance of a transect from the site edge was 3 m. The first and second transects were parallel. The third and fourth transects were selected in a prolongation of the first and second transects. The density of bugs was based on numbers of adults and larvae per site, and species richness was based on the number of adult bug species per site.

Soil and environmental parameters

Soil and environmental parameters (= habitat parameters), which were shown to be important for the distribution of epigeic predatory arthropods in agroecosystems (Baker & Dunning 1975, Thiele 1977, Holopainen *et al.* 1995, Pfiffner & Luka 2000) were recorded to examine their influence on spider and carabid assemblages. In terms of vegetation cover, the proportion of bare ground and vegetation (dead and green material) covering the soil surface was estimated three times in late May, mid-June and early July 2001 at six randomly selected places per site. For each estimation, a 25 × 25 cm metal frame was placed on the ground, within which the vegetation was cut off 5 cm above the ground level to observe the actual cover on the surface. Samples were pooled over time resulting in one sample per site.

The volume of large pores in the soil was determined by taking five cylindrical soil samples (diameter = 5 cm; depth = 10 cm) at each study site in December 2000. The soil samples were soaked with water and the water content (% of volume) was measured with a time-domain-reflectometry (TDR)-probe (supplier: DMG AG, Fehraltorf, Switzerland) in the laboratory. Afterwards the samples were left to dry for 15 min (to let the air back into the larger pores) and the water content was measured again. The difference between the two measurements gave the percentage pore volume in the upper 10 cm of the soil. Sand content was measured from five soil samples per site, taken in December 2000. These were dried for seven days, and the large particles removed with a 2 mm-sieve. The remaining material (< 2 mm) was separated using a "wet siever" to determine the proportion of fine, medium and coarse sand (fine sand: particle size = 63–200 μm, medium sand: = 200–630 μm, coarse sand: = 630–2000 μm). The three fractions were weighed after drying and the percentages of fine and coarse sand were used in further analyses. The soil methods used follow Brucker and Kalusche (1976), Janetschek (1982), Kuntze *et al.* (1988) and Dunger and Fiedler (1997).

Field size, expressed as the area (in ha) of each study site, and the surrounding landscape structure were mapped in spring 2001. The latter measured the area of semi-natural habitats (extensively managed meadows, sown wildflower areas, ruderal areas, orchards, hedges, and forest) in a 150 m wide radius around each site.

Statistical analysis

One-way ANOVA was used to test for (1) differences in the density, biomass and species richness of epigeic spiders and carabids, (2) differences in the density and biomass of epigeic staphylinids, (3) differences in the density and richness of hypergeic bugs, and (4) differences in the individual weights of epigeic spiders, carabids and staphylinids among the five habitat types (individual weight = biomass/number of individuals). Tukey's HSD test was carried out for multiple comparisons. Where ANOVA revealed no significance ($p > 0.05$), contrasts between groups of interest were calculated to test for general group effects. Spearman's correlation coefficient was used to assess the relationship between successional age and arthropod density, biomass, species richness and individual weights of epigeic spiders, carabids and staphylinids. Here, wheat fields were excluded from the analysis as they were not part of the successional gradient of wildflower sites. All statistical procedures were carried out with SPSS 15.0. Canonical correspondence analysis (CCA) was

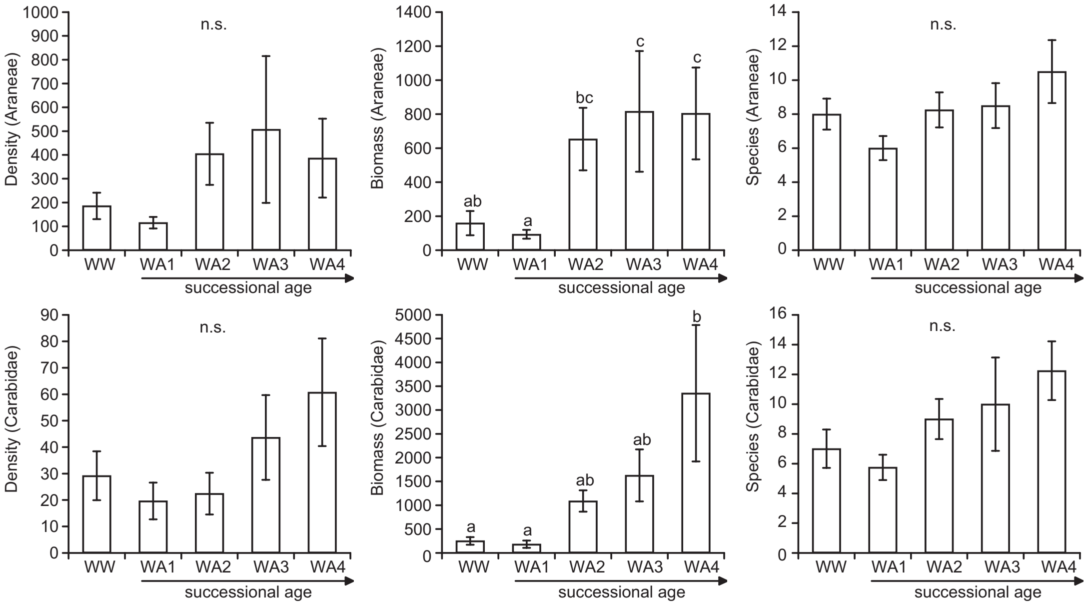

Fig. 1. Density, biomass and species richness of Araneae and Carabidae (mean ± SE) at winter wheat fields (WW) and 1- to 4-year-old wildflower sites (WA1–WA4). Different letters denote significant differences between habitat types (Tukey: $p < 0.05$, $n = 20$), n.s. = not significant. Arrows indicate the successional gradient for correlation analyses.

performed to characterize the spider and carabid assemblages relative to habitat parameters using Canoco 4.5 (Ter Braak & Smilauer 2002). The habitat parameters were standardized to z values and the number of individuals of each species was log-transformed ($y = \log_{10}[x + 1]$). Species represented by fewer than five individuals were omitted to minimise random effects and sampling errors (Pfiffner & Luka 2003). Thus, only the 19 most abundant spider and 22 carabid species were used in CCA. CCA was not performed for staphylinids as they were not determined to the species level. The response of bug assemblages to habitat parameters, including the predatory species considered in this work, is reported elsewhere (Frank & Künzle 2006).

Results

Spiders

Spider density did not differ significantly between any of the habitats (ANOVA: $F_{4,15} = 0.953$, $p = 0.461$, $n = 20$; Fig. 1). When testing for a general group effect, however, the comparison of 1- with 2- to 4-year-old wildflower sites revealed that spider density in the former was significantly lower than in the latter ($t = 2.500$, $p = 0.045$). Moreover, there was no significant correlation between spider density and age of wildflower sites (Spearman $r_s = 0.279$, $p = 0.269$, $n = 16$). Spider biomass was significantly lower at 1-year-old as compared with that at older wildflower sites (Fig. 1) and was significantly positively correlated with age ($r_s = 0.618$, $p = 0.011$, $n = 16$). The mean individual weight of spiders did not differ significantly among habitats, but increased significantly with the age of wildflower sites (Tables 1 and 2). There was no significant difference in spider species richness between any of the habitats ($F_{4,15} = 1.694$, $p = 0.204$, $n = 20$; Fig. 1), although richness responded significantly positively to the age of wildflower areas ($r_s = 0.550$, $p = 0.027$, $n = 16$). The spider assemblage was examined relative to habitat parameters using CCA, which explained 42.4% of the total variance (Fig. 2). Of the seven habitat parameters considered, only vegetation cover contributed significantly to the distribution of spiders, accounting for 14.8% of the variance. The remaining variance was explained by the

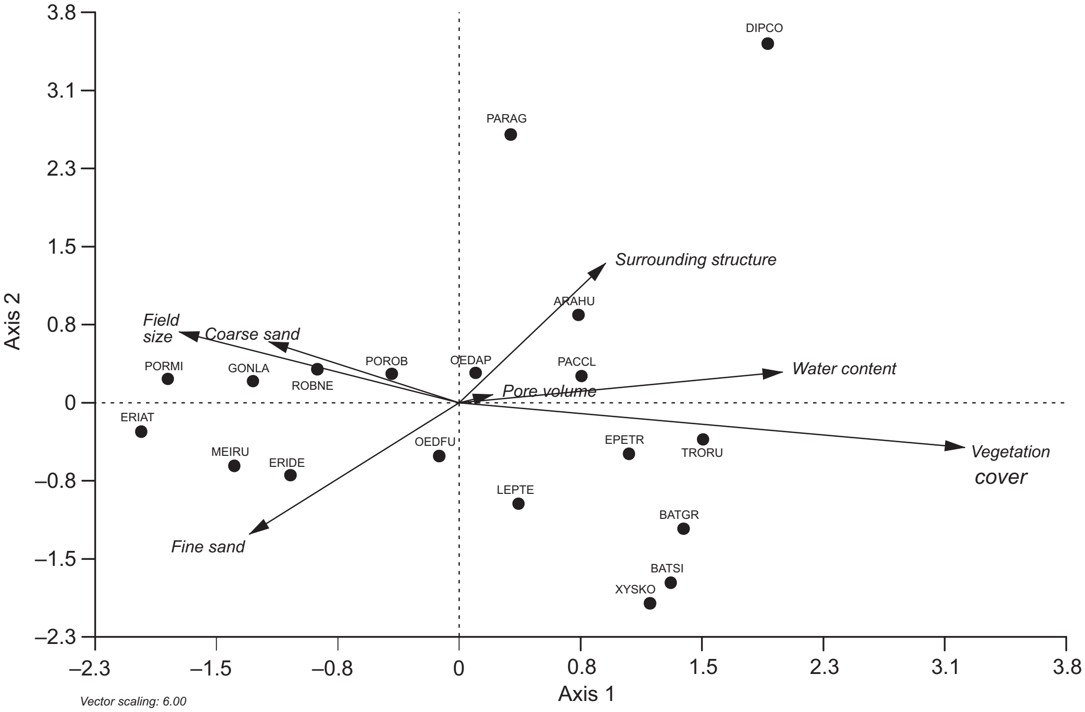

Fig. 2. Canonical correspondence analysis (CCA) showing the relation between the spider assemblage, based on the most abundant species, and habitat parameters. Species abbreviations: ARAHU = *Araeoncus humilis*, BATRGR = *Bathyphantes gracilis*, BATSI = *Bathyphantes similis*, DIPCO = *Diplostyla concolor*, EPETR = *Eperigone trilobata*, ERIAT = *Erigone atra*, ERIDE = *Erigone dentipalpis*, GONLA = *Gonglydiellum latebricola*, LEPTE = *Lepthyphantes tenuis*, MEIRU = *Meioneta rurestris*, OEDAP = *Oedothorax apicatus*, OEDFU = *Oedothorax fuscus*, PACCL = *Pachygnatha clercki*, PARAG = *Pardosa agrestis*, PORMI = *Porrhomma microphthalmus*, POROB = *Porrhomma oblitum*, ROBNE = *Robertus neglectus*, TRORU = *Trochosa ruricola*, XYSKO = *Xysticus kochi*. Explained variation by axis 1: 16.6%, and by axis 2: 8.7%. Habitat parameters most strongly correlated with axis 1: vegetation cover (0.843) and water content (0.539), and with axis 2: surrounding landscape structure (0.437).

Table 1. Individual weights of Araneae, Carabidae and Staphylinidae (mean ± SE, g m^{-2}) in winter wheat fields (WW) and 1- to 4-year-old wildflower sites (WA1–WA4). Different letters in the same line denote significant differences between habitat types (Tukey; $p < 0.05$). ns = not significant.

Arthropod group	WW	WA1	WA2	WA3	WA4
Araneae	0.76 ± 0.10^{ns}	0.81 ± 0.25^{ns}	2.28 ± 0.98^{ns}	3.07 ± 0.86^{ns}	4.07 ± 1.69^{ns}
Carabidae	9.77 ± 1.80^{a}	10.43 ± 5.42^{a}	59.29 ± 13.81^{b}	35.02 ± 8.71^{ab}	49.99 ± 6.98^{b}
Staphylinidae	2.13 ± 0.32^{ns}	1.35 ± 0.24^{ns}	1.96 ± 0.31^{ns}	2.89 ± 0.85^{ns}	6.56 ± 2.68^{ns}

Table 2. Correlation (Spearman r_s) between mean individual weights of arthropods (Araneae, Carabidae and Staphylinidae), and age of 1- to 4-year-old wildflower sites.

Arthropod group	r_s	p
Araneae	0.521	0.038
Carabidae	0.570	0.021
Staphylinidae	0.740	0.001

other parameters. A group of species (*Trochosa ruricola*, *Eperigone trilobata*, *Bathyphantes gracilis*) was preferentially or exclusively found at wildflower sites older than one year of age (Appendix 1) and were strongly correlated with vegetation cover. *Erigone atra* and *Porrhomma microphthalmum* revealed an opposite distribution. They were most abundant in winter wheat fields and were related to field size.

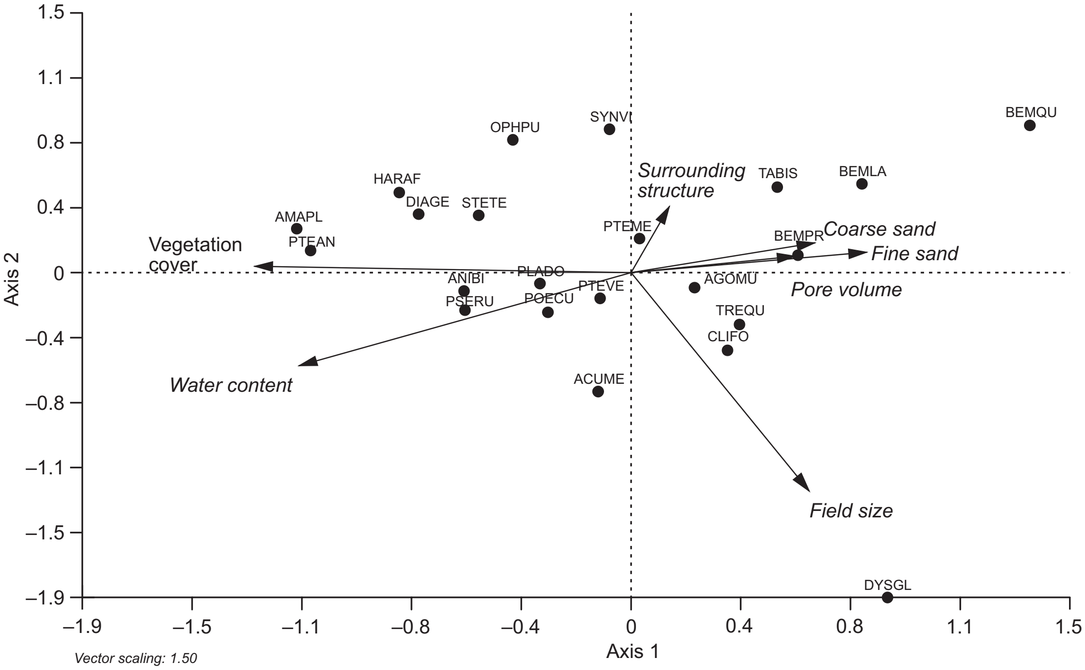

Fig. 3. Canonical correspondence analysis (CCA) showing the relation between the carabid assemblage, based on the most abundant species, and habitat parameters. Species abbreviations: ACUME = *Acupalpus meridianus*, AGOMÜ = *Agonum mülleri*, AMAPL = *Amara plebeja*, ANIBI = *Anisodactylus binotatus*, BEMLA = *Bembidion lampros*, BEMPR = *Bembidion properans*, BEMQU = *Bembidion quadristriatus*, CLIFO = *Clivina fossor*, DYSGL = *Dyschirius globosus*, DIAGE = *Diachromus germanus*, HARAF = *Harpalus affinis*, OPHPU = *Ophonus puncticeps*, PLADO = *Platynus dorsalis*, POECU = *Poecilus cupreus*, PSERU = *Pseudophonus rufipes*, PTEAN = *Pterostichus anthracinus*, PTEME = *Pterostichus melanarius*, PTEVE = *Pterostichus vernalis*, STETE = *Stenolophus teutonus*, SYNVI = *Synuchus vivalis*, TABIS = *Tachys bistriatus*, TREQU = *Trechus quadristriatus.* Explained variation by axis 1: 17.0%, and by axis 2: 10.5%. Habitat parameters most strongly correlated with axis 1: vegetation cover (–0.875) and water content (–0.756), and with axis 2: field size (–0.854).

Carabid beetles

Carabid density did not differ significantly between the habitat types ($F_{4,15}$ = 1.679, p = 0.207, n = 20; Fig. 1) but did increase significantly with advancing age of wildflower sites (r_s = 0.570, p = 0.021, n = 16). Significant differences were found in carabid biomass among the five habitat types ($F_{4,15}$ = 5.427, p = 0.007, n = 20; Fig. 1). Tukey's post-hoc test showed a significantly higher biomass at the 4-year-old *versus* 1-year-old wildflower sites and in wheat fields (p = 0.008 and p = 0.035, respectively). Biomass increased significantly with successional age (r_s = 0.740, p = 0.001; n = 16). Also, the mean individual weight of carabids was significantly positively correlated with habitat age and beetles were larger at the oldest sites when compared with those at the youngest wildflower sites and in wheat fields (Tables 1 and 2). The number of carabid species increased significantly from 1- to 4-year-old wildflower areas (r_s = 0.523, p = 0.037, n = 16), but no significant differences were observed between the five habitat types ($F_{4,15}$ = 1.805, p = 0.181, n = 20; Fig. 1). CCA explained 46.7% of the total variance of the carabid assemblage (Fig. 3). Vegetation cover (13.8%), field size (9.8%) and soil water content (7.5%) contributed significantly to the carabid assemblage and explained 31.3% of the total variance. Species particularly strongly correlated with vegetation cover either occurred exclusively at 4-year-old wildflower sites (*Amara plebeja*) or at 3- and 4-year-old sites with clear preference for the oldest stage (*Pterostichus anthracinus*, Appendix 2). Similarly, other species closely

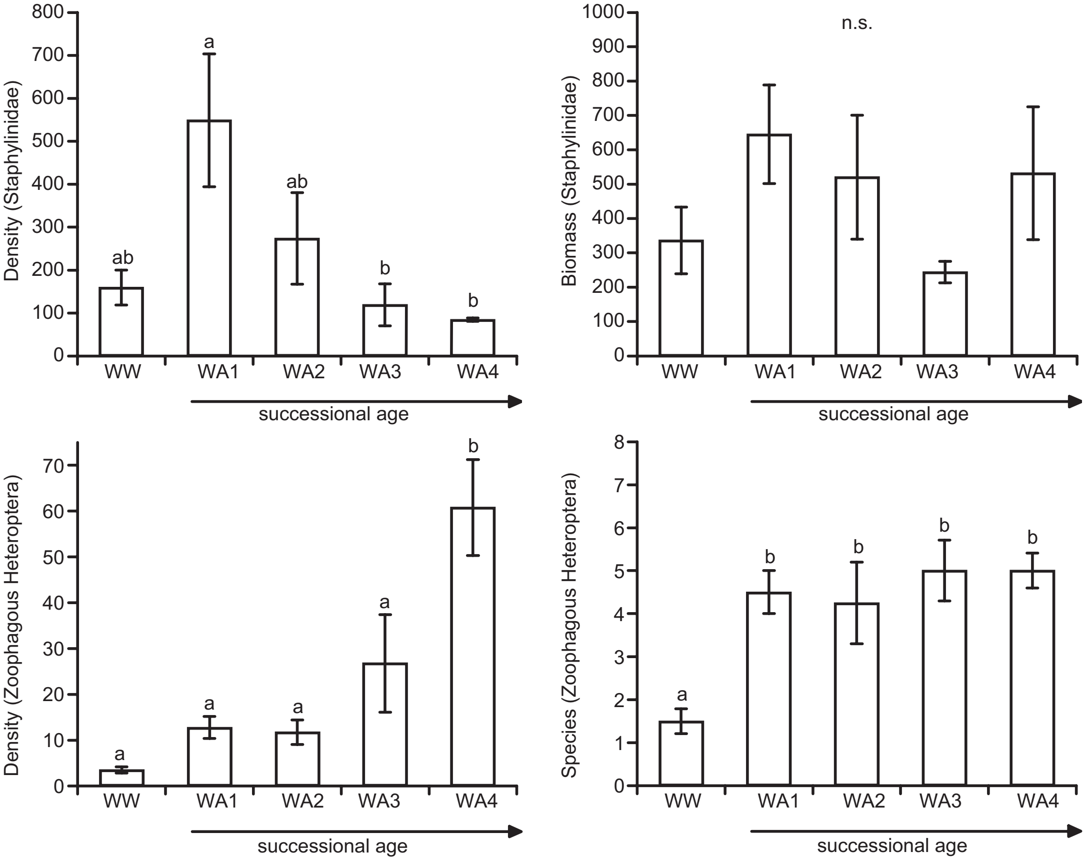

Fig. 4. Density and biomass of Staphylinidae and density and species richness of Heteroptera (mean ± SE) in winter wheat fields (WW) and 1- to 4-year-old wildflower sites (WA1–WA4). Different letters denote significant differences between habitat types (Tukey: $p < 0.05$, $n = 20$), n.s. = not significant. Arrows indicate the successional gradient for correlation analyses.

related to vegetation cover and water content were present at 2- to 4-year-old wildflower sites (*Harpalus affinis, Pseudophonus rufipes*) or only at 3- to 4-year-old sites (*Diachromus germanus*). By contrast, species with an opposite distribution were preferentially found at 1-year-old (*Bembidion quadrimaculatum*) or 1- and 2-year-old wildflower sites (*Bembidion lampros*).

Staphylinid beetles

Staphylinid density differed significantly among the five habitat types ($F_{4,15} = 4.600$, $p = 0.013$, $n = 20$; Fig. 4). It was highest at 1-year-old wildflower sites and decreased significantly with habitat age ($r_s = –0.778$, $p < 0.001$, $n = 16$). Staphylinid biomass was highest in 1-year-old and lowest at 3-year-old sites, but did not differ significantly among habitat types ($F_{4,15} = 1.231$, $p = 0.339$, $n = 20$; Fig. 4). Testing for a general group effect between staphylinid biomass at 3-year-old *versus* 1-, 2- and 4-year-old-wildflower sites showed a significantly lower biomass at the 3-year-old sites ($t = 4.637$, $p = 0.001$). There was no significant correlation between biomass and habitat age ($r_s = –0.255$, $p = 0.341$, $n = 16$), however, the mean individual weight of staphylinids increased significantly with the age of wildflower sites (Table 2).

Heteropteran bugs

Zoophagous bug density increased from 2- to 4-year-old wildflower sites, and was significantly higher at 4-year-old sites than in the other habitat types (Fig. 4). Density was positively correlated with age ($r_s = 0.700$, $p = 0.003$, $n = 16$). The number of zoophagous bug species was significantly lower in wheat fields than at 1- to 4-year-old wildflower sites, with no differences among successional ages (Fig. 4) and no significant correlation with habitat age ($r_s = 0.227$, $p = 0.398$, $n = 16$).

Discussion

Most beneficial arthropod groups investigated increased with successional age of wildflower areas in the parameters measured. White and Hassall (1994) reported an increase in species richness and biovolume, a feature highly correlated with biomass, of spiders within four years in uncropped headlands. Similarly, spider density increased with the age of a set-aside land over six years (Van Buskirk & Willi 2004). This corresponds to the positive response of spiders, carabids and zoophagous bugs with habitat age in the present study. Such a response should enhance the potential of biological pest control in adjacent crop fields because several authors have found increased carabid and spider dispersal from semi-natural habitats into fields. This led to higher predator densities as compared with those in fields without adjoining semi-natural areas (Coombes & Sotherton 1986, Cardwell, Hassall & White 1994, Lys *et al*. 1994, Lemke & Poehling 2002). Spiders and carabid and staphylinid beetles were observed to reduce populations of cereal and oilseed rape pests, thus being efficient beneficials in arable crops (Collins *et al*. 2002, Zaller *et al*. 2009).

The efficacy of predators as biological pest control agents apparently depends more on higher densities than on higher predator biodiversity (Straub & Snyder 2006), and Denys and Tscharntke (2002) showed that the biological control potential, based on predator–prey ratios, did not depend on predator species richness. This observation appears to be important for zoophagous bugs, whose density but not species richness increased significantly with advancing age of wildflower sites. However, density was significantly higher only at 4-year-old sites as compared with that at 1- to 3-year-old sites and in wheat fields. This indicates that large populations of zoophagous bugs developed only in the oldest successional stage studied. For carabid beetles, the positive response to habitat age was particularly obvious for biomass. Biomass reflects habitat productivity, and higher values indicate better conditions for insects. In fact, the nutritional condition of five common arable carabid species increased with habitat age at the same 1- to 4-year-old wildflower sites of the present study (Barone & Frank 2003, Frank *et al*. 2007).

The positive response of spiders, carabid beetles and zoophagous bugs to the successional age of wildflower areas supported our first hypothesis. As a general effect of advancing successional age, these beneficial arthropods may have profited from undisturbed developmental conditions where no pesticides and only extensive mechanical methods are allowed. As a consequence of succession, vegetation cover was significantly higher at 2- to 4-year-old wildflower sites as compared with that in wheat fields and at 1-year-old wildflower sites, and increased with habitat age at the wildflower sites investigated (Mosimann 2002). Vegetation cover seems to be an important factor explaining the continuous increase of density, biomass and species richness of epigeic spiders and carabids from 1- to 4-year-old sites: higher vegetation cover leads to better micro-environmental conditions for reproduction and larval survival for many carabid species (*see* Kromp 1999). More predatory arthropods in wildflowers sites as compared with winter wheat fields also supported the first hypothesis. This may simply reflect the above-mentioned favourable conditions in such semi-natural areas, as has already been observed elsewhere (e.g. Schmidt & Tscharntke 2005, Öberg *et al*. 2007). Except for bug species richness, however, species numbers at 1-year-old wildflower sites never differed from those in wheat fields; thus, newly sown wildflower sites have not yet built up large populations of predators. By contrast, density of the Staphylinidae decreased across the successional gradient. Even though staphylinid beetle density was shown not to increase within the first two years of succession in field margins (Olson & Wäckers 2007), our observation is in contradiction with our first hypothesis. Many staphylinids perhaps preferred younger wildflower sites with more open ground, which may provide more suitable conditions ($r_{\text{s Staphylinidae } vs. \text{ Vegetation cover}} = –0.718$, $p = 0.002$, $n = 16$). Alternatively, staphylinids may have preferred younger areas because they were out-competed or preyed upon by spiders and carabids in older areas, as intraguild predation among groups of generalist predators is well known (Müller & Brodeur 2002, Snyder & Ives 2003). However, predation and competition among epigeic predators must be interpreted with caution because there were only trends towards negative relations between spiders and staphylinids ($r_s = –0.399$, $p = 0.125$, $n = 16$) and carabids and staphylinids ($r_s = –0.315$, $p = 0.234$, $n = 16$).

Classical r-K strategy (Nentwig *et al.* 2007) could explain the overall pattern of a significant increase in the average individual weights of epigeic spiders, carabids and staphylinids with habitat age; i.e. young wildflower sites were mainly colonised by small pioneer species (r-strategists), which were perhaps replaced by larger species over time (K-strategists), thus an average individual at a 4-year-old wildflower site was larger than an average individual at a 1-year-old site. Consistently, among the two most abundant spider families, the smaller-sized Linyphiidae and the larger Araneidae comprised 93.81% and 0.51% of spiders collected at 1-year-old wildflower sites, respectively. At 4-year-old wildflower sites, however, 45.15% belonged to Araneidae and 35.28% to Linyphiidae. Similarly, the three carabid species of the genus *Bembidion*, which are typical small-sized pioneer species (Koch 1989), comprised 75.76% and 0.98% of carabids collected at 1- and 4-year-old wildflower sites, respectively. On the other hand, 4-year-old sites were dominated by the fairly large *D. germanus* and *Anisodactylus binotatus*, comprising 47.38% of the carabids observed in the oldest successional stage, but were absent from 1-year-old wildflower sites. The increasing average individual weights of epigeic predators with habitat age suggest that there are changes in the habitat that support different types of species at different stages of early succession. For the large-sized, mainly phytophagous carabids *D. germanus* and *A. binotatus* (Marggi 1992), an increasing supply of seeds over time may have caused their predominance at the oldest wildflower sites. Overall, Odum (1969) suggested that variable nutrient supplies in later succession would favour larger animals, which further confirms our observations. In agreement with the present study, biomass and individual weights of spiders and carabids increased with the age of wood strips adjoining arable fields across a gradient from 2- to 7-years-old sites (Kajak & Oleszczuk 2004). Mean body weights of carabids were shown to increase with successional stage on abandoned — formerly agricultural — land even across a gradient from 7- to 80-year-old sites (Tyler 2008).

Vegetation cover was the most important habitat parameter characterizing both the spider and carabid assemblages. In CCA, there were two groups of species, which were either positively or negatively associated with vegetation cover and soil water content, thus supporting our second hypothesis. Species predominantly found at older wildflower sites obviously depend on more shaded and humid habitats, such as the carabid beetle *P. anthracinus* (Marggi 1992). This corresponds to our results as it preferred the oldest successional stage of wildflower areas with high vegetation cover and soil water content. Also, *A. plebeja* seems to prefer more humid soils (Marggi 1992) and exclusively occurred at 4-year-old wildflower sites. *D. germanus*, the most abundant carabid beetle, is regarded as a stenoecious, mainly phytophagous species (Marggi 1992, Pfiffner & Luka 1996), feeding on pollen and seeds. It depends on areas with late cutting or no mowing, and indicates a successional stage towards permanent grassland (Pfiffner & Luka 1996), which corresponds well with its exclusive occurrence at 3- and 4-year-old wildflower sites. The spider *T. ruricola* is known to occur in forest edges, crop land and meadows of medium humidity and shade (Hänggi *et al.* 1995, Bellmann 1997), which corresponds with its exclusive occurrence at 2- to 4-year-old wildflower sites. Similarly, *B. gracilis* can be observed in humid and shadowy forests and meadows (Heimer & Nentwig 1991), explaining its preference for wildflower sites older than two years with higher vegetation covers and soil water content. *E. trilobata*, an invasive species from North America, can preferentially be observed in meadows, pastures and rural areas (Kreuels 2007). This mode of life explains its close relation to vegetation cover.

Bembidion quadrimaculatum, which was negatively correlated with vegetation cover and water content, was almost exclusively found at 1-year-old wildflower sites, where distinct daily fluctuations of microclimatic conditions due to sparse vegetation cover is expected. It is a pioneer species typical to areas free of vegetation and is considered xerophilous (Koch 1989, Kromp 1990). *Bembidion lampros* can be observed more frequently in arable land than in old meadows and pastures (Thiele 1977); thus the high vegetation cover in the older wildflower sites might be the reason for its rareness there. The spiders *E. atra* and *P. microphthalmum* are typical agrobionts (Heimer & Nentwig 1991, Hänggi *et al*. 1995) predominantly occurring in winter wheat fields. This explains their negative response to vegetation cover and water content because these parameters are less pronounced in wheat. The strong correlation between field size and *Dyschirius globosus* must be assessed with caution because it was only found at two of the 20 sites, namely one large wheat field and the largest wildflower site. This exceptional relation may generally explain the significant impact of field size on carabid assemblage. During the early successional stages of wildflower areas, a change in the vegetation appeared to be the main driver for promoting guilds differentiation. The first two years were favourable to xerophilous pioneers and afterwards more hygrophilous species appeared, which both comprised species that can function as antagonists of arable pests.

Conclusions

As predicted, arthropod species richness increases with successional age. Due to the absence of disturbance, density and biomass of most predators studied also increased with the age of wildflower sites. However, populations of these arthropods at 1-year-old wildflower sites were similar to those in wheat fields and large populations of predators only developed after the first year. Therefore, benefits from wildflower areas to farmers by many beneficials invading crop fields from wildflower sites nearby may only be expected after the first year of sowing. We therefore recommend maintaining wildflower areas for several years in the same place instead of removing them after two to three years and resowing elsewhere. This recommendation has practical relevance because (i) many farmers currently remove wildflower areas already after two to three years fearing that older areas enhance weed infestation, and (ii) wildflower areas belong to agri-environment schemes subsidized by European governments.

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Appendix 1. Number of Araneae in the 20 study sites of winter wheat fields (WW) and 1- to 4-year-old wildflower areas (WA1–WA4).

		WW				WA1				WA2				WA3				WA4				Σ
Taxon	Family[3]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Agelenidae[1]	AGE																			1		1
Araeoncus humilis	LIN			3									4			1			1		1	10
Araneidae[1]	ARA	2	10	2					1	15	2	40	3	4	9	442	2	5	2	277	7	823
Arctosa leopardus	LYC														2	1					1	4
Arctosa sp.	LYC																				19	19
Bathyphantes gracilis	LIN		1					1		2	1	1		2	6				1		18	33
Bathyphantes similis	LIN							1													4	5
Bathyphantes sp.	LIN									3										1	8	12
Bianor aurocinctus	SAL																	1				1
Centromerus sylvaticus	LIN											1										1
Clubiona lutescens	CLU																1					1
Clubiona sp.	CLU											1									2	3
Cyclosa sp.	ARA														8							8
Diaea sp.	THO														1							1
Dicymbium nigrum	LIN																			1	1	2
Diplocephalus cristatus	LIN												3									3
Diplocephalus latifrons	LIN													1						2		3
Diplostyla concolor	LIN												11	4								15
Eperigone trilobata	LIN				1			1		1		1	4		2		3	1	2	1	2	19
Erigone atra	LIN			4	3	1	1															9
Erigone dentipalpis	LIN	1		3	2	2	15	4	1						1			1				30
Euophrys aperta	SAL														1							1
Euophrys lanigera	SAL						1															1
Gongylidiellum latebricola	LIN					3	1			1												5
Heliophanus flavipes	SAL																	2				2
Larinioides cornutus	ARA														1			1				2
Lepthyphantes sp.	LIN							1					1									2
Lepthyphantes tenuis	LIN		1	1						3		1			1		1	1				9
Linyphiidae[1]	LIN	37	20	32	18	40	29	11	10	172	44	191	17	18	6	78	7	27	5	4	89	855
Lycosidae[1]	LYC	77					3	1	3				15	2	133	1	5	7			5	252
Mangora acalypha	ARA														1							1
Meioneta rurestris	LIN	1	2	10	1	2			4			2										22
Micrargus subaequalis	LIN													1							2	3
Monocephalus fuscipes	LIN						1															1
Myrmarachne sp.	SAL																		1			1

Neottiura bimaculata	THE																				3	3
Nuctenea sp.	ARA																		1			1
Oedothorax apicatus	LIN	11	7	1	3	6	5		19	23	14	23		12	2	51		37	1		7	222
Oedothorax fuscus	LIN			1					1	1		3										6
Oedothorax sp.	LIN								1	10	4											15
Pachygnatha clercki	TET									2	1	1						1				5
Pachygnatha sp.	TET		2	1					1	1	2	6	1	1	2	1					1	19
Pardosa agrestis	LYC	4								6	1		3									14
Pardosa amentata	LYC																				1	1
Pardosa palustris	LYC									2				1				1				4
Pardosa sp.	LYC									2	3						3	3				11
Philodromus sp.	PHI																				1	1
Phrurolithus festivus	LIO																1					1
Pirata latitans	LYC																		1		1	2
Porrhomma campbelli	LIN														1						1	2
Porrhomma microphthalmum	LIN	5	1	2	3	2														1		14
Porrhomma oblitum	LIN	8	2	4	8	11	7	2		4	5	6	2	1		8		3	1	2	2	76
Porrhomma sp.	LIN				6																	6
Robertus lividus	THE				1																	1
Robertus neglectus	THE			1	5						2					2	3					13
Robertus sp.	THE				2																	2
Salticidae[1]	SAL																				1	1
Tetragnatha sp.	TET			1											1			1				3
Theridiidae[1]	THE												1		1							2
Tiso vagans	LIN	1						1												1		3
Trochosa ruricola	LYC											1	1	1	1		1	4				9
Trochosa sp.	LYC												7		1	2	2	5	1			18
Xysticus cristatus	THO													1						2		3
Xysticus kochi	THO														2	1	1	1	1	2	1	9
Xysticus sp.	THO									1		1		1	1			1	1	51	1	58
Zelotes praeficus	GNA																				1	1
Zelotes sp.	GNA																				1	1
Number of individuals		147	46	66	53	67	63	23	41	249	79	279	73	50	184	588	30	103	19	346	181	2687
Number of species[2]		7	6	10	9	7	7	6	4	10	6	10	7	9	12	6	7	12	7	8	15	43

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[1] juveniles that could not be determined to the genus level.

[2] only species considered that were determined to the species level (without sp.).

[3] AGE = Agelenidae, ARA = Araneidae, CLU = Clubionidae, GNA = Gnaphosidae, LIN = Linyphiidae, LIO = Liocranidae, LYC = Lycosidae, PHI = Philodromidae, SAL = Salticidae, TET = Tetragnathidae, THE = Theridiidae, THO = Thomisidae.

Appendix 2. Number of Carabidae at the 20 study sites of winter wheat fields (WW) and 1- to 4-year-old wildflower areas (WA1–WA4).

	WW				WA1				WA2				WA3				WA4				Σ
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Acupalpus meridianus	2		1							1							2	1			7
Agonum mülleri	1		1	2		1	1	2	1	6				5		2		1		3	26
Amara aenea									1								2				3
Amara plebeja																	4	1			5
Amara similata					1				1											2	4
Anisodactylus binotatus		1							9	2	2	5		16	12	1	29	29		9	115
Asaphidion flavipes			1	1								1									3
Bembidion lampros					1	1	10		8					3							23
Bembidion properans			1	5			9	9		21				6		22			2		75
Bembidion quadrimaculatum	1		2		12	13	19	1												1	49
Bradycellus csikii														1							1
Bradycellus verbasci														1					1		2
Clivina fossor	32		18	21			6			5		4	2	6	5	12	4		4	1	120
Diachromus germanus													1	16		32	40	2		36	127
Dyschirius globosus			4												7						11
Harpalus affinis												2				2	1	8		1	14
Harpalus distinguendus												1									1
Harpalus rubripes																	2				2
Harpalus signaticornis					1										2						3
Loricera pilicornis			1						2												3
Ophonus ardosianus														1							1
Ophonus puncticeps												1					1	5	10		17
Platynus dorsalis								1	1	3		1		1			2				9
Poecilus cupreus							2		1	10				2	1	2	14	1			33
Pseudophonus rufipes										1	1	2		1	7	1	15	3	1	1	33
Pterostichus anthracinus														1			18				19
Pterostichus melanarius				1				2	3	2	3			2		1		1	3		18
Pterostichus vernalis	1	1	2	3			2			1	3		3	8	2	5	3	7		4	45
Stenolophus teutonus									1					6		11	6	1			25
Stomis pumicatus		1										1						2			4
Synuchus vivalis					1						1			1				1	2		6
Tachys bistriatus				5	1	1											2		2		11
Trechus quadristriatus	2	4	6	26			2			4		1		8	2		6		9		70
Number of individuals	39	7	37	64	17	16	51	15	28	56	10	19	6	85	38	91	151	63	34	58	885
Number of species	6	4	10	8	6	4	8	5	10	11	5	10	3	18	8	11	17	14	9	9	33