



## Research paper

## Spillover of arthropods from cropland to protected calcareous grassland – the neighbouring habitat matters



Filipe Madeira<sup>a,b</sup>, Teja Tschardt<sup>a</sup>, Zoltán Elek<sup>c</sup>, Urs G. Kormann<sup>a</sup>, Xavier Pons<sup>b</sup>, Verena Rösch<sup>a,d</sup>, Ferenc Samu<sup>e</sup>, Christoph Scherber<sup>a,f</sup>, Péter Batáry<sup>a,\*</sup>

<sup>a</sup> Agroecology, Georg-August University, Grisebachstr. 6, 37077 Göttingen, Germany

<sup>b</sup> Department of Crop and Forest Sciences, AGROTECNIO Center, University of Lleida, Rovira Roure 191, 25198 Lleida, Spain

<sup>c</sup> MTA-ELTE-MTM Ecology Research Group, Pázmány P. s. 1c, 1117 Budapest, Hungary

<sup>d</sup> Institute for Environmental Science, University of Koblenz-Landau, Fortstr. 7, 76829 Landau, Germany

<sup>e</sup> Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, PO Box 102, 1525 Budapest, Hungary

<sup>f</sup> Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany

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## ABSTRACT

Spillover effects of organisms from semi-natural habitats to adjacent crops have been frequently reported, yet evidence for the reversed process and associated functional consequences remains scarce. We examined the spillover of carabids, rove beetles and spiders from agricultural lands to protected, high-nature value calcareous grasslands by comparing two neighbourhood types: seven calcareous grasslands neighbouring intensively managed winter wheat fields and seven calcareous grasslands neighbouring intensively managed meadows in Germany. We examined arthropod activity density with repeated pitfall trapping in both the edge and the interior of all three habitat types (14 study sites). All three arthropod groups showed consistently higher activity density in calcareous grasslands adjacent to wheat fields than calcareous grasslands adjacent to meadows, apparently through spillover effects. Activity density of carabids and spiders exhibited a decline from the interior to the edge of the wheat fields and to even lower density at the edge and lowest density in the interior of the calcareous grassland. Carabid spillover from both neighbouring habitats to grasslands was driven by a dominant predatory species, *Pterostichus melanarius*, whereas *Oedothorax apicatus* was the dominant contributor to spider spillover from wheat to grasslands. Our results show that neighbourhood identity (wheat or meadow) can shape arthropod density and community composition in semi-natural habitats due to spillover of carabid beetles, spiders and rove beetles from adjacent crop fields. Neighbourhood effects on spillover are thus more accentuated at the cropland-grassland interface compared to the meadow-grassland boundary, with small grasslands being particularly affected due to their high edge-to-interior ratios. Our results suggest that meadows around high-nature value, protected grassland reserves, may be important conservation elements by attenuating arthropod spillover from arable crops. Such spillover may compromise the identity, structure and functioning of endangered communities.

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## 1. Introduction

During the last decades, agricultural land-use intensity has markedly increased (Tilman et al., 2001). This has resulted in the fragmentation of the remaining natural and semi-natural habitats, while the size of arable fields has increased, leading to landscapes dominated by only few crop types (Robinson and Sutherland,

2002; Tschardt et al., 2012). The loss of natural areas and the extension of monocultures can negatively affect biodiversity and ecosystem services such as biological control (Tews et al., 2004; Bianchi et al., 2006; Schmidt et al., 2008). Invertebrate populations in agro-ecosystems undergo strong fluctuations through pesticide use and mechanical pest control, short-term availability of resources (e.g. mass flowering crops), crop senescence (e.g. peak-ripening) and/or abrupt resource depletion (cutting/harvest) (Kennedy and Storer, 2000; Holzschuh et al., 2011) that could boost spillover effects (Rand et al., 2006). Generalist predators (mainly spiders, carabids and rove beetles), important to the suppression of

\* Corresponding author at: Grisebachstr. 6, 37077 Göttingen, Germany.

E-mail address: [pbatary@gmail.com](mailto:pbatary@gmail.com) (P. Batáry).

crop pests (e.g. Symondson et al., 2002), generally immigrate to arable fields from adjacent habitats in spring (e.g. Tscharrntke et al., 2005; Bianchi et al., 2006; Rusch et al., 2010). This process is important for an efficient natural pest control, because early colonization of crop fields by natural enemies may prevent serious pest outbreaks later in the season (Tscharrntke et al., 2005), but evidence of the opposite process is rare (see Rand et al., 2006; Blitzer et al., 2012; Schneider et al., 2013). However, as the high productivity of arable fields during the growing season locally enhances arthropod densities, a massive and large-scale spillover of organisms from crop to non-crop areas can be expected (Tscharrntke et al., 2005). Spillover, i.e. the dispersal or foraging of organisms across habitat borders, can affect ecosystem functioning and food web interactions of local communities (Schneider et al., 2013). The potential impact of this spillover on adjacent natural and semi-natural habitats has largely been a neglected, and is scarcely known (Tscharrntke et al., 2012). Spillover of insect predators from agricultural to natural habitats and back may be underestimated (Blitzer et al., 2012).

Calcareous grasslands, a semi-natural grassland type, represent one of the most species-rich habitats for plants and insects in Western Europe and are therefore of major conservation priority (Tscharrntke et al., 2002; van Swaay, 2002). In Lower Saxony (Germany), they generally occur as small, fragmented patches embedded in a landscape dominated by agriculture. The majority of the remaining calcareous grasslands are located adjacent to arable fields or intensively managed meadows.

In this study, we examined the spillover of ground-dwelling arthropods (carabid beetles, rove beetles and spiders) in two neighbouring habitat types (calcareous grasslands next to wheat fields vs. calcareous grasslands next to meadows). During the growing season, wheat fields may act as source habitats for predators invading adjacent calcareous grassland, because wheat fields exhibit higher productivity than meadows and more pronounced seasonal changes in productivity (crop ripening). We hypothesise that the high productivity donor habitat (wheat field) will generate larger spillover effects than the low productivity donor habitat (meadow).

## 2. Materials and methods

### 2.1. Study sites and study design

The study was conducted before wheat harvest (when wheat started drying) and hay cutting in July and August 2011 in the vicinity of Göttingen, Lower Saxony, Germany (see Appendix A1 in Supplementary material). The study area consisted of a mosaic of cereal fields (mainly wheat, barley and maize) and other crops (e.g. oilseed rape and sugar beet), fertile, intensively managed meadows and less intensively managed, semi-natural landscape elements such as field margins, hedges, deciduous forests and calcareous grasslands. The meadows in the study area are permanent and have been managed continuously for more than 10 years, while the crop rotation of arable fields may include maize, oilseed rape, barley and sugar beet. In this landscape mosaic, calcareous grasslands are mostly located directly adjacent to crop fields and meadows on south-facing slopes with forest on the top of these slopes. We selected fourteen study sites (area of calcareous grasslands (mean  $\pm$  SEM):  $0.45 \pm 0.18$  ha) with two different habitat combinations: seven sites where intensively managed winter wheat fields (W) bordered calcareous grasslands (CG) and seven sites where intensively managed meadows (M) bordered calcareous grasslands (CG). Due to an unexpected withdrawal of permission to use one of the grasslands by its owner, we used two different borders of the same calcareous grassland in two comparisons (for both CG next to W (CG-W) and CG next to M

(CG-M)). However, the study areas of this fragment were separated by more than 90 m in a straight line from each other. Based on Moran's I, activity density data were spatially independent for each of the three sampled taxa (see Appendix A2 in Supplementary material). Finally, there was always a direct contact between CG and W or M without any specific boundary vegetation.

The selected wheat fields and meadows received the typical conventional management of the study region:  $\sim 200$  and  $\sim 100$  kg nitrogen/ha in wheat fields and meadows, respectively, and ca. five pesticide treatments (generally herbicide and fungicide) on wheat fields; whereas meadows received less than one herbicide treatment (Batáry et al., 2012; own observations by P. Batáry). The meadows were mown between one to four times from mid-May. Calcareous grasslands were either managed by extensive mowing (N=2; 1 CG-W and 1 CG-M), extensive grazing by sheep (N=3; 1 CG-W and 2 CG-M) or abandoned (N=9; 5 CG-W and 4 CG-M), leaving them to succession for several years. While grazing only occurred in winter, mowing could happen at different times throughout the season from July onwards. We selected calcareous grassland fragments that harboured more than ten of the plant species that are typical for calcareous grasslands in the study area (Krauss et al., 2004). We did not try to avoid differences in habitat quality and management, because we intended to mirror the actual condition of calcareous grasslands in the study area.

### 2.2. Arthropod sampling

Arthropod samples (carabids, rove beetles and spiders) were collected using pitfall traps (plastic cups 15 cm deep and 10 cm in diameter). In each habitat, three pitfall traps were placed at a distance of 2 m from the margin ("edge transects") parallel to the edge, and another three pitfall traps at a distance of 10 m from the margin ("interior transects") (N=168). This distance has been chosen for two reasons: 1.) 10 m is easily accessible from the first track root in wheat; 2.) a rapid decline in arthropod numbers can be expected already at this distance in wheat. Pitfall traps within transects were separated by 10 m. Since the edge transects in the two adjacent neighbouring habitats were shifted by 5 m compared to each other, the minimum distance of traps from the two habitats was more than 6 m.

Pitfall traps were filled with saltwater (15 vol.%, one third of the cup), covered with a plastic roof (15  $\times$  15 cm), and remained in the field for seven days. The samples were then stored in ethanol (70 vol.%) and kept at 10 °C until sorting. All carabids, rove beetles and adult spiders were identified to species level.

In each habitat we performed two pitfall trapping sampling periods before wheat harvest (between 9th and 28th of July) or hay cutting (between 10th of July and 7th of August). The first sampling in the wheat fields corresponded to the milk-ripening stage of wheat, while the second one corresponded to the peak-ripening period. The time spans between the first and second sampling were between 2 and 4 and 1–4 days for CG-W and CG-M sites, respectively. For the analyses, pitfall trap data were summed per transect for the two sampling periods.

### 2.3. Statistical analyses

We analysed the activity densities in calcareous grasslands in relation to neighbourhood type (calcareous grassland next to wheat vs. calcareous grassland next to meadow) and transect positions within study site (interior–edge–edge–interior). Prior to the analyses, the data of the two sampling occasions were pooled by taking the sum. Transect positions within study site was used as a numeric variable in the following way: 1–calcareous grassland interior, 2–calcareous grassland edge, 3–edge of neighbouring wheat/meadow, 4–interior of neighbouring wheat/meadow. A

significant effect of transect position therefore is indicated by significant (linear) changes in activity density from the interior to the edge of the neighbouring habitat (wheat/meadow) and to the edge and interior of calcareous grassland. We conducted separate analyses for the activity density of all species per carabid, rove beetle and spider taxa and for the activity density of the most abundant species per taxon. We applied generalized linear mixed-effects models (GLMM) with negative binomial distribution since data were overdispersed, where the full models also contained the two-way interaction of neighbourhood type and transect position (number of observations: 14 study sites  $\times$  4 transect positions = 56). Since we had four transects per study site, study site was used as a random factor. Models were simplified by single term deletions to arrive at the most parsimonious model based on AIC value using the “drop1” function in lme4 package (Bates et al., 2014) in R (R Development Core Team, 2015).

Since we focused on changes in the number of individuals, we did not consider analysing species richness data. However, we performed redundancy analyses (RDA) to explore which species might have been responsible for the observed spillover effect in GLMM. Prior to the analyses, the species matrix was transformed by Hellinger transformation (Legendre and Gallagher, 2001). This transformation allows for Euclidean-based ordination methods with community composition data containing many zeros, i.e. characterised by long gradients. The species matrix was constrained by transect position as numeric variable, while study site was included as a conditional variable. Separate RDAs were performed for the two neighbourhood types. We did this because parallel inclusion of neighbourhood type (as constrained variable) and study site (as conditional variable) resulted in that study site took all variation potentially explained by neighbourhood type (i.e. zero variation in case of the latter variable). Additionally, our main interest in these analyses was to explore whether and which species contribute to transect position effect and not whether the community composition of the two neighbourhood types are different or not. Calculations were performed using the ‘vegan’ package (Oksanen et al., 2015) in R (R Development Core Team, 2015).

### 3. Results

#### 3.1. Carabids

During the two sampling rounds we collected 1792 carabid individuals belonging to 27 species in wheat, 394 carabid individuals belonging to 26 species in calcareous grassland next to wheat (CG next to W), 239 carabid individuals belonging to 24 species in meadow and 69 carabid individuals belonging to 19 species in grassland next to meadow (CG next to M) (see Table A1

in Supplementary material). Carabids were significantly more abundant (approx. six times more) in CG next to W than in CG next to M (Table 1, Fig. 1a). Additionally, transect position significantly influenced activity densities (independent of neighbourhood type), with activity densities gradually decreasing from the interior of M or W, respectively, towards the interior of CG (Table 1). *Pterostichus melanarius* was the most common species in all habitats, representing 60% and 49% of all individuals caught in CG next to W and CG next to M, respectively. It showed the same significant neighbourhood type and transect position effects as all species taken together (Table 1, Fig. 1a).

In the ordination, transect position explained a significant part of the variation in the species matrix only in the case of CG-W sites, but not for CG-M sites (Table 2, see Fig. A1 in Supplementary material). In order to further visualize the distribution of individuals of carabid species identified as responsible for transect position effect by RDA, we plotted their activity densities against transect position per study site (see Fig. A2 in Supplementary material). These figures show that three out of six species were affected by spillover in some way, but with a clear effect in each study site only in case of *P. melanarius*.

#### 3.2. Rove beetles

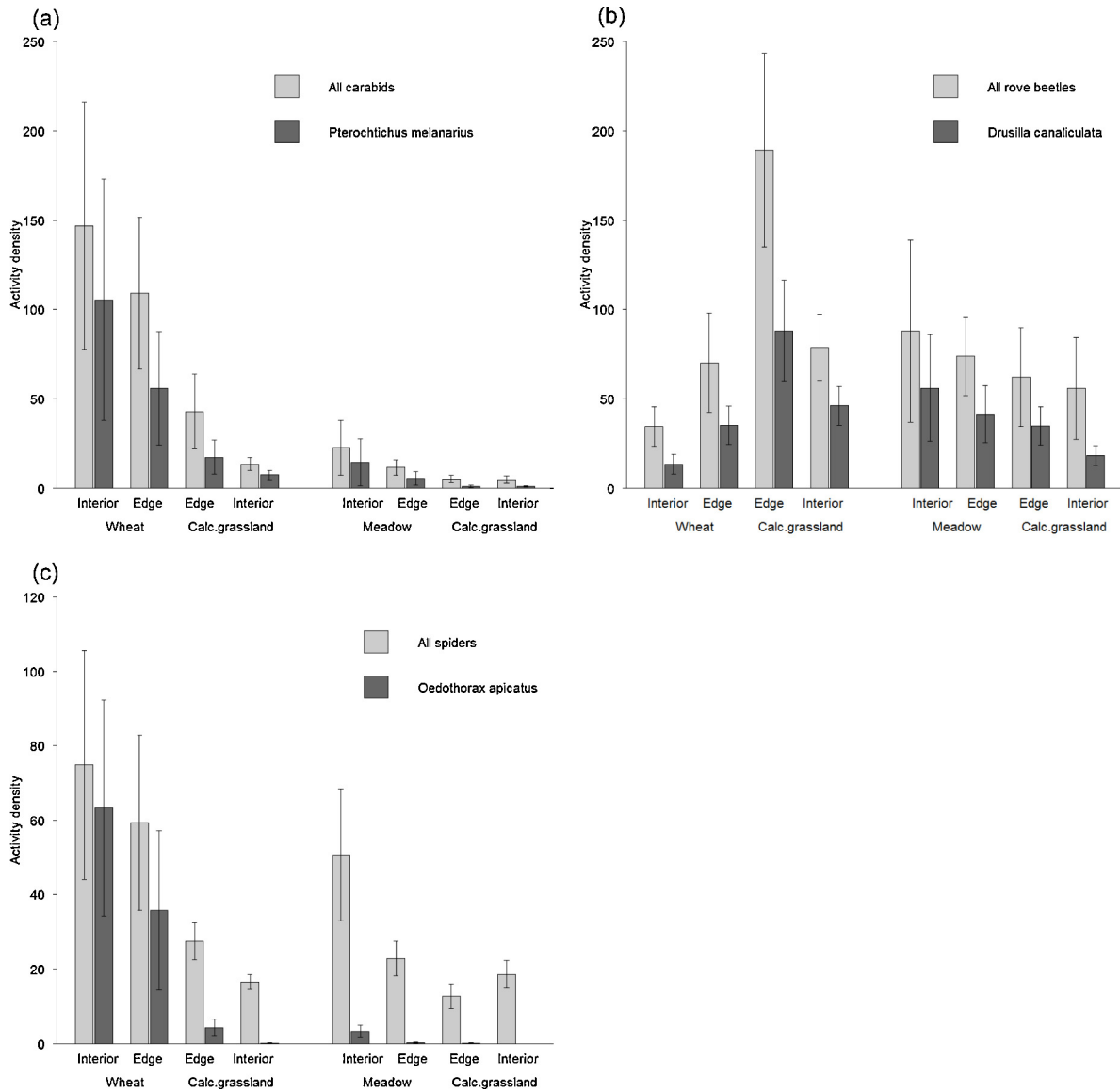
In wheat, we captured 732 adult rove beetle individuals belonging to 27 species, in CG next to W 1876 individuals belonging to 31 species, in meadow 1132 individuals belonging to 36 species and in CG next to M 825 individuals belonging to 25 species (see Table A2 in Supplementary material). For all species, there was a significant effect of neighbourhood type with more individuals captured in CG next to W than in CG next to M (Table 1, Fig. 1b). Additionally, the interaction of neighbourhood type and transect position was also significant, indicating a decrease of activity density in CG next to M, but an increase in CG next to W with exceptionally high activity density in calcareous grassland edges (Table 1). *Drusilla canaliculata* was the most abundant rove beetle caught, representing 49% and 54% of the individuals caught in CG next to W and CG next to M, respectively. *D. canaliculata* showed also the same significant interaction between neighbourhood type and transect position (Table 1, Fig. 1b).

In the ordination biplot, transect position explained a significant part of the variation in the species matrix only in case of CG-W sites, but not for CG-M sites (Table 2, see Fig. A3 in Supplementary material). The figures on distribution of individuals of rove beetle species identified as responsible for transect position effect by RDA showed no sign of spillover effect when we investigated them per study site (see Fig. A4 in Supplementary material).

**Table 1**

Parameter estimates  $\pm$  95% CI of the minimal adequate mixed-effects models testing the effects of neighbourhood type (N: calcareous grassland–wheat field vs. calcareous grassland–meadow), transect position within study site (T: interior–edge–edge–interior) and their interaction on the activity density of carabids, rove beetles and spiders and the most dominant species per taxon. \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

	Neighbourhood type (N)	Transect position (T)	N $\times$ T
Carabid activity density			
All species	1.85 $\pm$ 0.99 ***	0.63 $\pm$ 0.27 ***	–
<i>Pterostichus melanarius</i>	2.41 $\pm$ 1.40 ***	0.78 $\pm$ 0.40 ***	–
Rove beetle activity density			
All species	1.95 $\pm$ 1.12 ***	0.12 $\pm$ 0.26	–0.56 $\pm$ 0.36 **
<i>Drusilla canaliculata</i>	2.62 $\pm$ 0.76 ***	0.26 $\pm$ 0.03 ***	–0.81 $\pm$ 0.03 ***
Spider activity density			
All species	0.45 $\pm$ 0.06 ***	0.37 $\pm$ 0.05 ***	–
<i>Oedothorax apicatus</i>	3.47 $\pm$ 1.39 ***	1.78 $\pm$ 0.58 ***	–



**Fig. 1.** Mean activity density of (a) all carabids and the dominant species *Pterostichus melanarius*, (b) all rove beetles and the dominant species *Drusilla canaliculata* and all spiders and the dominant species *Oedothorax apicatus* in two different calcareous grassland neighbourhood types (next to wheat field and next to meadow) and transect positions within study site (interior–edge–edge–interior). Although transect positions within study site was used as a continuous variable in mixed effects models, barplots are used here for a better presentation of results. Error bars represent SEM.

**Table 2**

Results of redundancy analysis to test the effect of transect position within study site (interior–edge–edge–interior) on species composition of carabids, rove beetles and spiders in calcareous grassland–wheat field and in calcareous grassland–meadow neighbourhood types. Percentage of explained variation and F-values are given. \*\*p < 0.01, \*\*\*p < 0.001.

	Variation (%)	F
Wheat field – Calcareous grassland		
Carabids	7.64	2.74**
Rove beetles	6.89	2.31**
Spiders	19.88	7.40***
Meadow – Calcareous grassland		
Carabids	3.83	1.40
Rove beetles	2.39	0.88
Spiders	9.18	3.51**

### 3.3. Spiders

During the two sampling occasions we caught 939 adult spider individuals belonging to 26 species in wheat, 309 individuals belonging to 27 species in CG next to W, 515 individuals belonging to 26 species in meadow and 219 adult spiders belonging to 22 species in CG next to M (see Table A3 in Supplementary material). In the case of all spider species we also found a significant effect of neighbourhood type with more individuals captured in CG next to W than in CG next to M (Table 1, Fig. 1c). Transect position also significantly influenced activity densities (independent of neighbourhood type), with activity densities gradually decreasing from the interior of M or W, respectively, towards the interior of CG. In the case of spiders the most abundant species were different in each habitat (see Table A3 in Supplementary material). In total, the web-building spider *Oedothorax apicatus* was the most abundant species caught, representing 58% and less than 4% of individuals caught in CG next to W and CG next to M, respectively. This species

showed the same significant neighbourhood type and transect position effects as all species taken together (Table 1, Fig. 1c).

In the ordination, transect position explained a significant part of the variation in the species matrix in both CG-W and CG-M models (Table 2, see Fig. A5 in Supplementary material). However, investigating the figures on distribution of individuals of spider species identified as responsible for transect position effect by RDA, we found that only one species, *O. apicatus*, in CG-W sites was affected by spillover (see Figs. A6, A7 in Supplementary material).

#### 4. Discussion

Ground-dwelling arthropod (carabid beetles, rove beetles and spiders) activity densities were significantly higher in CG-W than in CG-M, suggesting a strong directional spillover from wheat fields to adjacent calcareous grassland before wheat harvest. Species abundance and diversity in terrestrial habitat patches can be strongly influenced by neighbouring habitats (Cook et al., 2002). The characteristics of the adjacent habitat type are likely to be the reason for the higher arthropod activity densities in CG next to W compared to CG next to M in this study. Although denser vegetation structure might impede arthropod movements, suggesting higher catches in wheat than in the denser meadows due to a potential methodological bias of pitfall trapping (Melbourne, 1999). However, the spillover of carabids and spiders to CG was not moderated by neighbourhood type *per se*, but being seemingly density dependent. Usually, intensive monocultures such as wheat fields, which experience an excessive use of agrochemicals, are highly productive and exhibit high (pest) prey and predator densities (Altieri and Nicholls, 2003). The organisms present within these unstable agro-ecosystems are usually characterised by rapid development, high growth rates and a high capacity to disperse to alternative habitats (Opatovsky and Lubin, 2012). The increase of predator densities may lead to higher predator emigration rates to less productive habitats, when prey densities become low at the time of crop ripening (Rand et al., 2006).

Rand and Louda (2006) showed in one of the few studies on crop–non-crop spillover that beetles can be three to six times more abundant in native grasslands surrounded by crop-dominated landscapes than in grassland-dominated landscapes. In non-crop areas, parasitism rates of *Meligethes aeneus* (Coleoptera, Nitidulidae) on a native Brassicaceae host plant increased with an increasing proportion of its crop host plants (oilseed rape) in the landscape (Gladbach et al., 2011). Our results agree with theoretical models, predicting that spillover generally takes place from more to less productive habitats (Holt and Hochberg, 2001).

Another reason for the observed increase in arthropod densities in calcareous grasslands near cropland could be the pronounced fluctuations of resource availability in croplands during the growing season. Cereals are ephemeral, senescing relatively early in the growing season and are harvested in mid-season in all over Europe. Thus, they provide food resources only during a limited period of the year (Wissinger, 1997). Shortage of resources forces invertebrates to move to neighbouring habitats (Tylianakis et al., 2005; Rand et al., 2006). Hence, the movement of predators from their agricultural habitat to nearby semi-natural habitats can be a response to declining habitat quality, as documented for spiders, carabids and rove beetles (Thorbek and Bilde, 2004). In general, harvesting/cutting increases the movement of arthropods into adjacent habitats (Ribera et al., 2001; Thorbek and Bilde, 2004; Eyre et al., 2013; Madeira and Pons 2016). Previous studies showed that carabid and running crab spider activity densities increased in adjacent habitats after wheat harvest (French et al., 2001; Opatovsky and Lubin, 2012). However, in our study, we observed that arthropod spillover to adjacent calcareous grasslands started

before wheat harvest. This suggests that movement occurs when the crop no longer provides a suitable environment in terms of microclimate and food resources as observed for some carabid species (Thomas et al., 2002). This threshold may be reached at different times for different arthropod groups, explaining the different patterns for the two beetle taxa. Rove beetles seem to have started to move to CG earlier than carabids, showing higher activity-densities in CG compared to carabids at the time of sampling. Duelli et al. (1990) and di Lascio et al. (2016) also observed that coccinellids moved from maize fields to adjacent habitats once the aphid population on maize declined. Alternatively, the pattern of rove beetles might be related to the two overly dominant species (*D. canaliculata* and *Falagrioma thoracica*). These two related species can be considered as polyphagous predators with a preference for ant larvae leading to an avoidance of ploughed sites, especially wheat interiors (Hoffmann et al., 2016). Finally, the fact that transect position explained a significant part of the variation in the arthropod community composition in case of CG next to W, but not for CG next to M (except for spider) also suggests that spillover from wheat fields to calcareous grasslands occurs before wheat harvesting.

The reason for the higher activity density of spiders in CG next to W than in CG next to M could be that they show a higher preference for wheat fields earlier in the season (Pluess et al., 2008; Batáry et al., 2012). Web-building spiders' activity density is influenced by vegetation structure and architectural complexity (Rypstra et al., 1999; Richardson and Hanks, 2009) and philodromid spiders (hunting spiders) have been found to spillover from wheat fields into a semi-desert habitat (Pluess et al., 2008).

Spillover effects are accentuated along patch edges, and this is why small patches of semi-natural habitat are more affected than large patches, given their higher edge-interior ratios (Cook et al., 2002). Our results on carabids (including *P. melanarius*) and spiders (including *O. apicatus*) coincide with the distribution patterns of synanthropic species with higher activity densities in crop than non-crop habitats (Duelli and Obrist, 2003; but see the opposite pattern by Lemke and Poehling, 2002 for an earlier spillover from weed strip to cereal). These suggest that the neighbourhood type (cropland vs. grassland) moderates the absolute amount of spillover to calcareous grassland by functionally important groups, thereby probably also shaping ecosystem processes such as predation. However, the spillover of carabids and spiders from wheat fields or meadows into grasslands does not necessarily mean that individuals moving from these habitats stayed in grassland for any length of time. For investigating this, i.e. whether individuals spilled over, remained in the recipient habitat for feeding, reproducing or overwintering, further studies are needed with individual marking or tracking.

In the redundancy analyses, for all three taxa transect position explained a significant part of the variation in the species matrix in CG next to W, but in CG next to M only for spiders. However, the spillover was not caused by all observed species equally. Generally speaking, the species that were found responsible for the spillover are specific for cropland (Thomas et al., 1991; Lemke and Poehling, 2002; Samu and Szinetár, 2002; Frank and Reichhart, 2004; Öberg and Ekblom, 2006). These species can be assumed to build up large populations during the growth of the crop when conditions are favourable. When resources become more scarce at the time of crop senescence they are prone to disperse to adjacent habitats. Furthermore, we think that spillover can be detectable only in frequent species, where the donor habitat bears a lot of individuals. In such cases with simple trapping methods spillover becomes indirectly measurable. Alternatively marking individuals by paints, trace-elements or stable isotopes can deliver a direct proof of spillover, but also only for frequent species (e.g. Madeira and Pons, 2016).

The spillover of predators from crop to non-crop was considered recently (Rand et al., 2006; Blitzer et al., 2012). Our study shows that spillover from cropland to natural habitats can occur before crop harvesting when habitat quality declines, and allows us to improve the understanding of crop arthropod (including predatory species) spillover events to non-crop habitats. More studies over the whole vegetation season should be conducted to examine the ecological consequences of predator spillover effects from cropland to adjacent protected calcareous grassland.

## 5. Conclusion

Neighbourhood identity (wheat or meadow in this case) can shape density and functional consequences of arthropods due to spillover effects. Calcareous grasslands experienced higher arthropod spillover from adjacent cropland than from adjacent meadows. Small calcareous grasslands can be expected to experience relatively stronger effects by nearby cropland than grasslands, since their higher edge-to-interior ratio should result in proportionally higher crop–non-crop spillover of predatory generalist species, potentially enhancing predation rates. Therefore, we conclude that buffer areas such as meadows around protected grassland reserves may help to reduce spillover from arable crops that may compromise the identity, structure and functioning of endangered communities.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2016.10.012>.

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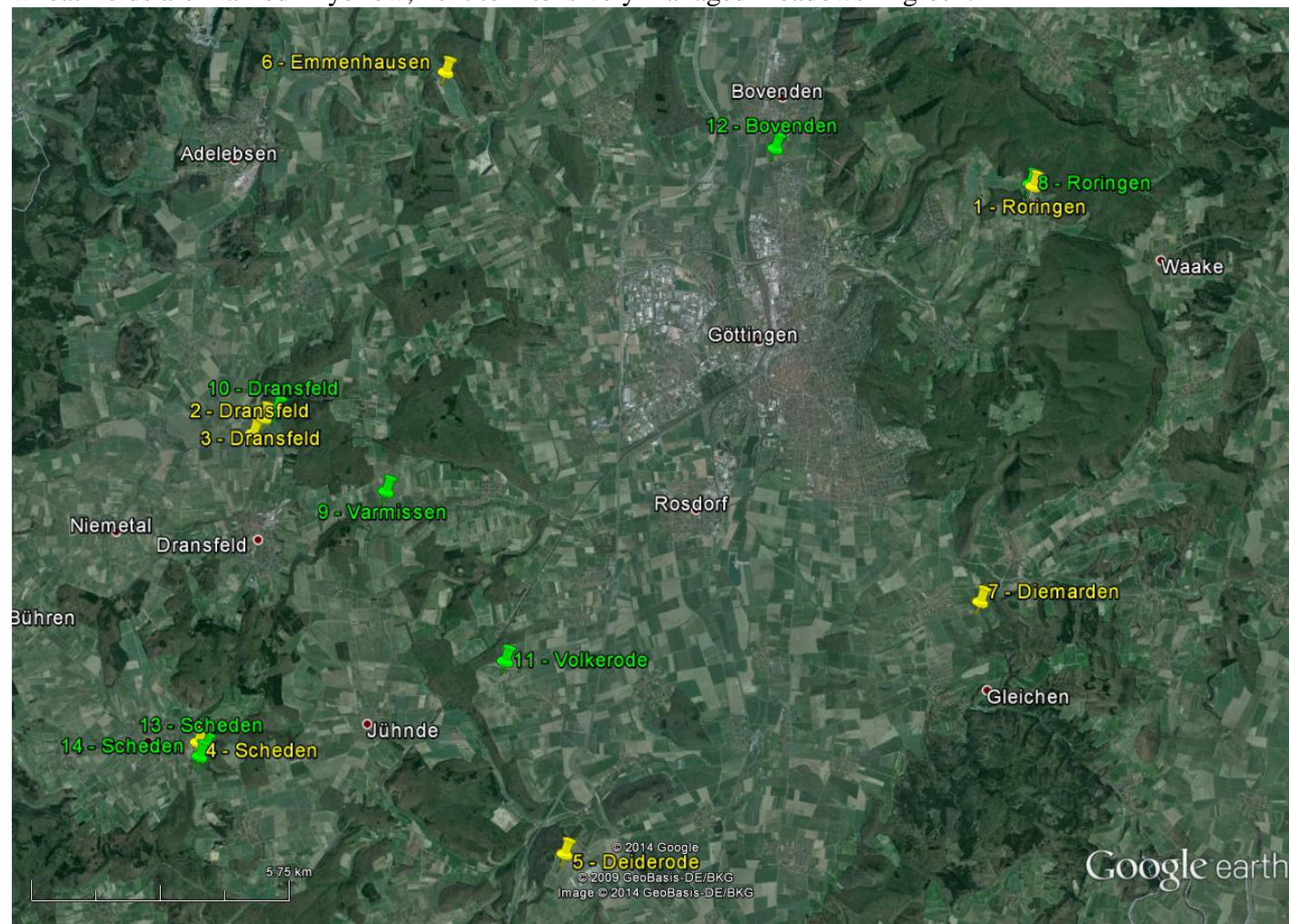
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## SUPPLEMENTARY MATERIAL

### Appendix A1

Location of the 14 calcareous grasslands with the city of Göttingen in the centre of the map. Calcareous grasslands next to intensively managed wheat fields are marked in yellow, next to intensively managed meadows in green.





## Appendix A2

Moran's I test based on nearest-neighbourhood distances for all 14 CG sites. For all three sampled taxa there was no significant spatial autocorrelation (Moran's  $I \pm SD$  for carabids:  $-0.03 \pm 0.02$ ,  $p = 0.386$ ; rove beetles:  $0.19 \pm 0.04$ ,  $p = 0.101$ ; spiders:  $0.05 \pm 0.03$ ,  $p = 0.235$ ; spdep package (Bivand et al., 2014) in R (R Development Core Team, 2013)).

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**Table A1.** Number of individuals of carabids collected in wheat fields, calcareous grasslands next to wheat field (CG-W), meadows and calcareous grasslands next to meadow (CG-M).

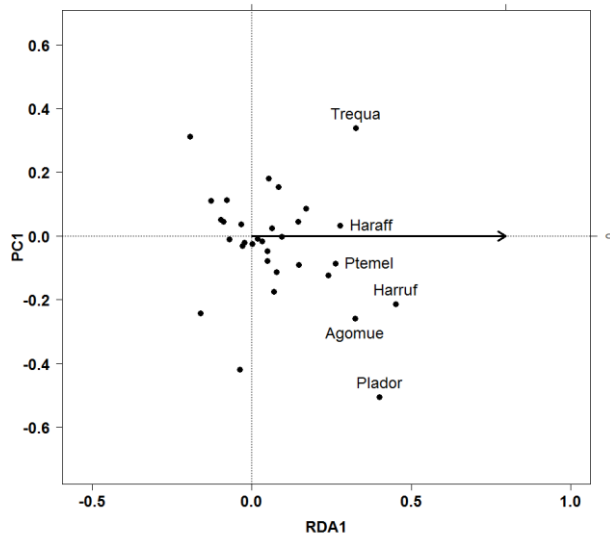
Scientific name*	Wheat	CG-W	Meadow	CG-M
<i>Abax parallelus</i>	0	1	0	0
<i>Agonum muelleri</i>	23	3	1	0
<i>Amara aenea</i>	0	5	4	0
<i>Amara equestris</i>	0	1	1	1
<i>Amara erratica</i> <sup>V</sup>	0	1	0	0
<i>Amara eurynota</i> <sup>V</sup>	2	2	6	1
<i>Amara nitida</i> <sup>3</sup>	0	0	1	1
<i>Amara ovata</i>	0	0	1	0
<i>Asaphidion flavipes</i>	1	0	0	0
<i>Bembidion lampros</i>	14	2	3	0
<i>Bembidion obtusum</i>	7	1	0	0
<i>Brachinus crepitans</i> <sup>V</sup>	33	34	2	0
<i>Brachinus explonens</i>	14	7	0	1
<i>Calathus fuscipes</i>	6	1	12	4
<i>Carabus auratus</i>	2	0	22	3
<i>Carabus convexus</i> <sup>3</sup>	10	6	0	1
<i>Carabus coricaeus</i>	4	1	1	1
<i>Carabus granulatus</i>	4	0	0	0
<i>Carabus nemoralis</i>	4	0	1	2
<i>Harpalus affinis</i>	53	9	0	0
<i>Harpalus distinguendus</i>	7	4	3	1
<i>Harpalus latus</i>	0	1	1	1
<i>Harpalus rufipes</i>	84	4	6	5
<i>Harpalus smaragdinus</i>	2	1	0	0
<i>Loricera pilicornis</i>	2	2	2	0
<i>Microlestes minutulus</i>	0	1	0	0
<i>Nebria brevicollis</i>	2	0	0	0
<i>Platynus dorsalis</i>	313	104	0	0
<i>Poecilus cupreus</i>	9	0	6	11
<i>Pterostichus madidus</i>	6	4	4	10
<i>Pterostichus melanarius</i>	1129	172	137	13
<i>Pterostichus melas</i>	19	17	18	5
<i>Pterostichus niger</i>	0	0	2	1
<i>Pterostichus vernalis</i>	2	0	1	0
<i>Synuchus vivalis</i>	3	5	2	2
<i>Trechus quardistriatus</i>	37	5	2	5
Total	1792	394	239	69

\*Red list status in Germany based on Binot et al. (1998). Codes: 0: extinct or missing, 1: critically endangered, 2: endangered, 3: vulnerable, G: unknown, R: extreme rare, V: near threatened, D: data deficient.

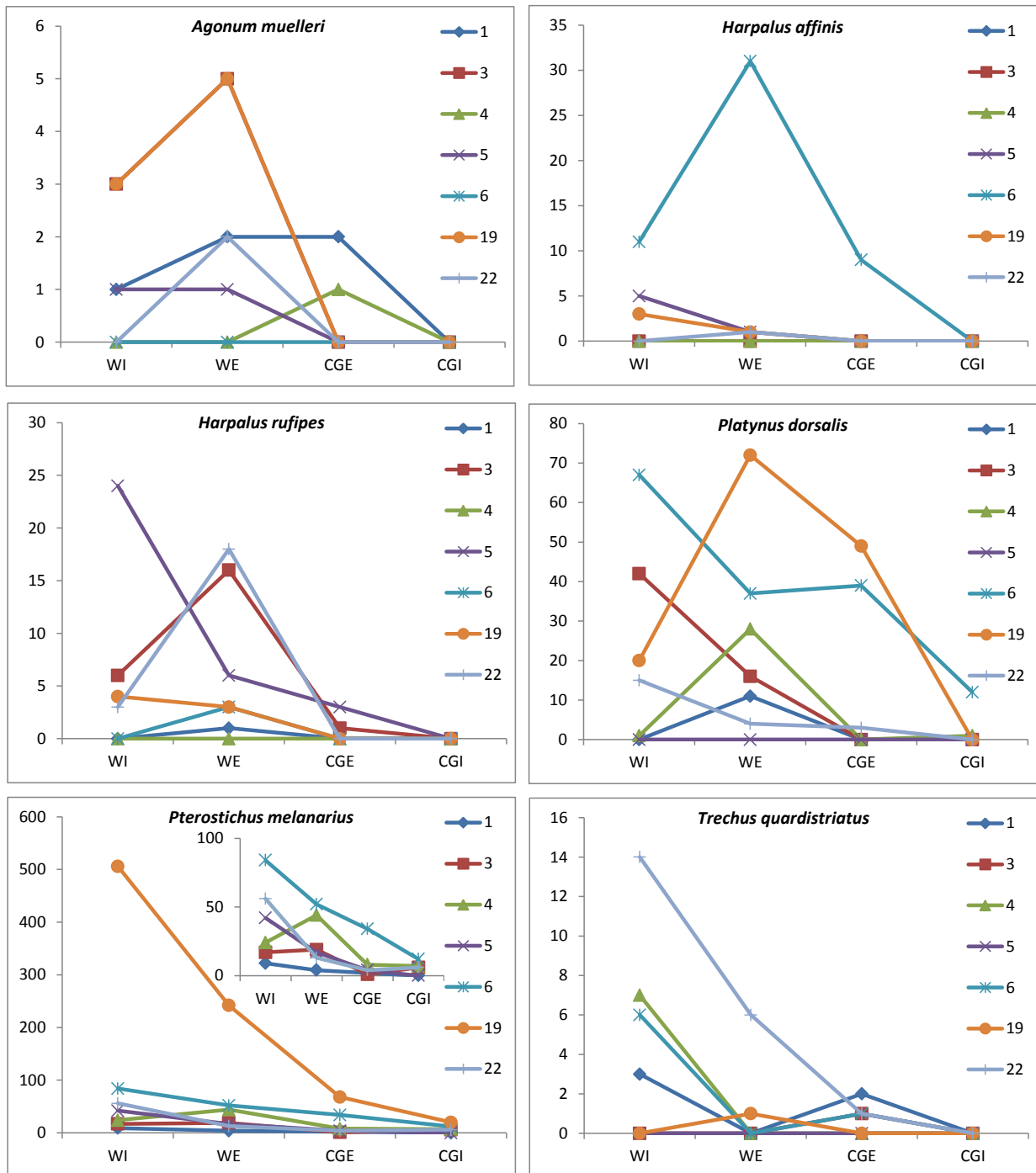
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Binot, M., Bless, R., Boye, P., Gruttke, H., Pretscher, P., (eds): Rote Liste gefährdeter Tiere Deutschlands. – 434 S., Bonn-Bad Godesberg (Bundesamt für Naturschutz); Schriftenreihe für Landschaftspflege und Naturschutz, Heft 55. ISBN 3-89624-110-9.

**Fig. A1.** RDA ordination biplot with carabid species (points) and transect position (arrow: wheat interior → wheat edge → calcareous grassland edge → calcareous grassland interior). Only species reacting in the same direction as transect position and with the highest fraction of variance fitted by the first factorial axis are indicated (Agomue: *Agonum muelleri*, Haraff: *Harpalus affinis*, Harruf: *Harpalus rufipes*, Plador: *Platynus dorsalis*, Ptemel: *Pterostichus melanarius*, Trequa: *Trechus quadristriatus*).



**Fig. A2.** Distribution of individuals of carabid species identified as responsible for transect position effect by RDA in the seven wheat–calcareous grassland study sites. In the case of *Pterostichus melanarius*, there is an inset figure without study site 19, where by far the most individuals were captured. WI: wheat interior, WE: wheat edge, CGE: calcareous grassland edge, CGI: calcareous grassland interior.



**Table A2.** Number of individuals of rove beetles collected in wheat fields, calcareous grasslands next to wheat field (CG-W), meadows and calcareous grasslands next to meadow (CG-M).

Scientific name*	Wheat	CG-W	Meadow	CG-M
<i>Aleochara bilineata</i>	0	0	2	0
<i>Aleochara bipustulata</i>	0	0	2	0
<i>Aleochara cuniculorum</i> <sup>3</sup>	0	0	0	1
<i>Aleochara curtula</i>	0	0	1	0
<i>Aleochara ruficornis</i>	0	1	0	0
<i>Aloconota sulcifrons</i>	1	0	0	0
<i>Amischa analis</i>	4	0	7	0
<i>Anotylus rugosus</i>	1	0	2	0
<i>Atheta britanniae</i>	0	2	0	0
<i>Atheta crassicornis</i>	0	0	1	1
<i>Atheta dilaticornis</i> <sup>2</sup>	0	0	0	1
<i>Atheta heymesii</i> <sup>3</sup>	0	2	2	0
<i>Bolitobius castaneus</i>	0	1	0	0
<i>Brachida exigua</i> <sup>3</sup>	0	9	0	0
<i>Callicerus obscurus</i>	1	0	0	0
<i>Dinaraea angustula</i>	0	0	4	2
<i>Drusilla canaliculata</i>	339	939	681	370
<i>Falagrioma thoracica</i>	207	779	204	376
<i>Geostiba circellaris</i>	20	0	0	0
<i>Heterothops niger</i>	0	0	2	0
<i>Ilyobates bennetti</i>	0	1	3	0
<i>Ischnosoma splendidum</i>	0	1	1	0
<i>Lathrobium fulvipenne</i>	2	0	0	0
<i>Lathrobium pallidum</i>	2	1	0	1
<i>Ocalea badia</i>	0	1	0	0
<i>Ocypus brunnipes</i>	0	2	0	0
<i>Ocypus fuscatus</i>	0	1	1	2
<i>Ocypus olens</i>	0	0	0	1
<i>Ocypus ophthalmicus</i>	1	1	1	3
<i>Ocypus picipennis</i>	0	0	0	1
<i>Paederus brevipennis</i>	0	6	1	1
<i>Parabolitobius formosus</i>	1	2	1	0
<i>Philonthus addendus</i>	1	0	0	0
<i>Philonthus carbonarius</i>	0	8	6	0
<i>Philonthus cognatus</i>	0	0	22	1
<i>Philonthus corruscus</i>	1	0	0	0
<i>Philonthus rotundicollis</i>	0	0	1	0
<i>Philonthus succicola</i>	0	0	1	0
<i>Plataraea brunnea</i>	0	0	1	0
<i>Platydracus latebricola</i>	0	2	1	2
<i>Platydracus stercorarius</i>	13	28	48	21
<i>Pycnota paradoxa</i>	9	9	0	0
<i>Quedius cruentus</i>	0	1	0	0
<i>Quedius longicornis</i>	0	0	0	1
<i>Quedius molochinus</i>	0	0	1	2
<i>Rugilus mixtus</i>	0	1	0	0
<i>Rugilus rufipes</i>	0	1	0	0
<i>Sepedophilus marshami</i>	2	0	0	0
<i>Staphylinus caesareus</i>	0	0	1	2
<i>Stenus clavicornis</i>	2	4	2	4

**Table A2.** Continued.

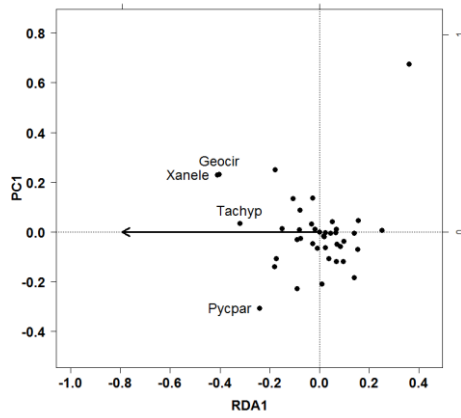
<b>Scientific name*</b>	<b>Wheat</b>	<b>CG-W</b>	<b>Meadow</b>	<b>CG-M</b>
<i>Stenus providus</i>	1	1	1	0
<i>Sunius melanocephalus</i>	1	0	0	0
<i>Tachinus corticinus</i>	0	0	1	0
<i>Tachinus rufipes</i>	9	3	94	4
<i>Tachyporus chrysomelinus</i>	4	16	9	2
<i>Tachyporus hypnorum</i>	6	0	1	2
<i>Tachyporus nitidulus</i>	4	2	1	0
<i>Xantholinus dvoraki</i>	1	0	0	0
<i>Xantholinus elegans</i>	67	39	19	18
<i>Xantholinus linearis</i>	1	7	2	3
<i>Xantholinus tricolor</i>	31	5	4	3
<b>Total</b>	<b>732</b>	<b>1876</b>	<b>1132</b>	<b>825</b>

\*Red list status in Germany based on Binot et al. (1998). Codes: 0: extinct or missing, 1: critically endangered, 2: endangered, 3: vulnerable, G: unknown, R: extreme rare, V: near threatened, D: data deficient.

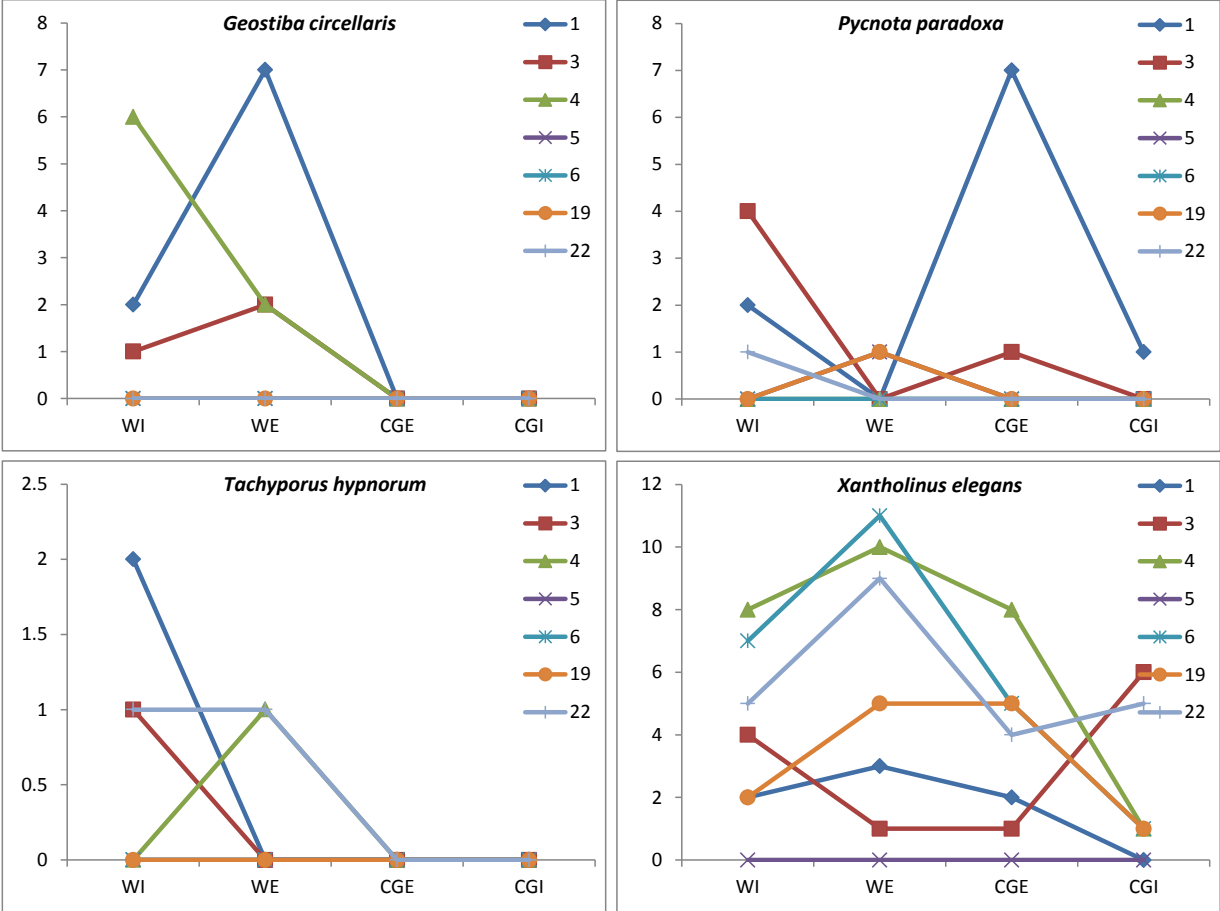
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Binot, M., Bless, R., Boye, P., Gruttke, H., Pretscher, P., (eds): Rote Liste gefährdeter Tiere Deutschlands. – 434 S., Bonn-Bad Godesberg (Bundesamt für Naturschutz); Schriftenreihe für Landschaftspflege und Naturschutz, Heft 55. ISBN 3-89624-110-9.

**Fig. A3.** RDA ordination biplot with rove beetle species (points) and transect position (arrow: wheat interior → wheat edge → calcareous grassland edge → calcareous grassland interior). Only species reacting in the same direction as transect position and with the highest fraction of variance fitted by the first factorial axis are indicated (Geocir: *Geostiba circellaris*, Pycpar: *Pycnota paradoxa*, Tachyp: *Tachyporus hypnorum*, Xanele: *Xantholinus elegans*).



**Fig. A4.** Distribution of individuals of rove beetle species identified as responsible for transect position effect by RDA in the seven wheat–calcareous grassland study sites. WI: wheat interior, WE: wheat edge, CGE: calcareous grassland edge, CGI: calcareous grassland interior.





**Table A3.** Number of individuals of spiders collected in wheat fields, calcareous grasslands next to wheat field (CG-W), meadows and calcareous grasslands next to meadow (CG-M).

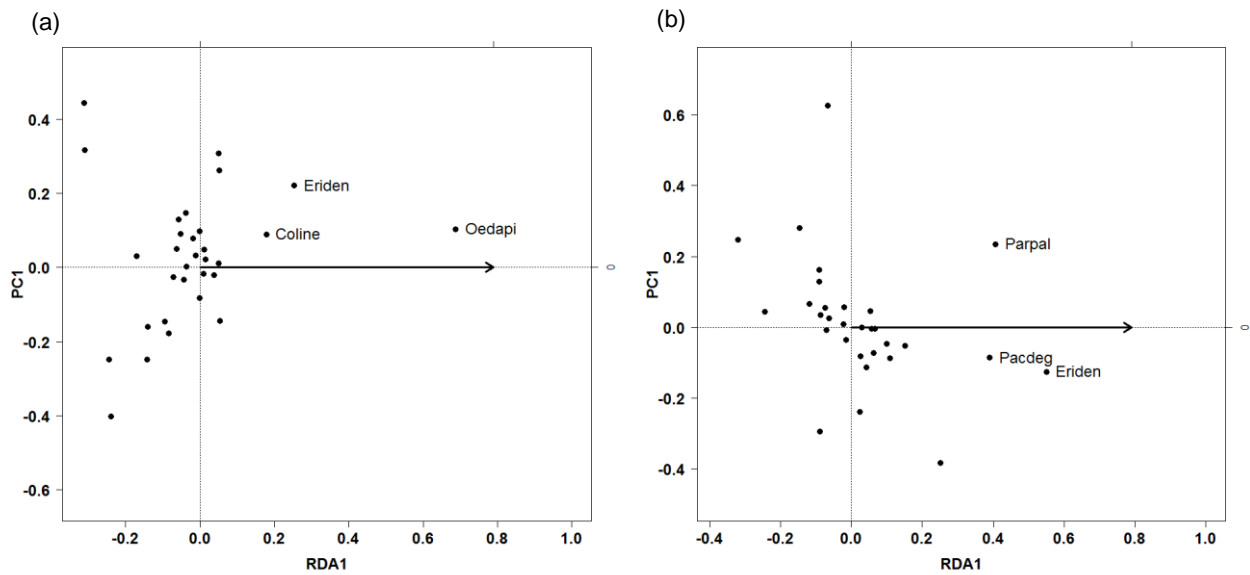
Scientific name*	Wheat	CG-W	Meadow	CG-M
<i>Alopecosa pulverulenta</i>	1	11	20	19
<i>Asagena phalerata</i>	0	1	0	0
<i>Aulonia albimana</i>	2	21	16	60
<i>Bathypantes parvulus</i>	2	3	0	1
<i>Centromerus sylvaticus</i>	0	0	1	0
<i>Clubiona neglecta</i>	0	0	3	0
<i>Cnephalocotes obscurus</i>	0	1	0	0
<i>Collinsia inerrans</i>	15	0	7	0
<i>Diplostyla concolor</i>	20	6	2	1
<i>Drassodes lapidosus</i>	1	0	0	1
<i>Drassyllus praeficus</i>	1	8	6	7
<i>Drassyllus pusillus</i>	0	0	1	1
<i>Drassyllus villicus</i> <sup>3</sup>	1	0	0	0
<i>Dysdera erythrina</i> <sup>R</sup>	0	1	0	0
<i>Dysdera ninnii</i>	0	0	2	0
<i>Erigone dentipalpis</i>	66	21	173	1
<i>Haplodrassus signifer</i>	2	1	3	13
<i>Histoipona torpida</i>	0	1	0	0
<i>Meioneta rurestris</i>	9	6	7	0
<i>Meioneta simplicatarsis</i> <sup>3</sup>	1	0	0	0
<i>Micrargus herbigradus</i>	1	3	0	0
<i>Micrargus subaequalis</i>	0	0	1	0
<i>Neottiura bimaculata</i>	0	0	0	1
<i>Oedothorax apicatus</i>	693	31	25	1
<i>Oedothorax retusus</i>	35	5	14	0
<i>Ozyptila trux</i>	0	5	0	0
<i>Pachygnatha degeeri</i>	6	9	80	8
<i>Pachygnatha listeri</i>	1	0	0	0
<i>Pardosa palustris</i>	3	3	35	4
<i>Pardosa pullata</i>	25	54	42	24
<i>Phrurolithus festivus</i> <sup>3</sup>	9	10	8	14
<i>Scotina celans</i>	0	0	0	9
<i>Semljicola faustus</i>	4	1	1	0
<i>Tenuiphantes tenuis</i>	25	84	37	26
<i>Trochosa terricola</i>	8	10	19	14
<i>Walckenaeria vigilax</i>	6	2	2	0
<i>Xysticus bifasciatus</i>	0	0	1	0
<i>Xysticus kochi</i>	1	1	2	2
<i>Zelotes latreillei</i>	0	6	7	8
<i>Zelotes petrensis</i>	0	0	0	2
<i>Zora spinimana</i>	1	4	0	2
Total	939	309	515	219

\*Red list status in Germany based on Binot et al. (1998). Codes: 0: extinct or missing, 1: critically endangered, 2: endangered, 3: vulnerable, G: unknown, R: extreme rare, V: near threatened, D: data deficient.

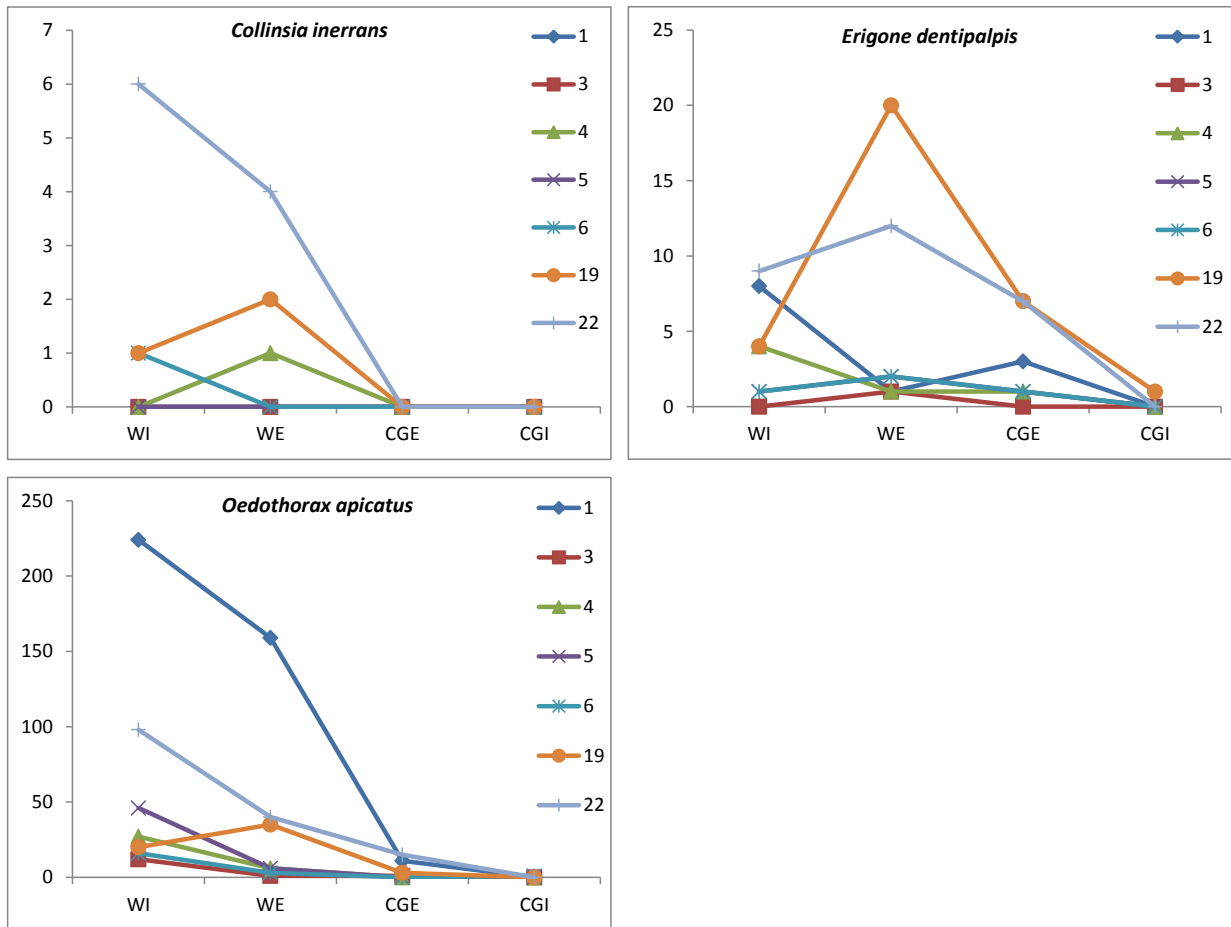
#### Reference

Binot, M., Bless, R., Boye, P., Gruttke, H., Pretscher, P., (eds): Rote Liste gefährdeter Tiere Deutschlands. – 434 S., Bonn-Bad Godesberg (Bundesamt für Naturschutz); Schriftenreihe für Landschaftspflege und Naturschutz, Heft 55. ISBN 3-89624-110-9.

**Fig. A5.** RDA ordination biplots with spider species (points) and transect position (arrow: wheat/meadow interior → wheat/meadow edge → calcareous grassland edge → calcareous grassland interior) in (a) calcareous grassland–wheat field and (b) in calcareous grassland–meadow neighbourhood types. Only species reacting in the same direction as transect position and with the highest fraction of variance fitted by the first factorial axis are indicated (Coline: *Collinsia inerrans*, Eriden: *Erigone dentipalpis*, Oedapi: *Oedothorax apicatus*, Pacdeg: *Pachygnatha degeeri*, Parpal: *Pardosa palustris*).



**Fig. A6.** Distribution of individuals of spider species identified as responsible for transect position effect by RDA in the seven wheat–calcareous grassland study sites. WI: wheat interior, WE: wheat edge, CGE: calcareous grassland edge, CGI: calcareous grassland interior.



**Fig. A7.** Distribution of individuals of carabid species identified as responsible for transect position effect by RDA in the seven meadow–calcareous grassland study sites. In case of *Erigone dentipalpis*, there is an inset figure without the study site 11, where by far the most individuals were captured. WI: wheat interior, WE: wheat edge, CGE: calcareous grassland edge, CGI: calcareous grassland interior.

