

## Journal Pre-proof

Can rare arable plants benefit biological pest control potential of cereal aphids in croplands?

Alina Twerski , Harald Albrecht , Róbert Gallé , Fabian Sauter , Péter Császár , Christina Fischer

PII: S1439-1791(22)00098-6  
DOI: <https://doi.org/10.1016/j.baae.2022.12.003>  
Reference: BAAE 51529



To appear in: *Basic and Applied Ecology*

Received date: 24 November 2021

Accepted date: 11 December 2022

Please cite this article as: Alina Twerski , Harald Albrecht , Róbert Gallé , Fabian Sauter , Péter Császár , Christina Fischer , Can rare arable plants benefit biological pest control potential of cereal aphids in croplands?, *Basic and Applied Ecology* (2022), doi: <https://doi.org/10.1016/j.baae.2022.12.003>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2022 Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie.  
This is an open access article under the CC BY-NC-ND license  
(<http://creativecommons.org/licenses/by-nc-nd/4.0/>)

## Journal

Special issue (Managing agrobiodiversity) of *Basic and Applied Ecology*

## Title

**Can rare arable plants benefit biological pest control potential of cereal aphids in croplands?**

## Authors

Alina Twerski \*<sup>a, b</sup>, Harald Albrecht<sup>a</sup>, Róbert Gallé<sup>c</sup>, Fabian Sauter<sup>a</sup>, Péter Császár<sup>d</sup>,  
Christina Fischer<sup>a, e</sup>

<sup>a</sup> Restoration Ecology, School of Life Sciences, Technical University of Munich, Emil-Ramann-Str. 6, 85354 Freising, Germany

<sup>b</sup> Faculty of Sustainability, Leuphana University Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany

<sup>c</sup> “Lendület” Landscape and Conservation Ecology, Institute of Ecology and Botany, Centre for Ecological Research, Vácrátót, Hungary

<sup>d</sup> University of Szeged, Doctoral School of Environmental Sciences, 6720, Rerrich Béla tér 1., Szeged, Hungary

<sup>e</sup> Faunistics and Wildlife Conservation, Department of Agriculture, Ecotrophology and Landscape Development, Anhalt University of Applied Sciences, Strenzfelder Allee 28, 06406 Bernburg, Germany

\* **Corresponding author.** Tel.: +49 8161 714142; Fax: +49 8161 71-4143

E-Mail Adresse: alina.twerski@tum.de

### **Keywords**

agroecology, spider, carabid, weed, biocontrol potential, arable land, trophic interaction, agricultural landscape, phytodiversity

### **Highlights**

- Rare arable plant cover can reduce the total number of aphids
- Cereal aphids decreased through predation of active hunting spiders
- Direct effects of rare arable plants only on active hunting spiders

### **Abstract**

In agricultural landscapes, arable plants are negatively affected by management intensification. These species can fulfill various ecosystem functions, such as biological pest

control, by supporting predators. The ecosystem functions of common plant species are widely known. By contrast, the contribution of rare arable plants (RAPs) to biocontrol in cereal fields remains poorly understood. This study investigated the effect of RAPs on biocontrol potential. We compared cropped plots with and without sowing of rare and threatened arable plant species and investigated the effects on cereal aphids and their antagonistic predators, active hunting, and web-building spiders, as well as carnivorous/omnivorous carabids. We counted the total number of aphids on cereal shoots and trapped ground-dwelling arthropods on an experimental field and on 10 agricultural farms in the vicinity of Munich, Germany, in 2018 and 2019. The effects of the presence of RAP were analyzed using linear mixed-effect models, whereas cover of RAPs was analyzed using structural equation models. Linear models revealed that the presence of RAPs did not significantly affect the aphid density and the activity densities of spiders and carabids. Structural equation models revealed direct negative effects of RAP cover on aphid density. However, no indirect effects via the predators of aphids were detected. Direct negative effects of active hunting spiders on aphids were determined, but not of the other potential predators. The weak impact of RAPs on spiders and carabids suggests that the species richness of plant communities exerts only little influence on organisms at higher trophic levels. Our results suggest that RAPs may indirectly impact aphid infestation, however, the activity density of spiders and carabids were unsuitable indicators for such interactions.

## Introduction

Over the past decades, intensification of agricultural production has substantially increased crop yields. However, it has also become a threat for numerous species and has caused a strong decline in agrobiodiversity (Matson, Parton, Power, & Swift, 1997; Raven & Wagner, 2021; Stoate et al., 2001). Increased synthetic fertilizer and pesticide usage, reduced crop

diversity, increased crop density, narrow crop rotations, loss of natural and semi-natural habitats, and the homogenization of agricultural landscapes have been the main drivers causing this decline (Stoate et al., 2001). As biodiversity is strongly associated with ecosystem functions (Cardinale et al., 2012), this loss of agrobiodiversity may diminish associated ecosystem functions, including biological pest control (biocontrol) through predator species (Hooper et al., 2005).

Cereal aphids are among the most harmful agricultural pests, and their infestations can substantially reduce crop yield, causing economic losses (Dedryver, Le Ralec, & Fabre, 2010). To control aphid abundance and reduce crop damages, farmers commonly apply pesticides, which can in turn also reduce the number of natural predators (Geiger et al., 2010). Numerous authors have reported on the importance of beneficial insects for aphid control (Martin et al., 2019; Schmidt et al., 2003; Thies et al., 2011), which constitutes an alternative biocontrol management strategy (Ben-Issa, Gomez, & Gautier, 2017; Landis, Wratten, & Gurr, 2000). The concept of biocontrol involves the use of living organisms for preventing or reducing damage caused by harmful organisms (Stenberg et al., 2021). In biocontrol, considering the entire interaction networks and including trait-based functional groups are necessary (De Heij & Willenborg, 2020; Letourneau & Bothwell, 2008). The prey capture strategies (active hunting vs. web-building) of spiders (Araneae) and feeding traits (carnivorous/omnivorous vs. predominantly granivorous) of carabids (Carabidae) may affect predator communities through cannibalism and intraguild predation (multiple predator taxa compete for prey and consume each other) and may cause a reduction in biocontrol function (Currie, Spence, & Niemelä, 1996; Frank, Shrewsbury, & Denno, 2010).

Spiders and carabid beetles are generalist biocontrol agents in agroecosystems that can improve ecosystem services (Dainese et al., 2019; González, Seidl, Kadlec, Ferrante, & Knapp, 2020). Because aphids are a significant part of their diet, facilitation of these predators

constitutes effective biocontrol against aphids (Diekötter, Wamser, Wolters, & Birkhofer, 2010; Symondson, Sunderland, & Greenstone, 2002). Biocontrol can be enhanced by managing habitats and landscapes to ensure favorable conditions for natural enemies (Landis et al., 2000). Such management may include the provision of alternative food resources, the creation of moderate microclimate, and the provision of shelter from adverse abiotic conditions such as extreme weather conditions or pesticides (Landis et al., 2000). Habitat management that diversifies the vegetation structure in terms of plant species richness, vegetation height coverage, and density may positively affect spiders and carabids, and therefore, it improves the biocontrol potential within fields and at the landscape scale (Diehl, Mader, Wolters, & Birkhofer, 2013; Gaba et al., 2020; Schirmel, Thiele, Entling, & Buchholz, 2016).

The non-crop vegetation within cereal fields, namely common arable plants, can fulfill various ecosystem functions such as the provision of food and habitat for arthropods (Bretagnolle & Gaba, 2015; Kells, Holland, & Goulson, 2001; Marshall et al., 2003; Twerski, Albrecht, Fründ, Moosner, & Fischer, 2022). Gaba et al. (2020) reported that arable plant diversity enhanced the multifunctionality of arable land. More specifically, arable plant diversity increased the species richness and abundance of carabids and thus also aphid predation rates. Similarly, Seyfulina (2005) identified a positive relationship between common arable plants and the abundance of web-building spiders, and the meta-analysis of Letourneau et al. (2011) proved the positive effects of plant diversity on enemy enhancement and herbivore suppression in agricultural crops. However, because of agricultural intensification, 35% of the typical arable plants of Germany are presently recorded in the red list (Metzing, Garve, & Matzke-Hajek, 2018). Formerly common arable species have become rare (Hurford, Wilson, & Storkey, 2020; Walker et al., 2007) and the impact of their decline

and extinction on ecosystem functionality is unclear. Therefore, studying the biocontrol potential of rare and endangered arable plants is crucial.

In this study, we sowed a mixture of 10 rare arable plant (RAP) species (according to red list status and/or decline in abundance) on an experimental field to study the relationships between RAP, ground-dwelling arthropods, and aphid densities. To verify the results under practical field conditions, experimental plots were established on 10 agricultural farms in the vicinity of Munich, southern Germany. We counted the total number of aphids on 100 shoots per plot and placed pitfall traps to measure the activity densities of spiders and carabids. Our aim was to answer the following research questions:

1. How does the occurrence of RAP affect the activity density of aphids and their ground-dwelling predators, active hunting, and web-building spiders, as well as carnivorous/omnivorous carabids?
2. How do crop and RAP cover affect food web interactions between aphids, spiders, and carabids with distinct feeding behavior?

## Materials and methods

### *Study area and experimental design*

The study was conducted in the Munich Plain in Bavaria, southern Germany, in 2018 and 2019 (see Appendix A Fig. 1). The area is characterized by nutrient-poor and shallow soils with a high percentage of calcareous gravel in the top soil, which leads to a low water holding capacity and high pH levels (Fetzer et al., 1986). Barley, rye, oilseed rape, and potatoes are the most frequent crops in this region (Bayerisches Landesamt für Statistik, 2016). The mean annual temperature and precipitation are 9.2 °C and 757 mm, respectively (Station: Munich airport ID: 1262; DWD, 1993–2019). On 10/06/2019, a strong hailstorm damaged the crops

and vegetation on the experimental field (DWD, 2019; further details: Twerski, Fischer, & Albrecht, 2021). After the hailstorm, the vegetation structure had changed completely, so that the data from the experimental field in 2019 were excluded from our analysis.

To study biocontrol potential under experimental and practical field conditions, one experimental field with randomized blocks was used in Gräfelfing, southwest of Munich, and in addition, 10 private farm fields that were distributed over the Munich Plain were used (Twerski et al., 2021). The effects of RAP sowing on biocontrol potential were tested by sowing 10 archaeophytic RAP species: *Buglossoides arvensis*, *Consolida regalis*, *Kickxia spuria*, *Lathyrus tuberosus*, *Legousia speculum-veneris*, *Neslia paniculata*, *Papaver rhoeas*, *Sherardia arvensis*, *Silene noctiflora*, and *Valerianella dentata* (see Appendix A Fig. 2; species nomenclature according to The Plant List, 2013). These species were classified as rare based on the red list status of eight species (Metzing et al., 2018; Scheuerer & Ahlmer, 2003). Two species *Lathyrus tuberosus* and *Papaver rhoeas* rarely occur and decrease in the Munich Plain (Albrecht, 1989; Scheuerer & Ahlmer, 2003). Further selection criteria were a low to intermediate competitive capacity and the affiliation to different plant families (see Appendix A: Table 1). RAP sowing was conducted manually at the start of the experiments in March 2018. Sowing densities varied from 50 to 300 seeds per square meter (Twerski et al., 2021). The management of the private farms and the experimental field was comparable to each other: spring crops in the first, autumn crops in the second vegetation period. During the experiment, no mechanical weed control and no pesticide or fertilizer were applied on any of the experimental plots.

#### *Experimental field*

The effects of RAPs were tested under controlled conditions on experimental plots established on an arable field owned by the organic farming Seidlhof Foundation in Gräfelfing, southwest of Munich (48°07'42" N, 11°24'58" E; see Appendix A Fig. 1). There, two treatments (crops



with and without sowing of RAP) were applied. In the first year of the study (2018), hulless oat was sowed in March, which was followed by spelt in September 2018. Between harvesting and sowing, ploughless tillage with a rotary cultivator was performed. The treatment with RAPs (+RAP) had 20 replications, and the treatment without RAPs (-RAP) had 10 replications per study year. The data that were analyzed in this study were part of an overarching project with various research questions and treatment combinations. Therefore, our treatments varied in the number of replicates. The plot size was  $6.0 \times 2.3$  m, and plots were arranged in a randomized block design with five blocks and two (-RAP) or four (+RAP) replicates per block (Twerski et al., 2021).

### *Field study*

To test the effects of RAPs on biocontrol potential not only on one experimental field, but also under different practical and environmental conditions, additionally 10 fields on different agricultural farms in the Munich Plain were selected (see Appendix A Fig. 1). At each field, a +RAP and a -RAP plot were established. Plots measured  $5.0 \times 2.3/3.0$  m (adapted to the machining width of the farms) and were situated 25.0 m apart. In the first study year, all sown crops were spring cereals. In the second study year, winter cereals were sown. The choice of cereal crops, crop sowing densities, and row distances varied among farms (see Appendix A: Table 2; Twerski et al., 2021). Due to the paired design, landscape characteristics were identical for the +RAP and -RAP plots of the agricultural farms (landscape characteristics within 1000 m radius around the different agricultural farms are shown in Appendix A: Table 3 and Table 4).

### *Aphid and ground-dwelling predator sampling*

Aphids were counted on 50 randomly selected shoots in two crop rows (100 shoots in total) per plot and sampling round. To reduce edge effects, rows with less than 20 cm to the edge

were excluded. Counting took place twice a year, that is, once during crop flowering (BBCH 61; beginning of aphid population growth) and once during crop milk ripening stage (BBCH 75).

To compare the activity densities of ground-dwelling predators between treatments with and without RAPs, spiders and carabids were sampled using pitfall traps, which were set up after each round of aphid counting (one per plot, twice per year; Brown & Matthews, 2016). The traps (with a volume of 400 mL and a width of 90 mm) were filled with a mixture of water and ethylene glycol (1:1; 120 mL) and dug at ground level into the middle of each plot. The traps were covered with a plastic roof and a metal grid (15 × 15 mm grid size) to avoid overflowing during rain and accidental rodent catches (Császár, Torma, Gallé-Szpisjak, Tölgyesi, & Gallé, 2018). The traps were activated for 7 days. Subsequently, all arthropods were transferred into 70% ethanol. Spiders and carabids were identified to species according to Nentwig, Blick, Gloor, Hänggi, and Kropf (2019) and Hurka (1996). Carabid feeding behavior was classified according to Homburg, Homburg, Schäfer, Schuldt, and Assmann (2014). To simplify the dataset, carabid feeding behavior was classified as predominantly granivorous (species mainly feeds on seeds and fruits) or as carnivorous/omnivorous, because carnivorous and omnivorous species are potentially feeding on aphids and other non-plant material. Spider hunting strategy (active hunter or web-builder) was used as the feeding trait according to Cardoso, Pekár, Jocqué, and Coddington (2011). For statistical analyses, the numbers of aphids, spiders, and carabids were summed for the two sampling rounds per plot.

#### *Vegetation sampling*

To analyze the effect of vegetation on ground-dwelling predators and aphids, vegetation surveys were performed once per study year in July. The cover of each plant species (%) was visually estimated per plot. Subsequently, plant species were divided into (1) RAP and (2)

spontaneously occurring arable plants (SAP). Finally, crop cover (%) per plot was estimated. Because crop and SAP plant cover were negatively correlated in the field study ( $r_s = -0.59$ ,  $p < 0.001$ ,  $n = 38$ , Spearman's rank correlation), only crop and RAP cover were included in the analyses for both the experimental field and the field study.

### *Statistical analyses*

All statistical analyses were performed with the software R, version 4.0.3 (R Core Team, 2020). The experimental field and field study were analyzed separately. The effects of treatments (+/-RAP) on the response variables (total number of aphids and activity density of ground-dwelling predators) were modeled using linear mixed-effect models with implemented maximum likelihood (*lme*; library *nlme* version 3.1-150, Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2020). The two study years of the field study were analyzed together, and "year" was included as a fixed effect. On the experimental field "block" ( $n = 5$ ) and on the field study "agricultural farm" ( $n = 10$ ) were used as random intercepts to account for spatial nestedness. The response variables were log+1, log or square root transformed. In the text, means  $\pm$  SD are given (*ddply*; library *plyr* version 1.8.6, Wickham, 2011).

To determine the impact of RAPs and crop cover on the direct and indirect food web interactions between aphids and ground-dwelling predator densities, structural equation models (SEM) were applied (*psem*; library *piecewiseSEM* version 2.1.0, Lefcheck, 2016). The analysis was based on the following hypothesized relationships: (1) vegetation structure (crop and RAP cover) affects aphid abundance and ground-dwelling predator activity densities (Diehl et al., 2013; Honěk & Jarošík, 2000; Langellotto & Denno, 2004; Schirmel et al., 2016); (2) active hunting spiders and carnivorous/omnivorous carabids decimate aphid abundance (Diehl et al., 2013; Schmidt et al., 2003; Thies et al., 2011); and (3) interactions between activity densities of carnivorous/omnivorous carabids, active hunting spiders, and

predominantly granivorous carabids (De Heij & Willenborg, 2020; Rusch et al., 2016; Straub, Finke, & Snyder, 2008; for the full SEM model, see **Appendix A Fig. 3, Lists 1 and 2**). The component models were adapted to the linear mixed-effect models: the data for the experimental field and field study were analyzed separately. For the experimental field, the data of 2019 were excluded from the analyses; the two years of the field study were analyzed together and “year” was included as a fixed effect in all hypothesized relationships; the variable transformations and random factors were the same as those described above.

Because landscape characteristics may affect biocontrol, the proportion of semi-natural habitats and cropland were included as fixed effects in the linear mixed effects models. Since these analyses showed only marginal effects, we decided not to account for landscape parameters in this study. However, the results are shown in the Appendix A Tables 5 and 6.

## Results

The total number of aphids per 100 shoots was lower, although not significantly, when rare arable plants (RAP) were sown (see Appendix A: Table 7). For the field study, the number of aphids per 100 shoots varied between years ( $103.8 \pm 86.5$  in 2018 and  $21.2 \pm 22.3$  in 2019) and farms (lowest abundance:  $12.8 \pm 8.5$ ; highest abundance:  $104.4 \pm 139.7$ ).

In total, 1622 adult spiders from 47 species were recorded in this study: 360 individuals and 26 species on the experimental field in 2018 and 1262 individuals from 42 species in the field study during both years (see Appendix A: Tables 7 and 8). We recorded 1678 carabids from 63 species on the experimental field (215 individuals; 20 species; only 2018) and the field study (1463 individuals; 50 species; both study years; see Appendix A: Tables 7 and 9).

No significant effects of the presence of RAPs on the number of aphids, activity densities of active hunting and web-building spiders, or on carnivorous/omnivorous and predominantly

granivorous carabids were observed (in both the experimental field and field study; Table 1). In the field study, the number of aphids and activity densities of active hunting spiders and carnivorous/omnivorous carabids varied significantly between the study years (Table 1).

A direct negative relationship between the total number of aphids and RAP cover occurred only on the experimental field. No such direct effects were observed between crop cover and the total number of aphids neither on the experimental field nor in the field study. In the field study, increasing crop cover was related to a decreasing activity density of active hunting spiders and predominantly granivorous carabids, and RAP cover decreased the activity density of active hunting spiders. Regarding the effect of predators on the numbers of aphids, we observed a decline with increased activity densities of active hunting spiders on the experimental field, but not in the field study. No measurable effects exerted by carnivorous/omnivorous carabids on the total number of aphids were observed. No interactions between the activity densities of active hunting spiders and predominantly granivorous carabids occurred. The activity density of carnivorous/omnivorous carabids and active hunting spiders revealed a positive relationship in the field study. However, the number of aphids and the activity densities of active hunting and web-building spiders and of carnivorous/omnivorous carabids showed significant variation between the study years (Fig. 1 and Appendix A: Table 10). Fisher's C statistics, p-values, and marginal and conditional  $R^2$ -values are presented in Fig. 1 and Appendix A: Table 10.

## Discussion

### *Effects of rare arable plants on aphids and predators*

Higher rare arable plant (RAP) cover was associated with decreasing numbers of aphids on the experimental field. This result may support the associated resistance-hypothesis (Barbosa et al., 2009), which states that neighboring plant species can strengthen the associated resistance of crops against herbivores. The mechanisms implicit in the associated resistance

hypothesis are diverse: Neighboring plants can camouflage the crops (Perrin & Phillips, 1978) and can therefore decrease their visibility for herbivore pests (*sensu* Feeny, 1976). Since RAPs are rare by definition, they are not expected to have a large impact on aphids when considered alone. Thus, also our study showed only small effects of RAP on aphid densities. However in interaction with other spontaneous plants RAPs may impact biocontrol.

In contrast to Gaba et al. (2020), Langellotto and Denno (2004), and Letourneau et al. (2011), the increased phytodiversity of RAP sowing in our study did not enhance the activity densities of spiders and carabids neither on the experimental field nor in the field study. The low effects of RAP on predators in our study may be caused by the high species richness of resident arable plants (Twerski et al., 2021), which may already have provided suitable habitats for ground-dwelling predators and reduced the negative effects of bare ground, for example, on carabids (Seidl, González, Kadlec, Saska, & Knapp, 2020). Therefore, even the substantial increase of total plant cover and species richness after sowing the rare and low competitive arable plants (Twerski et al., 2021) could have been insufficient in affecting higher trophic levels due to the already high suitability of the habitats. Such a saturation effect became evident in the relationship curve of plant and predator diversity in a grassland experiment (Scherber et al., 2010). Reduced positive effects of plant species richness for organisms of higher trophic levels were also observed in a grassland biodiversity experiment (Scherber et al., 2010). However, the SEM calculated for the field study revealed that higher RAP cover decreased the activity density of active hunting spiders (but see Seyfulina, 2005). Introducing RAPs into a dense arable plant community may have even impaired living conditions for spiders. Furthermore, because carabids and spiders in agricultural fields often have a broad food spectrum and no diet specialization compared to vegetation-associated taxa, plant species richness generally seems to be less important for ground-dwelling arthropods (Ebeling et al., 2018). Moreover, landscape composition can affect ground-dwelling arthropods

(Schmidt, Thies, Nentwig, & Tschardtke, 2007). However, often arthropods, such as spiders and carabids respond more strongly to in-field management than to landscape scale effects (Gallé, Happe, Baillod, Tschardtke, & Batáry, 2019; Schmidt, Roschewitz, Thies, & Tschardtke, 2005).

Regarding the sampling of predators using pitfall traps, some uncertainty remains. First, pitfall traps may collect more carnivorous carabid species than other sampling techniques like hand searching do (Knapp, Knappová, Jakubec, Vonička, & Moravec, 2020). Second, pitfall traps are more selective and therefore biased toward ground-dwelling active hunting and not web-building spiders. Nonetheless, the bias of our sampling method is identical across all plots and therefore comparable between treatments.

### ***Biocontrol potential***

In this study, a negative relationship between the activity densities of active hunting spiders and aphid density was observed in the experimental field, revealing effective pest control potential. This supports the important role of ground-dwelling predators in agroecosystems (Diehl et al., 2013; González et al., 2020; Schmidt et al., 2003). However, our results did not suggest reduced aphid densities caused by web-building spiders and carnivorous/omnivorous carabids. The insignificant effect of web-building spiders on aphid density could also be caused by the bias of the sampling technique. In an experiment by Berg, Thies, Tschardtke, and Scheu (2009), generalist predators, including spiders and carabids, reduced aphid numbers only when aphid densities were high ( $14.0 \pm 3.8$  individuals per shoot at the end of the experiment) but not at medium ( $2.7 \pm 0.7$ ) to low ( $2.2 \pm 1.6$ ) densities. Furthermore, the predators preferred to feed on alternative prey such as click beetles, subsequently switching to feeding on aphids at high aphid densities (Berg et al., 2009; Gabriel, Roschewitz, Tschardtke, & Thies, 2006). Although sampling was performed during suitable crop development stages, the number of aphids collected in our study was low (experimental field:  $0.7 \pm 0.4$  individuals

per shoot; field study:  $0.6 \pm 0.8$ ). This suggests that web-building spiders and carnivorous/omnivorous carabids could have been feeding mainly on alternative prey and did not reach the stage where aphids became the preferred diet. Furthermore, the effects of RAP cover on ground-dwelling predators and aphids were not consistent between the experimental field and the field study. This suggests that factors like management history or actual practices like the choice of crops can cause large variation between agricultural farms. In general, positive (facilitation) and negative (intraguild predation or cannibalism) interactions between distinct predator guilds are known, which can enhance or decrease biocontrol (De Heij & Willenborg, 2020; Rusch et al., 2016; Thies et al., 2011). De Heij and Willenborg (2020) promoted ecological approaches in which direct and indirect interactions between pests, multiple predator groups, and the spatial environment should be considered. We tried to implement this approach in our study. However, besides a positive interaction between the activity density of carnivorous/omnivorous carabids and active hunting spiders in the field study, no interactions between ground-dwelling predators were detected. The densities of vegetation-dwelling predators and aphid mummies were sampled but were too low for statistical analyses. In turn, conclusions on the interactions between ground- and vegetation-dwelling predators could not be drawn. The low effect of sowing RAPs on biocontrol potential may be due to the extensive land use performed at the study sites. This favored a dense and species-rich spontaneous vegetation with a low prey infestation, which was already established from the outset. Theoretically, the impact of RAP occurrence on biocontrol potential might have been stronger in conventional (intensive) farming systems with a low species diversity. However, RAPs usually do not survive under such conditions. Under low management intensity, where the occurrence of low competitive RAP is more realistic, their contribution to biocontrol potential seems to be limited.



## Conclusion

The occurrence of rare arable plants (RAP) diversifies plant communities and increases phytodiversity (Twerski et al., 2021). Our study investigated biodiversity effects on higher trophic levels. However, such effects were scarce. Only on the experimental fields was, RAP cover directly associated with increased biocontrol potential through reduced aphid densities. In addition, active hunting spiders reduced aphid density. However, the underlying mechanisms of the biocontrol function are complex and remain unclear. De Heij and Willenborg (2020) invoked an approach where direct and indirect, positive and negative interactions among different pests and multitaxa predators should be combined. However, a holistic network needs to include a detailed analysis that includes parasitoids and the imagines and larvae of hoverflies and lacewings. Furthermore, the impact of rare and common arable plants at different densities and the impact of adjacent fields on the predator activity densities should be investigated in detail.

## Funding

This study was supported by The German Federal Environmental Foundation (DBU) [grant number AZ 34029/01].

## Author contribution

HA, CF designed the experiment; FS, AT, HA conducted the fieldwork; RG identified the spiders; PC identified the carabids; CF, AT, RG analyzed the data; AT wrote the manuscript, and all authors revised the manuscript.

## Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

## Acknowledgments

We thank the Seidlhof Foundation and the farmers for providing fields to perform the experiments. Thanks to Johannes Kollmann for commenting on the manuscript. We also thank the TUM Graduate School for proofreading and Stephan Haug, Thomas Wagner, and Jochen Fründ for statistical consulting. Sampling of living animals was permitted by the government of Upper Bavaria (reference: ROB-55.1-8646.NAT\_02-8-3-3).

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

## References

- Albrecht, H. (1989). *Untersuchungen zur Veränderung der Segetalflora an sieben bayerischen Ackerstandorten zwischen den Erhebungszeiträumen 1951/68 und 1986/88: Mit 31 Tabellen im Text und im Anhang*. Zugl.: München, Techn. Univ., Diss., 1989. *Dissertationes botanicae: Vol. 141*. Berlin, Stuttgart: Cramer in d. Borntraeger-Verl.-Buchh.
- Barbosa, P., Hines, J. [Jessica], Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational resistance and associational susceptibility: Having right or wrong

- neighbors. *Annual Review of Ecology, Evolution, and Systematics*, 40, 1–20. <https://doi.org/10.1146/annurev.ecolsys.110308.120242>
- Bayerisches Landesamt für Statistik (2016). Landwirtschaftszählung 2010 und Agrarstrukturerhebung 2016. Retrieved from [https://www.statistik.bayern.de/statistik/wirtschaft\\_handel/landwirtschaft/index.html](https://www.statistik.bayern.de/statistik/wirtschaft_handel/landwirtschaft/index.html)
- Ben-Issa, R., Gomez, L., & Gautier, H. (2017). Companion plants for aphid pest management. *Insects*, 8(4), 112. <https://doi.org/10.3390/insects8040112>
- Berg, K. von, Thies, C., Tschardt, T., & Scheu, S. (2009). Cereal aphid control by generalist predators in presence of belowground alternative prey: Complementary predation as affected by prey density. *Pedobiologia*, 53(1), 41–48. <https://doi.org/10.1016/j.pedobi.2009.03.001>
- Bretagnolle, V., & Gaba, S. (2015). Weeds for bees? A review. *Agronomy for Sustainable Development*, 35(3), 891–909. <https://doi.org/10.1007/s13593-015-0302-5>
- Brown, G. R., & Matthews, I. M. (2016). A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity. *Ecology and Evolution*, 6(12), 3953–3964. <https://doi.org/10.1002/ece3.2176>
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U. [David U.], Perrings, C., Venail, P., . . . Naeem, S. [Shahid] (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59–67. <https://doi.org/10.1038/nature11148>
- Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global patterns of guild composition and functional diversity of spiders. *PloS One*, 6(6), e21710.
- Császár, P., Torma, A., Gallé-Szpisjak, N., Tölgyesi, C., & Gallé, R. [Robert] (2018). Efficiency of pitfall traps with funnels and/or roofs in capturing ground-dwelling arthropods. *European Journal of Entomology*, 115, 15–24. <https://doi.org/10.14411/eje.2018.003>
- Currie, C. R., Spence, J. R., & Niemelä, J. (1996). Competition, cannibalism and intraguild predation among ground beetles (Coleoptera: Carabidae): A laboratory study. *The Coleopterists' Bulletin*, 135–148.
- Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., . . . Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, 5(10), eaax0121. <https://doi.org/10.1126/sciadv.aax0121>
- De Heij, S. E., & Willenborg, C. J. (2020). Connected carabids: Network interactions and their impact on biocontrol by carabid beetles. *Bioscience*, 70(6), 490–500. <https://doi.org/10.1093/biosci/biaa039>
- Dedryver, C.-A., Le Ralec, A., & Fabre, F. (2010). The conflicting relationships between aphids and men: A review of aphid damage and control strategies. *Comptes Rendus Biologies*, 333(6–7), 539–553.
- Diehl, E., Mader, V. L., Wolters, V., & Birkhofer, K. (2013). Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia*, 173(2), 579–589. <https://doi.org/10.1007/s00442-013-2634-7>
- Diekötter, T., Wamser, S., Wolters, V., & Birkhofer, K. (2010). Landscape and management effects on structure and function of soil arthropod communities in winter wheat.

- Agriculture, Ecosystems & Environment*, 137(1–2), 108–112.  
<https://doi.org/10.1016/j.agee.2010.01.008>
- DWD (1993–2019). CDC - Climate Data Center: Klimadaten Deutschland. Retrieved from <https://cdc.dwd.de/portal/>
- DWD (2019). Hagelunwetter in München und weitere schwere Gewitter an Pfingstmontag. Retrieved from [https://www.dwd.de/DE/wetter/thema\\_des\\_tages/2019/6/11.html](https://www.dwd.de/DE/wetter/thema_des_tages/2019/6/11.html)
- Ebeling, A., Hines, J. [Jes], Hertzog, L. R., Lange, M., Meyer, S. T., Simons, N. K., & Weisser, W. W. (2018). Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. *Basic and Applied Ecology*, 26, 50–63. <https://doi.org/10.1016/j.baae.2017.09.014>
- Feeny, P. (1976). Plant apparency and chemical defense. In J. W. Wallace & R. L. Mansell (Eds.), *Biochemical interaction between plants and insects* (pp. 1–40). Boston, MA: Springer US. [https://doi.org/10.1007/978-1-4684-2646-5\\_1](https://doi.org/10.1007/978-1-4684-2646-5_1)
- Fetzer, K. D., Grotenthaler, W., Hofmann, B., Jerz, H., Rückert, G., Schmidt, F., & Wittmann, O. (1986). Standortkundliche Bodenkarte von Bayern 1:50 000, München-Augsburg und Umgebung. *Bayerisches Geologisches Landesamt, München*.
- Frank, S. D., Shrewsbury, P. M., & Denno, R. F. (2010). Effects of alternative food on cannibalism and herbivore suppression by carabid larvae. *Ecological Entomology*, 35(1), 61–68. <https://doi.org/10.1111/j.1365-2311.2009.01156.x>
- Gaba, S., Cheviron, N., Perrot, T., Piutti, S., Gautier, J.-L., & Bretagnolle, V. (2020). Weeds enhance multifunctionality in arable lands in south-west of France. *Frontiers in Sustainable Food Systems*, 4. <https://doi.org/10.3389/fsufs.2020.00071>
- Gabriel, D., Roschewitz, I., Tschardtke, T., & Thies, C. (2006). Beta diversity at different spatial scales: Plant communities in organic and conventional agriculture. *Ecological Applications*, 16(5), 2011–2021. [https://doi.org/10.1890/1051-0761\(2006\)016\[2011:BDADSS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[2011:BDADSS]2.0.CO;2)
- Gallé, R. [Róbert], Happe, A.-K., Baillo, A. B., Tschardtke, T., & Batáry, P. (2019). Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *Journal of Applied Ecology*, 56(1), 63–72. <https://doi.org/10.1111/1365-2664.13257>
- Geiger, F., Bengtsson, J. [Jan], Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B., . . . Winqvist, C. (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, 11(2), 97–105.
- González, E., Seidl, M., Kadlec, T., Ferrante, M., & Knapp, M. (2020). Distribution of ecosystem services within oilseed rape fields: Effects of field defects on pest and weed seed predation rates. *Agriculture, Ecosystems & Environment*, 295, 106894. <https://doi.org/10.1016/j.agee.2020.106894>
- Homburg, K., Homburg, N., Schäfer, F., Schuldt, A., & Assmann, T. (2014). Carabids.org—a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity*, 7(3), 195–205. <https://doi.org/10.1111/icad.12045>
- 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. <https://doi.org/10.14411/eje.2000.080>

- Hooper, D. U. [D. U.], Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., . . . Wardle, D. A. [D. A.] (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35. <https://doi.org/10.1890/04-0922>
- Hurford, C., Wilson, P., & Storkey, J. (Eds.) (2020). *The changing status of arable habitats in Europe: A nature conservation review*. Cham, Switzerland: Springer.
- Hurka, K. (1996). *Carabidae of the Czech and Slovak republics*. Zlín, Czech Republic: Ing. Vit Kabourek.
- Kells, A. R., Holland, J. M., & Goulson, D. (2001). The value of uncropped field margins for foraging bumblebees. *Journal of Insect Conservation*, 5(4), 283–291. <https://doi.org/10.1023/A:1013307822575>
- Knapp, M., Knappová, J., Jakubec, P., Vonička, P., & Moravec, P. (2020). Incomplete species lists produced by pitfall trapping: How many carabid species and which functional traits are missing? *Biological Conservation*, 245, 108545. <https://doi.org/10.1016/j.biocon.2020.108545>
- Landis, D. A. [D. A.], Wratten, S. D. [S. D.], & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45, 175–201. <https://doi.org/10.1146/annurev.ento.45.1.175>
- Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, 139(1), 1–10. <https://doi.org/10.1007/s00442-004-1497-3>
- Lefcheck, J. S. (2016). piecewiseSEM : Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210X.12512>
- Letourneau, D. K., Armbrrecht, I., Rivera, B. S., Lerma, J. M., Carmona, E. J., Daza, M. C., . . . López, S. D. (2011). Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, 21(1), 9–21.
- Letourneau, D. K., & Bothwell, S. G. (2008). Comparison of organic and conventional farms: Challenging ecologists to make biodiversity functional. *Frontiers in Ecology and the Environment*, 6(8), 430–438. <https://doi.org/10.1890/070081>
- Marshall, E. J. P., Brown, V. K., Boatman, N. D., Lutman, P. J. W., Squire, G. R., & Ward, L. K. (2003). The role of weeds in supporting biological diversity within crop fields. *Weed Research*, 43(2), 77–89. <https://doi.org/10.1046/j.1365-3180.2003.00326.x>
- Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., . . . Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, 22(7), 1083–1094. <https://doi.org/10.1111/ele.13265>
- Matson, P. A., Parton, W. J., Power, A. G., & Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science*, 277(5325), 504–509.
- Metzing, D., Garve, E., & Matzke-Hajek, G. (2018). *Rote Liste und Gesamtartenliste der Farn- und Blütenpflanzen (Tracheophyta) Deutschlands: Naturschutz und Biologische Vielfalt 70. Naturschutz und biologische Vielfalt: Band 7*. Bonn-Bad Godesberg: Bundesamt für Naturschutz.

- Nentwig, W. [W.], Blick, T., Gloor, D., Hänggi, A., & Kropf, C. (2019). Spiders of Europe: Retrieved from [www.araneae.unibe.ch](http://www.araneae.unibe.ch).
- Perrin, R. M., & Phillips, M. L. (1978). Some effects of mixed cropping on the population dynamics of insect pests. *Entomologia Experimentalis Et Applicata*, 24(3), 585–593. <https://doi.org/10.1111/j.1570-7458.1978.tb02820.x>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2020). nlme: Linear and nonlinear mixed effects models: R package version 3.1-145. Retrieved from <https://cran.r-project.org/web/packages/nlme/index.html>
- The Plant List (2013). Version 1.1. Retrieved from <http://www.theplantlist.org/>
- R Core Team (2020). R: A language and environment for statistical computing [Computer software]. Vienna, Austria: R Foundation for Statistical Computing: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Raven, P. H., & Wagner, D. L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences*, 118(2). <https://doi.org/10.1073/pnas.2002548117>
- Rusch, A., Chaplin-Kramer, R., Gardiner, M. M., Hawro, V., Holland, J., Landis, D., . . . Bommarco, R. (2016). Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystems & Environment*, 221, 198–204. <https://doi.org/10.1016/j.agee.2016.01.039>
- Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B. [Bernhard], Voigt, W., Fischer, M., . . . Tschardtke, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468(7323), 553–556. <https://doi.org/10.1038/nature09492>
- Scheuerer, M., & Ahlmer, W. (2003). *Rote Liste gefährdeter Gefäßpflanzen Bayerns mit regionalisierter Florenliste* (Bearb. Stand 2002). *Schriftenreihe des Bayerisches Landesamt für Umweltschutz*, 165: Vol. 165. Augsburg: Bayer. Landesamt für Umweltschutz.
- Schirmel, J., Thiele, J., Entling, M. H., & Buchholz, S. (2016). Trait composition and functional diversity of spiders and carabids in linear landscape elements. *Agriculture, Ecosystems & Environment*, 235, 318–328. <https://doi.org/10.1016/j.agee.2016.10.028>
- Schmidt, M. H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M., & Tschardtke, T. (2003). Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1527), 1905–1909.
- Schmidt, M. H., Roschewitz, I., Thies, C., & Tschardtke, T. (2005). Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology*, 42(2), 281–287. <https://doi.org/10.1111/j.1365-2664.2005.01014.x>
- Schmidt, M. H., Thies, C., Nentwig, W. [Wolfgang], & Tschardtke, T. (2007). Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography*, 35(1), 157–166. <https://doi.org/10.1111/j.1365-2699.2007.01774.x>
- Seidl, M., González, E., Kadlec, T., Saska, P., & Knapp, M. (2020). Temporary non-crop habitats within arable fields: The effects of field defects on carabid beetle assemblages. *Agriculture, Ecosystems & Environment*, 293, 106856. <https://doi.org/10.1016/j.agee.2020.106856>

- Seyfulina, R. R. (2005). Microhabitat effect on spider distribution in winter wheat agroecosystem (Araneae). *Acta Zoologica Bulgarica*, *1*, 161–172.
- Stenberg, J. A., Sundh, I., Becher, P. G., Björkman, C., Dubey, M., Egan, P. A., . . . Viketoft, M. (2021). When is it biological control? A framework of definitions, mechanisms, and classifications. *Journal of Pest Science*, *94*(3), 665–676. <https://doi.org/10.1007/s10340-021-01354-7>
- Stoate, C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., Snoo, G. R. de, & Eden, P. (2001). Ecological impacts of arable intensification in Europe. *Journal of Environmental Management*, *63*(4), 337–365. <https://doi.org/10.1006/jema.2001.0473>
- Straub, C. S., Finke, D. L., & Snyder, W. E. (2008). Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control*, *45*(2), 225–237. <https://doi.org/10.1016/j.biocontrol.2007.05.013>
- Symondson, W. O., Sunderland, K. D., & Greenstone, M. H. (2002). Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, *47*(1), 561–594. <https://doi.org/10.1146/annurev.ento.47.091201.145240>
- Thies, C., Haenke, S., Scherber, C., Bengtsson, J. [Janne], Bommarco, R., Clement, L. W., . . . Gagic, V. (2011). The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecological Applications*, *21*(6), 2187–2196.
- Twerski, A., Albrecht, H., Fründ, J., Moosner, M., & Fischer, C. (2022). Effects of rare arable plants on flower-visiting wild bees in agricultural fields. *Agriculture, Ecosystems & Environment*, *323*, 107685. <https://doi.org/10.1016/j.agee.2021.107685>
- Twerski, A., Fischer, C., & Albrecht, H. (2021). Effects of rare arable plants on plant diversity, productivity and soil fertility in agricultural fields. *Agriculture, Ecosystems & Environment*, *307*, 107237. <https://doi.org/10.1016/j.agee.2020.107237>
- Walker, K. J., Critchley, C., Sherwood, A. J., Large, R., Nuttall, P., Hulmes, S., . . . Mountford, J. O. (2007). The conservation of arable plants on cereal field margins: An assessment of new agri-environment scheme options in England, UK. *Biological Conservation*, *136*(2), 260–270. <https://doi.org/10.1016/j.biocon.2006.11.026>
- Wickham, H. (2011). The split-apply-combine strategy for data analysis. *Journal of Statistical Software*, *40*(1). <https://doi.org/10.18637/jss.v040.i01>

**Table 1**

The results of the linear mixed-effect models depict the effect of rare arable plant occurrence (+RAP) on the response variables total number of aphids, activity densities of active hunting and web-building spiders, and carnivorous/omnivorous and predominantly granivorous carabids for the experimental field and the field study. The experimental field comprises one and the field study comprises two study years. For the field study, analyses “year” was included as a fixed effect. Values, standard error (SE), numerator degrees of freedom (DF), and t- and p-values from SUMMARY tables are provided.

Response variable		Experimental field					Field study					
		Value	SE	DF	t-value	p-value	Value	SE	DF	t-value	p-value	
Number of aphids <sup>a)</sup>	Intercept	4.99	0.08	24	62.16	<0.001	Intercept	5.19	0.25	26	20.63	< 0.001
	+ RAP	-0.15	0.1	24	-1.67	0.11	+ RAP	-0.17	0.18	26	-1.00	0.34
	-	-	-	-	-	-	Year 2019	-1.70	0.18	26	-9.40	< <b>0.001</b>
Active hunting spiders <sup>b)</sup>	Intercept	1.59	0.19	24	8.49	<0.001	Intercept	3.57	0.51	26	7.02	< 0.001
	+ RAP	-0.25	0.21	24	-1.18	0.25	+ RAP	-0.48	0.53	26	-0.91	0.37
	-	-	-	-	-	-	Year 2019	1.65	0.53	26	3.11	<b>0.01</b>
Web-building spiders <sup>c)</sup>	Intercept	2.11	0.20	24	10.48	<0.001	Intercept	2.55	0.27	26	9.29	< 0.001
	+ RAP	-0.28	0.25	24	-1.15	0.26	+ RAP	-0.17	0.23	26	-0.73	0.47
	-	-	-	-	-	-	Year 2019	-0.45	0.24	26	-1.91	0.07
Carnivorous/omnivorous carabids <sup>c)</sup>	Intercept	1.02	0.16	24	6.32	<0.001	Intercept	2.32	0.31	26	7.50	< 0.001
	+ RAP	0.32	0.20	24	1.61	0.12	+ RAP	0.16	0.18	26	0.90	0.40
	-	-	-	-	-	-	Year 2019	-0.46	0.18	26	-2.51	<b>0.02</b>



<b>Predominantly granivorous carabids</b> <sup>b)</sup>	Intercept	1.68	0.20	24	8.61	< 0.001	Intercept	4.71	0.70	26	6.80	< 0.001
	+ RAP	-0.29	0.24	24	-1.20	0.24	+ RAP	-0.30	0.56	26	-0.52	0.61
	-	-	-	-	-	-	Year 2019	0.16	0.57	26	-0.28	0.78

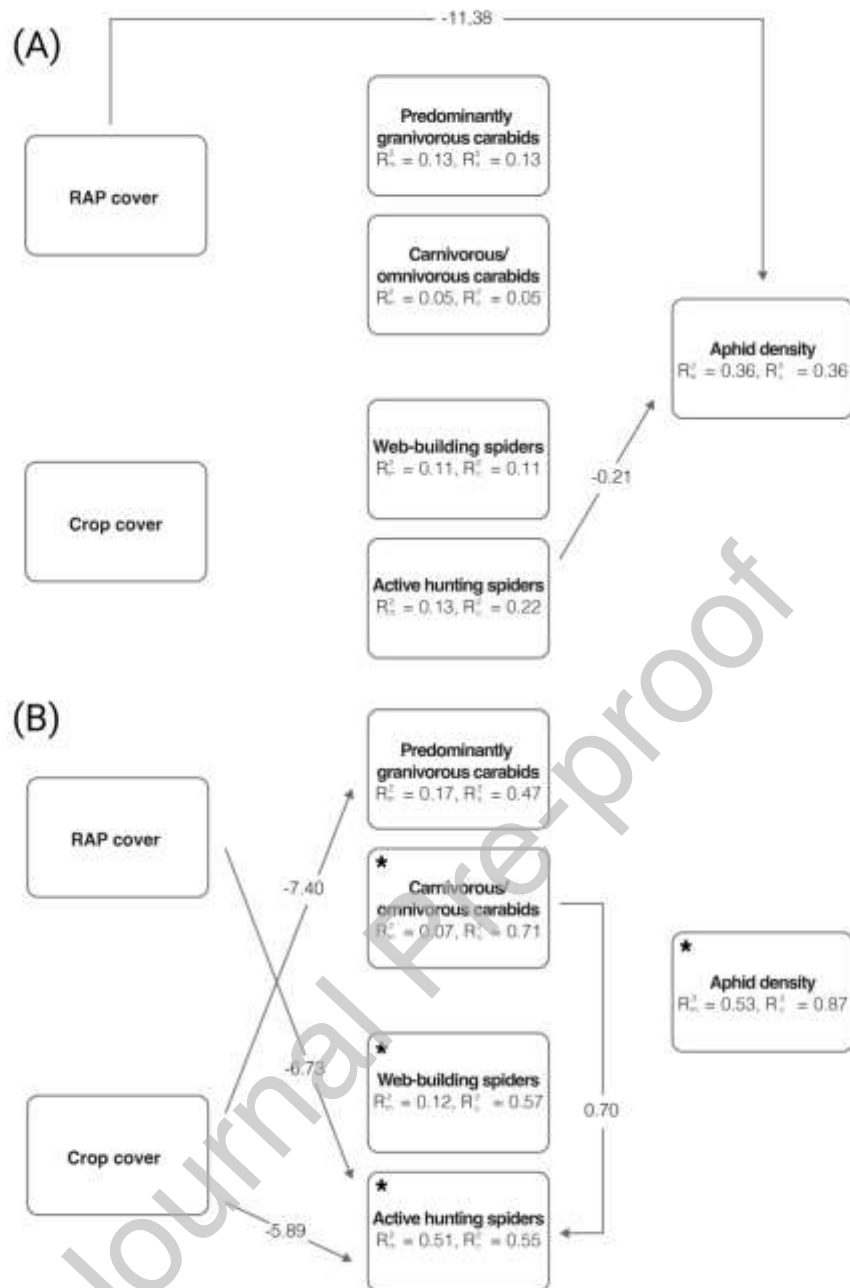
<sup>a)</sup> log-transformed

<sup>b)</sup> log-transformed for experimental field; sqrt-transformed for field study

<sup>c)</sup> log<sub>1p</sub>-transformed

**Fig. 1.** Results of the structural equation models (SEM). Multilevel analysis reveals the effects of crop and rare arable plant (RAP) cover on the activity patterns of active hunting and web-building spiders, carnivorous/omnivorous and predominantly granivorous carabids, and total number of aphids for (A) the experimental field and (B) the field study. Arrows represent unidirectional, significant ( $p < 0.05$ ) relationships. Estimates (above arrows) and marginal ( $R_m^2$ ) and conditional ( $R_c^2$ )  $R^2$ -values are provided. The asterisks indicate significant differences between the two study years in the field study.

Journal Pre-proof

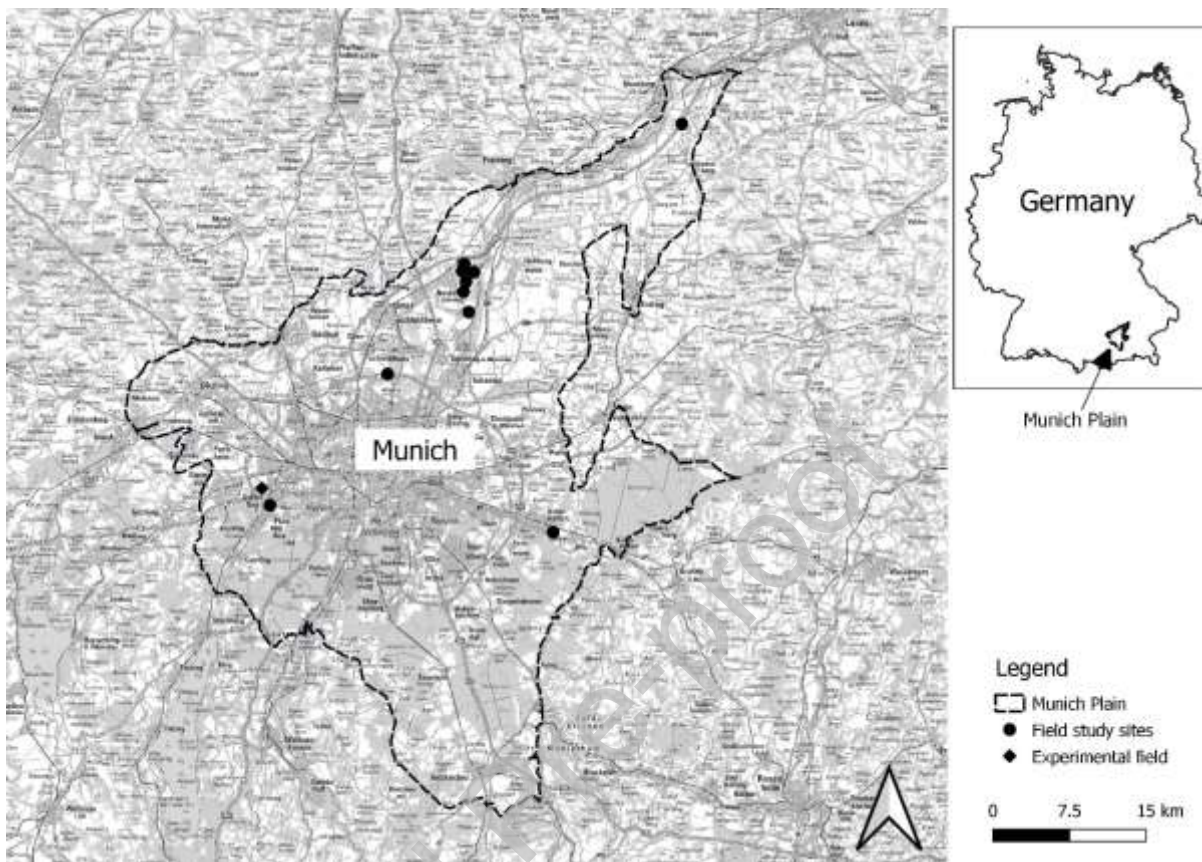


**Table 1**

List of rare arable plant (RAP) species and families (species nomenclature according to The Plant List, 2013), germination requirements, Red List of Germany and Federal State of Bavaria (Metzing et al., 2018; Scheuerer & Ahlmer, 2003), and sowing densities and competitive capacity (Holzner & Glauning, 2005). Competitive capacity: 1 = very low competitive species; 5 = highly competitive species. W = winter annual, S = summer annual, WS = no seasonal germination preference. Red List Status: \* = not endangered, V = near threatened, 3 = vulnerable, 2 = endangered (table and headline from Twerski et al., 2021).

Species	Family	Germination requirements	Red List Status		Sowing density (seeds/m <sup>2</sup> )	Competitive capacity
			Germany	Bavaria		
<i>Consolida regalis</i> Gray	Ranunculaceae	W	3	3	150	1–2
<i>Buglossoides arvensis</i> (L.) I.M.Johnst.	Boraginaceae	W	V	3	100	2
<i>Valerianella dentata</i> (L.) Pollich	Caprifoliaceae	W	V	*	150	1
<i>Legousia speculum-veneris</i> (L.) Durande ex Vill.	Campanulaceae	WS	2	3	150	2
<i>Silene noctiflora</i> L.	Caryophyllaceae	WS	3	V	100	2
<i>Papaver rhoeas</i> L.	Papaveraceae	WS	*	*	150	3
<i>Lathyrus tuberosus</i> L.	Fabaceae	S	*	*	50	-
<i>Neslia paniculata</i> (L.) Desv.	Brassicaceae	S	3	3	150	2
<i>Kickxia spuria</i> (L.) Dumort.	Plantaginaceae	S	3	3	300	-
<i>Sherardia arvensis</i> L.	Rubiaceae	S	V	V	100	1

**Fig. 1.** Study area depicting (the *Munich Plain*) the locations of the experimental field and the agricultural farms in the federal state of Bavaria, Germany (from Twerski, Fischer, & Albrecht, 2021).



**Fig. 2.** Plots with rare arable plants (RAP) sowed among different crop types: (A) *Consolida regalis* with rye in the field study 2019, (B) *Legousia speculum-veneris* and *Valerianella dentata* with oat on the experimental field 2018, (C) *Consolida regalis* with oat on the experimental field 2018, and (D) *Silene noctiflora* with oat on the experimental field 2018.

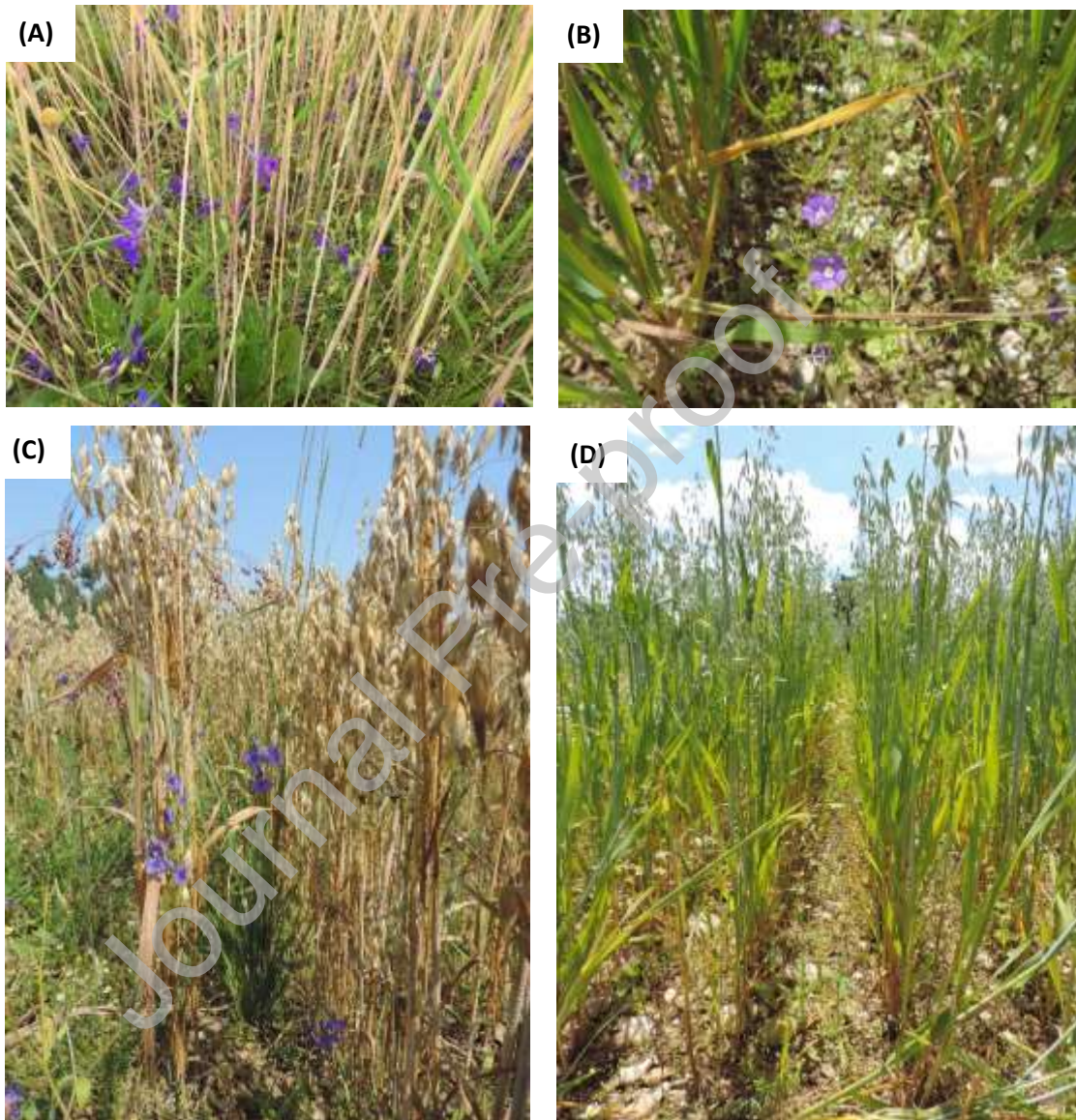


Table 2

Management type (organic vs. conventional), plot width, seed row distance, sowing date, crop (including variety), and sowing rate of the field study (table and headline from Twerski et al., 2021).

Management	Location	Plot width [m]	Reduced seed row distance [cm]	Sowing date	Crop	Reduced sowing rate [kg/ha]
Organic farming	Munich (48°08'N 11°35'E)	2.34	22	28.03.2018	Oat var. <i>Saul</i>	70
				28.09.2018	Spelt var. <i>Oberkulmer Rotkorn</i>	95
		2.50	26	26.03.2018	Spring barley var. <i>Margret</i>	NA
				29.09.2018	Winter rye var. <i>Amilio</i>	55
	Neufahrn near Freising (48°18'N 11°39'E)	2.50	25	10.04.2018	Oat var. <i>Saul</i>	70
				06.09.2018	Winter wheat var. <i>Capo</i>	90
		3.00	27	19.04.2018	Oat var. 50% <i>Saul</i> & 50% <i>SinaBa</i>	70
				11.10.2018	Spelt var. <i>Oberkulmer Rotkorn</i>	95
		2.50	25	13.04.2018	Oat var. <i>Poseidon</i>	80
				06.10.2018	Winter rye var. <i>Inspector</i>	60
	Oberschleißheim (48°15'N 11°33'E)	3.00	30	12.04.2018	Oat var. <i>Max</i>	65
				10.10.2018	Winter wheat var. <i>Wiwa</i>	102.5
	Langenpreising (48°26'N 11°58'E)	3.00	25	08.04.2018	Oat var. <i>Scorpion</i>	66
				09.10.2018	Spelt var. <i>Oberkulmer Rotkorn</i>	95
Zorneding (48°05'N 11°49'E)	3.00	25	12.04.2018	Spring barley var. <i>Avalon</i>	NA	
			06.10.2018	Winter rye var. <i>Dukato</i>	65	
Conventional farming	Neufahrn near Freising (48°18'N 11°39'E)	3.00	24	04.04.2018	Spring barley var. <i>Marthe</i>	70
				04.10.2018	Winter rye var. 90% <i>SU Forsetti</i> & 10% <i>Dukato</i>	31.5
	Dietersheim near Eching (48°16'N 11°40'E)	3.00	30	04.04.2018	Oat var. <i>Max</i>	NA
				08.10.2018	Triticale var. <i>Lombardo</i>	85

**Table 3**

Land cover (in %) within 1000 m radius of the agricultural farms in the field study.

Farm	Settlement	Forest	Grassland	Crop	Semi-natural habitat
1	2.70	12.40	5.70	72.00	2.80
2	19.00	7.60	4.50	64.10	1.10
3	2.80	0.00	13.50	65.50	10.80
4	3.20	56.40	6.20	15.50	12.50
5	30.20	0.00	3.00	57.90	4.40
6	12.90	0.90	4.30	56.90	6.50
7	78.80	2.30	4.70	2.30	2.10
8	30.50	41.40	4.30	17.00	0.70
9	5.60	42.30	8.20	28.40	2.30
10	20.50	34.20	4.50	28.20	1.10



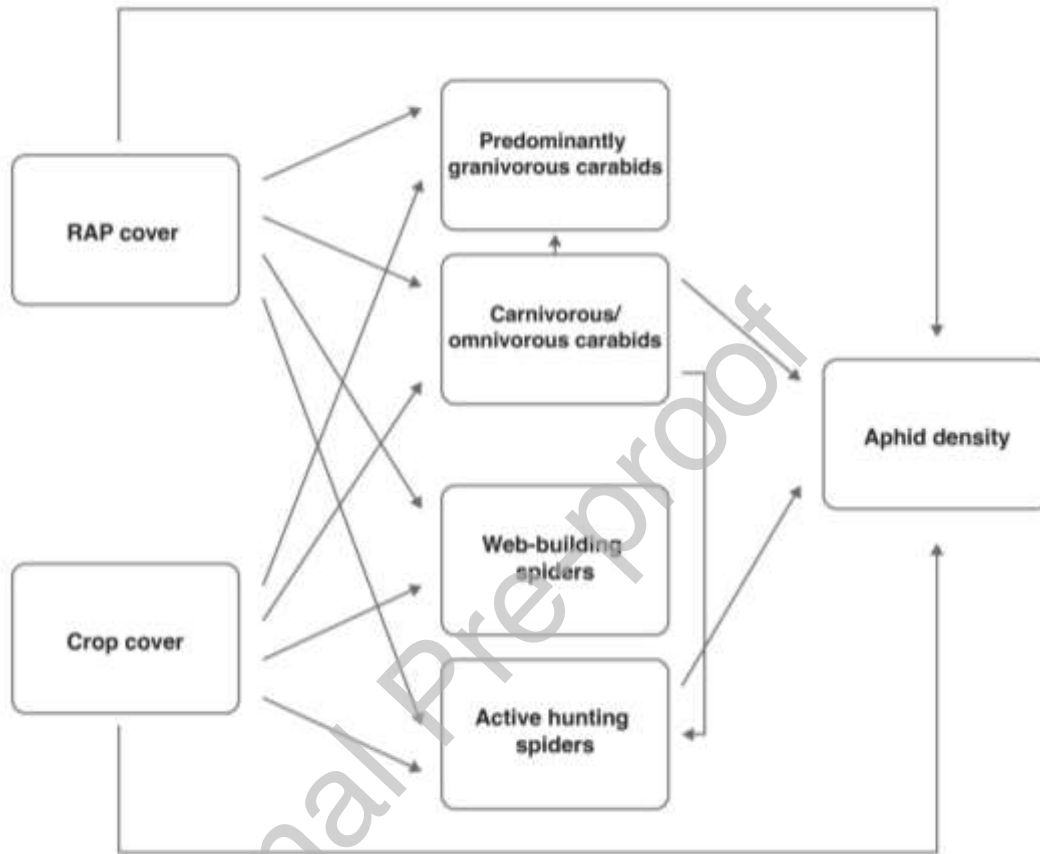
**Table 4**

Mean, standard deviation (SD), minimum and maximum values of land cover within 1000 m of the agricultural farms in the field study.

	<b>Mean</b>	<b>SD</b>	<b>Min</b>	<b>Max</b>
<b>Settlement</b>	20.62	23.10	2.70	78.80
<b>Forest</b>	19.75	21.53	0.00	56.40
<b>Grassland</b>	5.89	3.02	3.00	13.50
<b>Crop</b>	40.78	25.12	2.30	72.00
<b>Semi-natural habitat</b>	4.43	4.20	0.70	12.50

Journal Pre-proof

**Fig. 3.** Structural equation model of the hypothesized impact of crop and rare arable plant (RAP) cover on the direct/and indirect food web interactions between aphids and carabids and spiders with different feeding behaviors.



**List 1**

Structural equation model of the causal relationship between the rare arable plant (RAP) and crop cover and the direct/and indirect food web interactions between aphids, carabids, and spiders with different feeding behaviors on the experimental field. The model is depicted: Fisher's C = 7.89 with p-value = 0.79; AIC = 65.89.

```
SEM_G_1_all<-psem(
```

```
Ara_web = lme(Araneae_webBuilder_log1p ~ RAP_cover + Crop_cover_log, random = ~1|WH, data = G_SEM, method = "ML"),
```

```
Ara_hunt = lme(Araneae_activHunt_log ~ RAP_cover + Crop_cover_log + Carabidae_carni_log1p, random = ~1|WH, data = G_SEM, method = "ML"),
```

```
Cara_carni = lme(Carabidae_carni_log1p ~ RAP_cover + Crop_cover_log, random = ~1|WH, data = G_SEM, method = "ML"),
```

```
Cara_herbi = lme(Carabidae_herbi_log1p ~ Crop_cover_log + RAP_cover+Carabidae_carni_log1p, random = ~1|WH, data = G_SEM, method = "ML"),
```

```
Aphid = lme(N_aphid_log ~ Crop_cover_log + RAP_cover + Araneae_activHunt_log + Carabidae_carni_log1p, random= ~1|WH, data=G_SEM, method="ML"))
```

## List 2

Structural equation model of the causal relationship between rare arable plant (RAP) and crop cover and the direct/and indirect food web interactions between aphids, carabids, and spiders with different feeding behaviors on the field study. The model is depicted: Fisher's C = 19.76 with p-value = 0.07; AIC = 87.76.

```
SEM_L_1_all<-psem(
```

```
Ara_web = lme(Araneae_webBuilder_log1p ~ RAP_cover_asin + Crop_cover + Year, random = ~1|Farm, data = L_SEM, method = "ML"),
```

```
Ara_hunt = lme(Araneae_activHunt_sqrt ~ RAP_cover_asin + Crop_cover + Carabidae_carni_log1p + Year, random = ~1|Farm, data = L_SEM, method = "ML"),
```

```
Cara_carni = lme(Carabidae_carni_log1p ~ RAP_cover_asin + Crop_cover + Year, random = ~1|Farm, data = L_SEM, method = "ML"),
```

```
Cara_herbi = lme(Carabidae_herbi_sqrt ~ RAP_cover_asin + Crop_cover + Carabidae_carni_log1p + Year, random = ~1|Farm, data = L_SEM, method = "ML"),
```

```
Aphid = lme(N_aphid_log ~ RAP_cover_asin + Crop_cover + Araneae_activHunt_sqrt + Carabidae_carni_log1p + Year, random = ~1|Farm, data = L_SEM, method = "ML"))
```

Table 5

The results of the linear mixed-effect models depict the effect of rare arable plant occurrence (+RAP) on the response variables total number of aphids, activity densities of active hunting and web-building spiders, and carnivorous/omnivorous and predominantly granivorous carabids for the field study. The factors “year” and “cover of semi-natural habitats in 1000 m radius” were included as a fixed effect. Values, standard error (SE), numerator degrees of freedom (DF), and t- and p-values from SUMMARY tables are provided.

Response variable		Value	SE	DF	t-value	p-value
Number of aphids a)	Intercept	4.76	0.30	26	15.92	< 0.001
	+ RAP	-0.17	0.18	26	-0.96	0.34
	Year 2019	-1.69	0.18	26	-9.34	< 0.001
	Semi-nat. habitat cover in 1000 m	0.10	0.05	8	2.13	0.07
Active hunting spiders b)	Intercept	3.58	0.65	26	5.50	< 0.001
	+ RAP	-0.48	0.53	26	-0.90	0.38
	Year 2019	1.65	0.54	26	3.07	0.01
	Semi-nat. habitat cover in 1000 m	-0.004	0.09	8	-0.04	0.97
Web-building spiders c)	Intercept	2.55	0.37	26	6.82	< 0.001
	+ RAP	-0.17	0.24	26	-0.72	0.48
	Year 2019	-0.45	0.24	26	-1.88	0.07
	Semi-nat. habitat cover in 1000 m	-0.001	0.06	8	-0.01	0.99
Carnivorous/omnivorous carabids c)	Intercept	2.54	0.44	26	5.81	< 0.001
	+ RAP	0.16	0.18	26	0.86	0.40
	Year 2019	-0.46	0.19	26	-2.47	0.02
	Semi-nat. habitat cover in 1000 m	-0.05	0.07	8	-0.71	0.50

		1000 m				
Predominantly granivorous carabids b)	Intercept	4.13	0.91	26	4.53	< 0.001
	+ RAP	-0.29	0.57	26	-0.51	0.62
	Year 2019	0.13	0.58	26	0.23	0.82
	Semi-nat. habitat cover in 1000 m	0.13	0.14	8	0.94	0.38

a) log-transformed

b) log-transformed for experimental field; sqrt-transformed for field study

c) log<sub>1p</sub>-transformed

Table 6

The results of the linear mixed-effect models depict the effect of rare arable plant occurrence (+RAP) on the response variables total number of aphids, activity densities of active hunting and web-building spiders, and carnivorous/omnivorous and predominantly granivorous carabids for the field study. The factors “year” and “crop cover in 1000 m radius” were included as a fixed effect. Values, standard error (SE), numerator degrees of freedom (DF), and t- and p-values from SUMMARY tables are provided.

Response variable		Value	SE	DF	t-value	p-value
Number of aphids a)	Intercept	5.47	0.45	26	12.26	< 0.001
	+ RAP	-0.17	0.18	26	-0.960	0.34
	Year 2019	-1.70	0.18	26	-9.26	< 0.001
	Crop cover in 1000 m	-0.01	0.01	8	-0.76	0.47

Active hunting spiders b)	Intercept	2.51	0.68	26	3.69	<	0.001
	+ RAP	-0.48	0.54	26	-0.89	0.38	
	Year 2019	1.60	0.54	26	2.98	0.01	
	Crop cover in 1000 m	0.03	0.01	8	2.15	0.06	
Web-building spiders c)	Intercept	1.79	0.37	26	4.87	<	0.001
	+ RAP	-0.17	0.24	26	-0.71	0.48	
	Year 2019	-0.48	0.24	26	-2.01	0.06	
	Crop cover in 1000 m	0.02	0.01	8	2.69	0.03	
Carnivorous/omnivorous carabids c)	Intercept	2.32	0.58	26	4.00	0.00	
	+ RAP	0.16	0.18	26	0.90	0.40	
	Year 2019	-0.46	0.18	26	-2.47	0.02	
	Crop cover in 1000 m	-0.01	0.01	8	-0.03	0.98	
Predominantly granivorous carabids b)	Intercept	4.80	1.16	26	3.28	<	0.001
	+ RAP	-0.29	0.57	26	-0.51	0.82	
	Year 2019	0.13	0.58	26	0.23	0.82	
	Crop cover in 1000 m	0.02	0.02	8	0.97	0.36	

a) log-transformed

b) log-transformed for experimental field; sqrt-transformed for field study

c) log<sub>1p</sub>-transformed

Table 7

Group means  $\pm$  SD of the effect of rare arable plant (RAP) sowing (+RAP) on the response variables total number of aphids per 100 shoots, activity densities of active hunting and web-building spiders, and carnivorous/omnivorous and predominantly granivorous carabids for the experimental field and the field study per plot (sum of two rounds per year). The experimental field comprises one and the field study comprises two study years. Group means  $\pm$  SD are provided.

		Experimental field mean $\pm$ SD	Field study mean $\pm$ SD
Number of aphids	- RAP	76.2 $\pm$ 42.5	68.4 $\pm$ 84.0
	+ RAP	64.5 $\pm$ 33.0	61.0 $\pm$ 68.9
Active hunting spiders	- RAP	5.7 $\pm$ 3.9	22.4 $\pm$ 17.3
	+ RAP	4.4 $\pm$ 2.4	18.5 $\pm$ 16.5
Web-building spiders	- RAP	8.9 $\pm$ 7.6	13.1 $\pm$ 13.7
	+ RAP	6.3 $\pm$ 3.8	12.4 $\pm$ 11.1
Carnivorous/omnivorous carabids	- RAP	2.0 $\pm$ 1.2	11.3 $\pm$ 12.3
	+ RAP	3.3 $\pm$ 2.2	14.9 $\pm$ 18.5
Predominantly granivorous carabids	- RAP	5.1 $\pm$ 3.3	28.4 $\pm$ 25.0
	+ RAP	3.9 $\pm$ 3.2	22.4 $\pm$ 13.7



**Table 8**

Hunting traits (active hunting/web-building) and abundances (N) of collected spider species for the experimental field (only 2018) and in the field study (2018 and 2019) (according to Cardoso, Pekár, Jocqué, & Coddington, 2011).

Species	N exp. field	N field study	Hunting
<i>Agyneta affinis</i> (Kulczyński, 1898)	11	0	web
<i>Agyneta rurestris</i> (C. L. Koch, 1836)	6	75	web
<i>Alopecosa pulverulenta</i> (Clerck, 1757)	1	1	active
<i>Araeoncus humilis</i> (Blackwall, 1841)	6	10	web
<i>Bathyphanes gracilis</i> (Blackwall, 1841)	0	1	web
<i>Cicurina cicur</i> (Fabricius, 1793)	1	0	web
<i>Dicymbium nigrum</i> (Blackwall, 1834)	0	1	web
<i>Diplocephalus cristatus</i> (Blackwall, 1833)	0	2	web
<i>Diplostyla concolor</i> (Wider, 1834)	1	5	web
<i>Drassyllus lutetianus</i> (L. Koch, 1866)	1	3	active
<i>Drassyllus pusillus</i> (C. L. Koch, 1833)	1	6	active
<i>Erigone atra</i> Blackwall, 1833	5	28	web
<i>Erigone dentipalpis</i> (Wider, 1834)	56	91	web
<i>Evarcha arcuata</i> (Clerck, 1757)	0	1	active
<i>Micaria micans</i> (Blackwall, 1858)	4	4	active
<i>Micrargus subaequalis</i> (Westring, 1851)	4	2	web
<i>Neottiura bimaculata</i> (Linnaeus, 1767)	1	2	web
<i>Oedothorax apicatus</i> (Blackwall, 1850)	72	215	web
<i>Oedothorax fuscus</i> (Blackwall, 1834)	1	0	web
<i>Ozyptila praticola</i> (C. L. Koch, 1837)	0	1	active
<i>Ozyptila trux</i> (Blackwall, 1846)	0	2	active
<i>Pachygnatha degeeri</i> Sundevall, 1830	47	37	web
<i>Pardosa agrestis</i> (Westring, 1861)	48	277	active
<i>Pardosa agricola</i> (Thorell, 1856)	0	10	active
<i>Pardosa amentata</i> (Clerck, 1757)	0	1	active
<i>Pardosa fulvipes</i> (Collett, 1876)	0	6	active
<i>Pardosa lugubris</i> (Walckenaer, 1802)	1	23	active
<i>Pardosa palustris</i> (Linnaeus, 1758)	15	162	active
<i>Pardosa prativaga</i> (L. Koch, 1870)	65	88	active
<i>Pardosa pullata</i> (Clerck, 1757)	0	1	active
<i>Pardosa riparia</i> (C. L. Koch, 1833)	0	2	active
<i>Pelecopsis parallela</i> (Wider, 1834)	1	1	web
<i>Phlegra fasciata</i> (Hahn, 1826)	0	1	active
<i>Phrurolithus festivus</i> (C. L. Koch, 1835)	3	2	active
<i>Piratula latitans</i> (Blackwall, 1841)	0	1	active
<i>Porrhomma errans</i> (Blackwall, 1841)	0	1	web
<i>Porrhomma microphthalmum</i> (O. P.-Cambridge, 1871)	1	0	web
<i>Tegenaria campestris</i> (C. L. Koch, 1834)	0	1	web
<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	0	4	web
<i>Trochosa ruricola</i> (De Geer, 1778)	5	38	active

<i>Trochosa terricola</i> Thorell, 1856	1	0	active
<i>Walckenaeria atrotibialis</i> (O. Pickard-Cambridge, 1878)	0	1	web
<i>Walckenaeria dysderoides</i> (Wider, 1834)	0	1	web
<i>Walckenaeria vigilax</i> (Blackwall, 1853)	2	7	web
<i>Xerolycosa miniata</i> (C. L. Koch, 1834)	0	144	active
<i>Xysticus kochi</i> Thorell, 1872	0	1	active
<i>Zelotes subterraneus</i> (C. L. Koch, 1833)	0	2	active

---

Journal Pre-proof

**Table 9**

Feeding traits and abundances (N) of collected carabid species for the experimental field (only 2018) and the field study (2018 and 2019) (according to Homburg, Homburg, Schäfer, Schuldt, & Assmann, 2014).

Species	N exp. field	N field study	Food
<i>Abax parallelus</i> (Duftschmid, 1812)	1	0	carni
<i>Acupalpus interstitialis</i> (Reitter, 1884)	0	6	omni
<i>Agonum muelleri</i> (Herbst, 1784)	1	12	carni
<i>Agonum sexpunctatum</i> (Linne, 1758)	0	11	carni
<i>Amara aenea</i> (De Geer, 1774)	4	129	pre. grani
<i>Amara aulica</i> (Panzer, 1796)	1	1	pre. grani
<i>Amara communis</i> (Panzer, 1797)	0	14	pre. grani
<i>Amara consularis</i> (Duftschmid, 1812)	0	4	pre. grani
<i>Amara curta</i> (Dejean, 1828)	1	0	pre. grani
<i>Amara eurynota</i> (Panzer, 1796)	0	6	pre. grani
<i>Amara familiaris</i> (Duftschmid, 1812)	0	6	pre. grani
<i>Amara ingenua</i> (Duftschmid, 1812)	0	1	pre. grani
<i>Amara lunicollis</i> (Schiodte, 1837)	0	4	pre. grani
<i>Amara montivaga</i> (Sturm, 1825)	1	2	pre. grani
<i>Amara nitida</i> (Sturm, 1825)	0	1	pre. grani
<i>Amara plebeja</i> (Gyllenhal, 1810)	0	1	pre. grani
<i>Amara similata</i> (Gyllenhal, 1810)	0	6	pre. grani
<i>Anchomenus dorsalis</i> (Pontoppidan, 1763)	2	90	carni
<i>Anisodactylus binotatus</i> (Fabricius, 1787)	0	11	pre. grani
<i>Anisodactylus nemorivagus</i> (Duftschmid, 1812)	0	7	pre. grani
<i>Badister bullatus</i> (Schrank, 1798)	4	0	carni
<i>Badister sodalis</i> (Duftschmid, 1812)	1	1	carni
<i>Bembidion quadrimaculatum</i> (Linne, 1761)	0	3	carni
<i>Calathus fuscipes</i> (Goeze, 1777)	0	23	omni
<i>Calathus melanocephalus</i> (Linne, 1758)	0	1	omni
<i>Carabus cancellatus</i> (Linne, 1758)	0	42	carni
<i>Carabus granulatus</i> (Linne, 1758)	0	4	carni
<i>Carabus ullrichii</i> (Germar, 1824)	0	8	carni
<i>Diachromus germanus</i> (Linne, 1758)	0	13	pre. grani
<i>Harpalus affinis</i> (Schrank, 1781)	22	223	pre. grani
<i>Harpalus atratus</i> (Latreille, 1804)	0	1	pre. grani
<i>Harpalus distinguendus</i> (Duftschmid, 1812)	0	10	pre. grani
<i>Harpalus honestus</i> (Duftschmid, 1812)	0	17	pre. grani
<i>Harpalus rubripes</i> (Duftschmid, 1812)	1	39	pre. grani
<i>Harpalus tardus</i> (Panzer, 1797)	0	27	pre. grani
<i>Limodromus assimilis</i> (Paykull, 1790)	0	2	carni
<i>Loricera pilicornis</i> (Fabricius, 1775)	0	5	carni
<i>Metallina lampros</i> (Herbst, 1784)	37	36	carni

<i>Microlestes minutulus</i> (Goeze, 1777)	1	4	carni
<i>Nebria brevicollis</i> (Fabricius, 1792)	0	1	carni
<i>Notiophilus aestuans</i> (Dejean, 1826)	0	1	carni
<i>Notiophilus biguttatus</i> (Fabricius, 1779)	0	1	carni
<i>Ophonus azureus</i> (Fabricius, 1775)	22	32	pre. grani
<i>Ophonus puncticollis</i> (Paykull, 1798)	0	1	pre. grani
<i>Ophonus rufibarbis</i> (Fabricius, 1792)	0	3	pre. grani
<i>Ophous schaubergerianus</i> (Puel, 1937)	1	0	pre. grani
<i>Panagaeus bipustulatus</i> (Fabricius, 1775)	1	0	carni
<i>Poecilus cupreus</i> (Linne, 1758)	16	156	carni
<i>Poecilus versicolor</i> (Sturm, 1824)	2	41	carni
<i>Pseudoophonus rufipes</i> (De Geer, 1774)	76	332	pre. grani
<i>Pterostichus melanarius</i> (Illiger, 1798)	0	27	omni
<i>Pterostichus melas</i> (Creutzer, 1799)	20	16	carni
<i>Pterostichus vernalis</i> (Panzer, 1796)	0	2	carni
<i>Semiophonus signaticornis</i> (Duftschmid, 1812)	0	74	pre. grani
<i>Trechus quadristriatus</i> (Schrank, 1781)	0	5	carni

---

Table 10

Structural equation model results revealing the impact of rare arable plant (RAP) and crop cover on the direct/and indirect food web interactions between aphids, carabids, and spiders with different feeding behaviors for the experimental field and the field study. The experimental field comprises one and the field study comprises two study years. Estimate, standard error (SE), degrees of freedom (DF), critical value, p-value, standard estimate, and significance levels from SUMMARY-tables are provided.

	Response	Predictor	Estimate	SE	DF	Crit.Value	p-Value	Std.Estimate	Sig.Level
Experimental field	Web-building spiders	RAP cover	-15.09	10.18	23	-1.48	0.15	-0.27	
	Web-building spiders	Crop cover	-0.60	0.69	23	-0.86	0.40	-0.16	
	Active hunting spiders	RAP cover	-13.26	8.99	22	-1.47	0.15	-0.27	
	Active hunting spiders	Crop cover	0.50	0.63	22	0.79	0.44	0.15	
	Active hunting spiders	Carnivorous/ omnivorous carabids	0.30	0.20	22	1.51	0.15	0.27	
	Carnivorous/ omnivorous carabids	RAP cover	8.52	8.59	23	0.99	0.33	0.19	
	Carnivorous/ omnivorous carabids	Crop cover	-0.45	0.58	23	-0.77	0.45	-0.15	
	Predominantly granivorous carabids	Crop cover	-0.83	0.68	22	-1.22	0.24	-0.23	
	Predominantly granivorous carabids	RAP cover	-4.86	10.15	22	-0.48	0.64	-0.09	
	Predominantly granivorous carabids	Carnivorous/ omnivorous carabids	0.29	0.22	22	1.29	0.21	0.24	
	Aphid density	Crop cover	0.08	0.24	21	0.34	0.74	0.06	
	Aphid density	RAP cover	-11.38	3.75	21	-3.03	<b>0.01</b>	<b>-0.52</b>	**
	Aphid density	Active hunting spiders	-0.21	0.08	21	-2.77	<b>0.01</b>	<b>-0.47</b>	*
	Aphid density	Carnivorous/ omnivorous carabids	0.15	0.08	21	1.83	0.08	0.32	

		omnivorous carabids							
<b>Field study</b>	Web-building spiders	RAP cover	-2.91	1.55	25	-1.87	0.07	-0.27	
	Web-building spiders	Crop cover	0.98	1.35	25	0.73	0.47	0.12	
	Web-building spiders	Year	-0.29	0.24	25	-1.25	0.22	-0.16	
	Active hunting spiders	RAP cover	-6.73	2.94	24	-2.29	<b>0.03</b>	<b>-0.31</b>	*
	Active hunting spiders	Crop cover	-5.89	2.31	24	-2.55	<b>0.02</b>	<b>-0.34</b>	*
	Active hunting spiders	Carnivorous/ omnivorous carabids	0.70	0.26	24	2.65	<b>0.01</b>	<b>0.37</b>	*
	Active hunting spiders	Year	2.28	0.50	24	4.57	<b>0.00</b>	<b>0.59</b>	***
	Carnivorous/ omnivorous carabids	RAP cover	0.17	1.33	25	0.13	0.90	0.01	
	Carnivorous/ omnivorous carabids	Crop cover	0.85	1.19	25	0.71	0.48	0.09	
	Carnivorous/ omnivorous carabids	Year	-0.47	0.20	25	-2.33	0.03	-0.23	*
	Predominantly granivorous carabids	RAP cover	-2.37	3.85	24	-0.62	0.54	-0.09	
	Predominantly granivorous carabids	Crop cover	-7.40	3.27	24	-2.26	<b>0.03</b>	<b>-0.37</b>	*
	Predominantly granivorous carabids	Carnivorous/ omnivorous carabids	0.03	0.42	24	0.08	0.94	0.02	
	Predominantly granivorous carabids	Year	0.22	0.63	24	0.35	0.73	0.05	
	Aphid density	RAP cover	2.48	1.24	23	2.00	0.06	0.18	
	Aphid density	Crop cover	-0.83	1.14	23	-0.73	0.47	-0.08	
	Aphid density	Active hunting spiders	0.12	0.07	23	1.71	0.10	0.19	
	Aphid density	Carnivorous/ omnivorous carabids	0.06	0.16	23	0.38	0.71	0.05	
	Aphid density	Year	-1.99	0.25	23	-8.02	<b>0.00</b>	<b>-0.85</b>	***

## References

- Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global patterns of guild composition and functional diversity of spiders. *PloS One*, 6(6), e21710.
- Holzner, W., & Glauning, J. (2005). *Ackerunkräuter: Bestimmung, Biologie, Landwirtschaftliche Bedeutung* (3rd ed.). Graz, Stuttgart: Leopold Stocker Verlag.
- Homburg, K., Homburg, N., Schäfer, F., Schuldt, A., & Assmann, T. (2014). Carabids. org—a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity*, 7(3), 195–205.
- Metzing, D., Garve, E., & Matzke-Hajek, G. (2018). *Rote Liste und Gesamtartenliste der Farn- und Blütenpflanzen (Trachaeophyta) Deutschlands: Naturschutz und Biologische Vielfalt 70. Naturschutz und biologische Vielfalt: Band 7*. Bonn-Bad Godesberg: Bundesamt für Naturschutz.
- The Plant List (2013). Version 1.1. Retrieved from <http://www.theplantlist.org/>
- Scheuerer, M., & Ahlmer, W. (2003). *Rote Liste gefährdeter Gefäßpflanzen Bayerns mit regionalisierter Florenliste* (Bearb.-stand 2002). *Schriftenreihe des Bayerisches Landesamt für Umweltschutz 165: Vol. 165*. Augsburg: Bayer. Landesamt für Umweltschutz.
- Twerski, A., Fischer, C., & Albrecht, H. (2021). Effects of rare arable plants on plant diversity, productivity and soil fertility in agricultural fields. *Agriculture, Ecosystems & Environment*, 307, 107237. <https://doi.org/10.1016/j.agee.2020.107237>