Basic and Applied Ecology 80 (2024) 72–80

Contents lists available at ScienceDirect

Basic and Applied Ecology

journal homepage: www.elsevier.com/locate/baae

RESEARCH PAPER

High soil moisture promotes the emergence of ground beetles and spiders from soils in wheat fields

Klarissa Kober[a,b,*], Klaus Birkhofer[b], Michael Glemnitz[a]

[a] *Leibniz Centre for Agricultural Landscape Research, Research Area 2 "Land Use and Governance", Eberswalder Str. 84 15374 Müncheberg, Germany*
[b] *Brandenburg University of Technology Cottbus-Senftenberg, Faculty of Environment and Natural Sciences, Department of Ecology, Konrad-Wachsmann-Allee 6 03046 Cottbus, Germany*

ARTICLE INFO

Keywords:
Araneae
Carabidae
Crop edge
Distance gradient
Field boundaries
Generalist predators
Ponds
Potholes
Soil properties

ABSTRACT

Promoting arthropods in agricultural landscapes can contribute substantially to stop their decline and enhance pest control. Higher soil moisture and the presence of field margins can increase the abundance of arthropods in agricultural landscapes and influence their distribution within crop fields. However, little is known about the influence of soil moisture and distance from field margins on the overwintering of arthropods in arable fields. We investigated the influence of soil moisture and distance from a field margin on the numbers of arthropods, ground beetles and spiders emerging from soil in winter wheat fields. We established transects in winter wheat fields away from two different types of field margins: (i) around small standing water bodies (kettle holes) to capture a wide range of soil moisture values and (ii) other semi-natural landscape elements. At three distances (1 m, 20 m, 50 m), we sampled arthropods with emergence traps and measured soil moisture between March and June. We found that soil moisture had a positive effect on the emergence numbers of arthropods in general and ground beetles and spiders in particular. Distance from field margins generally had negative effects on the emergence numbers of ground beetles, but positive effects on the emergence numbers of spiders. Emergence numbers and soil moisture content did not differ significantly between the two types of field margins. The high emergence numbers inside the fields indicate that arable fields are important overwintering habitats for beneficial arthropods. Proper management of arable soils to promote soil water holding capacity and soil moisture content may have the added benefit of promoting the production of beneficial natural enemies from local soils.

Introduction

Arthropod populations worldwide are in decline (Cardoso et al., 2020; Wagner, 2020) and agricultural intensification is one of the major drivers of the ongoing biodiversity loss (Sánchez-Bayo & Wyckhuys, 2019). Agriculture benefits from a number of key ecosystem services provided by arthropods, mainly pest control (Landis et al., 2000), pollination (Klein et al., 2007) and decomposition of organic matter (Culliney, 2013). The local agricultural management not only affects the biodiversity of the farmed area but also of adjacent areas (Gabriel et al., 2010), including imbedded natural habitats and conservation areas (Brühl et al., 2021). Agricultural landscapes therefore need to be part of the solution to maintain arthropod biodiversity (Samways et al., 2020).

Arthropods need suitable habitats for overwintering, but agricultural fields are often characterised by adverse conditions: High intensity and frequent disturbance through management, for example ploughing, increases mortality of arthropods (Thorbek & Bilde, 2004) and a lack of vegetation cover in winter results in unfavourable microclimatic conditions (Bürki & Hausammann, 1993; Frank & Reichhart, 2004; Pfiffner & Luka, 2000). Consequently, field margins (Andersen, 1997; Clem & Harmon-Threatt, 2021; Ganser et al., 2019) and semi-natural habitats (Feng et al., 2021; Knapp et al., 2022) often harbour higher numbers of overwintering arthropods in agricultural landscapes compared to arable fields. Movement from these overwintering habitats into arable fields occurs in spring (Blitzer et al., 2012; Coombes & Sothertons, 1986; Wamser et al., 2011) and spillover of beneficial organisms contributes to the provision of ecosystem services, such as pest control (Dennis & Fry, 1992; Landis et al., 2000). Later in the crop growing season, spillover from semi-natural habitats into arable fields may, however, not provide a net benefit in terms of the number of pest control agents or pest control services (Birkhofer et al., 2018). In contrast, species overwintering in the field can account for a relevant proportion of the population during the

* Corresponding author.
E-mail address: klarissa.kober@zalf.de (K. Kober).

https://doi.org/10.1016/j.baae.2024.09.001
Received 20 January 2024; Accepted 1 September 2024
Available online 2 September 2024

growing season and thereby enhance pest control (Noordhuis et al., 2001).

Studies comparing the number of overwintering arthropods in semi-natural habitats or field margins to arable fields primarily sampled paired locations inside and outside the arable field (crop vs. non-crop habitat, e.g. Andersen (1997) [min. 20 m], Pfiffner and Luka (2000) [30 m], Ganser et al. (2019) [3 m], Clem and Harmon-Threatt (2021) [20 m]). Knapp et al. (2022) included a distance gradient in their design by placing additional sampling points at the edge between arable field and non-crop habitat. However, most studies that used a distance gradient focused on the distribution of arthropods in the growing season after emergence. With increasing distance into the fields, these studies often show changes in the activity-density of arthropods in general (Ng et al., 2018; Pollier et al., 2019) and amongst others for ground beetles (Anjum-Zubair et al., 2010; Birkhofer et al., 2014; Boetzl et al., 2019, 2020, 2024) (but see: Hof and Bright (2010)) and spiders (Birkhofer et al., 2014; Boetzl et al., 2019) (but see: Boetzl et al. (2020)).

Pitfall traps are the most common sampling technique for ground-dwelling arthropods such as ground beetles (Coleoptera, family Carabidae). The resulting estimates of local numbers are activity-densities without any reference to the origin of the beetles (Brown & Matthews, 2016). Emergence traps, in contrast, provide reliable estimates of the local production and emergence of arthropods overwintering in the soil and results can directly be linked to the properties of local soils (Holland et al., 2007). Soil moisture is an important soil characteristic and decreasing soil moisture inside agricultural fields leads to lower abundances of arthropods (measured with suction sampling), including ground beetles and spiders (Frampton et al., 2000; Zaller et al., 2014). However, knowledge about the influence of soil moisture on overwintering arthropods is scarce (but see: Holland et al. (2007)). Kettle holes, as small standing water bodies, provide a natural source of soil moisture. In Northeastern Germany, kettle holes are distributed with a density of up to 40 kettle holes per km^2 in agricultural landscapes (Kalettka & Rudat, 2006; Pätzig et al., 2012) and are regarded as hotspots of biodiversity (Pätzig et al., 2012; Vasic et al., 2020). These densities and their properties provide ideal conditions to study the influence of soil moisture and distance from field margins on the emergence of arthropods from soils of adjacent crop fields. The focus of this study is on ground beetles and spiders as numerically dominant generalist predators in agroecosystems, which contribute significantly to the biological control of pests and develop and emerge from soil (Birkhofer et al., 2013; Kromp, 1999; Michalko et al., 2019; Symondson et al., 2002).

We sampled arthropods with emergence traps along two distance gradients, with distances of 1, 20 and 50 m: (a) a distance gradient parting from the field margin of focal kettle holes into the surrounding wheat field and (b) a distance gradient from the field margin of another semi-natural landscape element into the same wheat fields. We hypothesize that (i) soil moisture is highest closest to the kettle hole field margins and that it decreases towards the centre of the wheat fields, (ii) numbers of arthropods, including ground beetles and spiders, emerging from soil generally increase with soil moisture and (iii) numbers of arthropods, including ground beetles and spiders, emerging from soil are highest near the kettle hole field margins, lower at other field margins and generally lowest in the field centres.

Materials and methods

Study area

The study area is located in the Uckermark region in the Federal State of Brandenburg in northeast Germany (Fig. 1). The landscape laboratory (AgroScapeLab Quillow, 2023) (https://comm.zalf.de/sites/aslq/SitePages/Home.aspx) is part of the Quillow catchment with an area of 160 km^2 which is intensively farmed. The undulating landscape was shaped by the Ice Age, leaving many small standing bodies of water called kettle holes which are often situated inside the arable fields (Appendix A: Fig. A.1). The study area is characterised by temperate climate with a mean air temperature of 8.9 °C and low annual precipitation (mean 498 mm), in the transition zone between subatlantic and

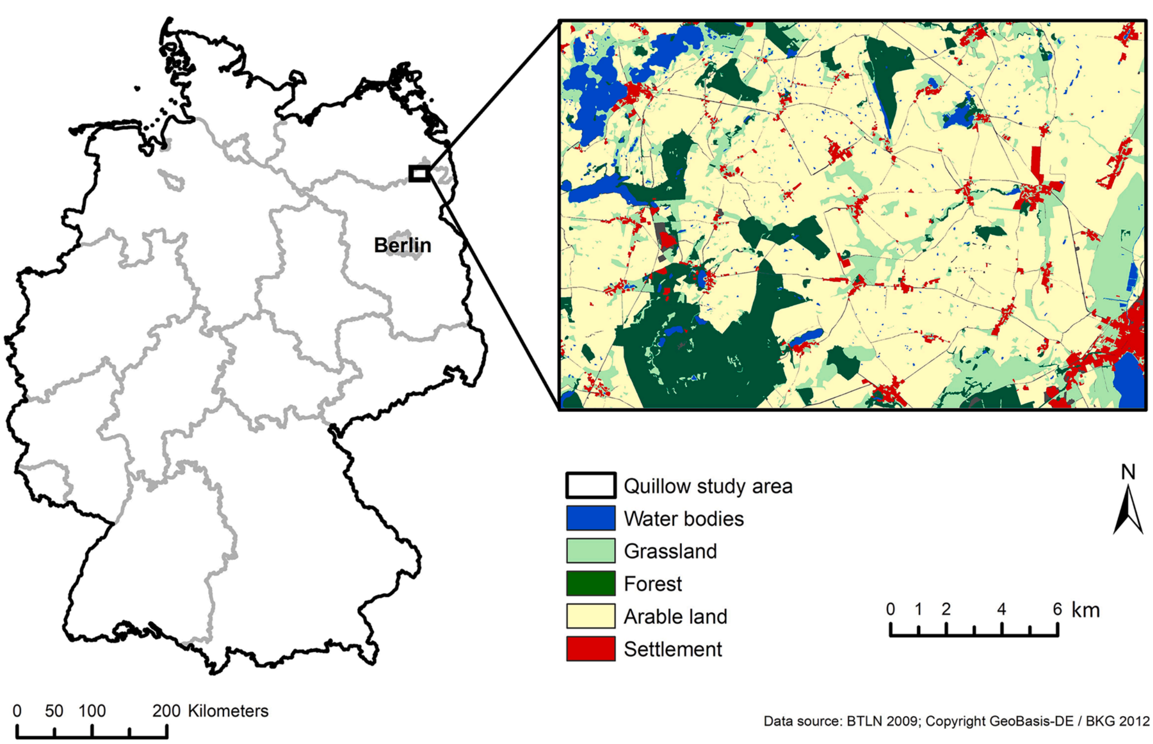


Fig. 1. Location of the study area. The landscape laboratory “AgroScapeLabs Quillow” is situated in the northeast German lowlands. Land cover types are indicated by colours. The area is dominated by arable land (yellow).

subcontinental impacts. The altitude varies between 20 and 110 m above sea level. Ranging mainly from sandy loam to loamy sand, soil types comprise a heterogeneous distribution of luvisols, arenosols, phaeozem, retisols, histosols, and planosols (Schultz et al., 2022). Due to a medium to high yield potential (winter wheat yield between 7.0 and 9.5 t/ha) (Schultz et al., 2022), land use is dominated by conventional farming with winter cereals (mostly wheat), silage maize and oilseed rape as the main crops (Raatz et al., 2019). The average field size amounts 27.5 ± 1.1 ha (Ullmann et al., 2020).

Study design

We selected ten kettle holes that were located entirely inside winter wheat fields ($N = 6$ fields; Fig. 2). These fields were all conventionally managed with maize as previous crop, did not border one another and were spread across the study area. The kettle holes had a distance to the field margin of at least 50 m and represented both the overflow and the storage type (Kalettka & Rudat, 2006). We established an orthogonal transect from the field margin around the kettle holes towards the centre of the surrounding wheat field ($N = 10$ transects). Additionally, we established a control transect from the field margin of another semi-natural landscape element (e.g. hedgerow or grassy margin) towards the centre of each of the same six fields that contained the selected kettle holes ($N = 6$ transects). The transects consisted of four sampling points for soil moisture at a distance of 1, 5, 20 and 50 m from the field margin (kettle hole or other margin) into the wheat field. We also collected arthropods with emergence traps at 1, 20 and 50 m. The number of sampling points differed for soil moisture and arthropods because we used a joint study design with other investigations analysing the impact of soil moisture. The sampling period started in mid-March and ended in late June 2020, just before the harvest.

Arthropod sampling

We set up commercially available (Emergence trap, 2023) (NHBS, https://www.nhbs.com/soil-emergence-trap-ii, Appendix A: Fig. A.2) to collect all invertebrates emerging from soil. We apply the term emergence in a broad sense to the process of individuals appearing from soil independent of (a change of) developmental stage. The traps (tents) were white and covered a surface of 60 × 60 cm (0.36 m^2). To catch all emerging individuals, we used the collecting bottle at the top of the tent for flying and climbing arthropods together with one pitfall trap in the centre of the tent for ground beetles, spiders and other ground-dwelling arthropods. Both sampling methods were combined to ensure that we captured the total amount of emerging individuals, taking into account their different modes of locomotion (Hanson et al., 2017). Bottles were filled with 200–300 ml of 70 % ethanol. For the pitfall traps we used glass cups (diameter 7.5 cm) half filled with a saturated salt solution and a drop of tenside to reduce the surface tension. Every two weeks, we replaced collecting bottles and pitfall traps over the sampling period of 16 weeks. We counted all arthropods, ground beetles and spiders in each sample but without consideration of larvae. We replaced missing values from lacking samples ($N = 157$ out of 2304) and outliers (criteria for definition: Cleveland dotplot and plausibility, $N = 4$) by the corresponding mean (i.e. the respective value of the means calculated for each trap type at each date at each distance at each field margin). To calculate the number of individuals emerging from soil (referred to as emergence numbers), we summed up all sampled individuals of arthropods or ground beetles or spiders over the entire sampling period for each emergence trap (i. e. for bottles and pitfall traps together as we focus on total emergence numbers). One value for the number of arthropods was implausibly high and was therefore replaced by the second highest value in the dataset.

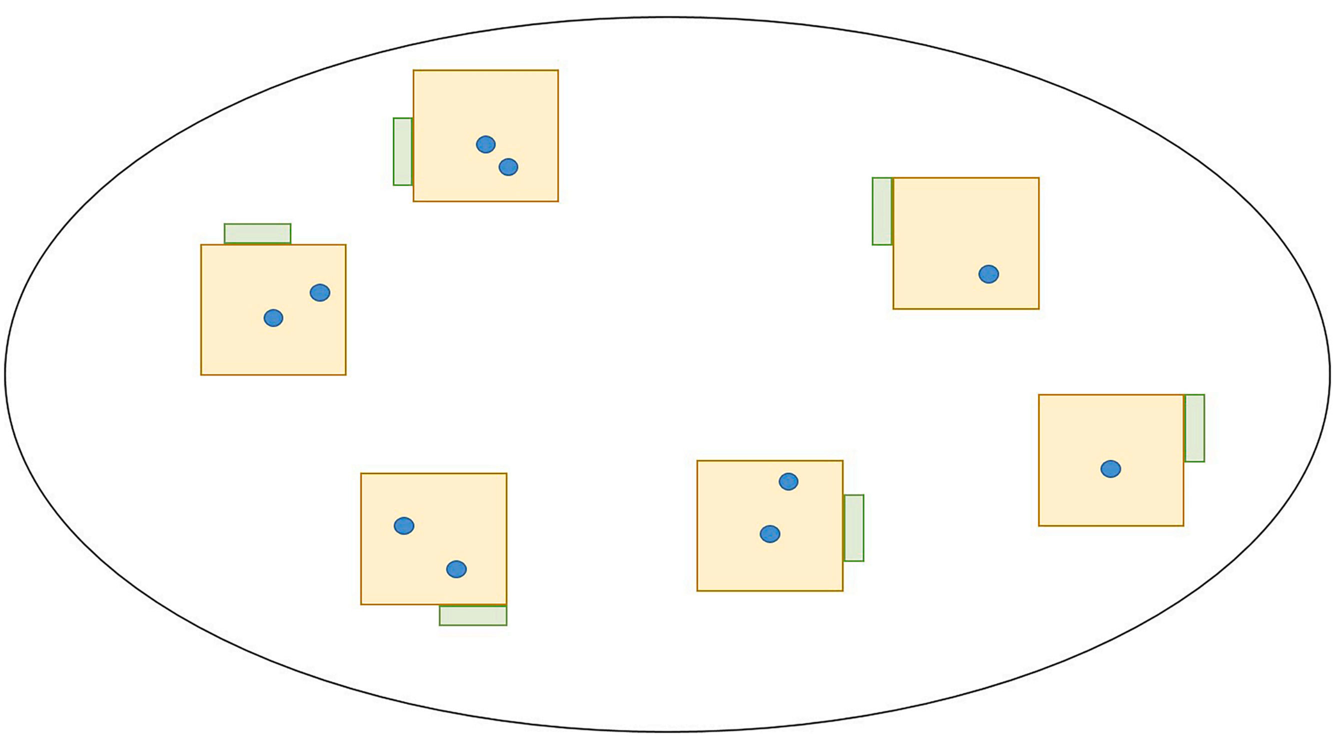


Fig. 2. Schematic illustration of the study design. The black line represents the outline of the study area. Blue circles: selected kettle holes ($N = 10$); yellow squares: fields containing the selected kettle holes ($N = 6$); green rectangles: selected other semi-natural habitats as control for each field ($N = 6$). Transects ran from the field margin of the kettle holes and the other semi-natural habitats towards the field centre ($N = 16$; not plotted). Smallest distance between fields: 2.4 km; greatest distance between fields: 13.4 km.

Soil moisture measurements

Next to the emergence traps, we measured the soil moisture (m^3/m^3, volumetric soil moisture content) using microclimatic measuring stations (Hobo H21 Micro Station, Onset Computer Corporation, MA, USA) with a soil moisture smart sensor (S-SMD-M005), which reported the soil moisture in a depth of approximately 10 cm continuously every hour. Due to technical problems, we did not get soil moisture values for the entire sampling period from all measuring stations. Therefore, we replaced the missing values ($N = 16{,}108$ out of 156,608) by the corresponding mean (according to the field margin type, distance and measurement time and date). We calculated mean soil moisture values over the entire measurement period as response variable.

Data analyses

To test for a soil moisture gradient from a field margin towards the field centre, we used a linear mixed-effect model. We included distance from a field margin (log-transformed to account for the non-linear relationship) and the type of the field margin (kettle hole vs. other semi-natural landscape element) as fixed factors and the field (Fields 1–6), in which the transects were placed, as random factor. To test for effects on emergence numbers of arthropods, a second linear mixed-effect model was used (Table 1). Emergence numbers were log-transformed prior to analyses to fit the model assumptions. This model included the mean soil moisture, distance from a field margin (log-transformed for arthropods and spiders to account for a non-linear relationship) and field margin type as fixed factors and the field as random factor. For all statistical analyses, we used R, version 4.1.3 (R Core Team, 2022) with the package "nlme" for linear mixed-effect models (Pinheiro et al., 2022). We confirmed model assumptions of homoscedasticity and normal distribution of the residuals visually. We selected the model with the lowest AIC value as minimum adequate model. To control the selection of the terms, we determined the statistical significance of fixed effects by Wald's chi-square tests on each of the full models (*Anova* function, 'car' package (Fox & Weisberg, 2019)). These tests confirmed the selected parameters (Appendix A: Table A.1).

Results

Soil moisture ranged between 0.12 m^3/m^3 to 0.38 m^3/m^3 for single measurement readings and between 0.22 m^3/m^3 to 0.33 m^3/m^3 for mean values per sampling point. Variation in soil moisture was best explained by distance from a field margin: Soil moisture declined with increasing distance (Fig. 3; estimate = −0.003, p = 0.021, 40.7 % explained variance). The field margin type was not selected as predictor of soil moisture in the model.

Table 1
Model parameters of the minimum adequate models. The effects of soil moisture, distance from a field margin and field margin type and the interaction between the factors on the emergence numbers of arthropods, ground beetles and spiders are shown with model estimate, p-value and the percentage of explained variance. "Not selected" means that the variable is not part of the minimum adequate model. Emergence numbers were log-transformed. Distance was log-transformed in the models on the emergence of arthropods and spiders.

	Arthropods		Ground beetles		Spiders	
	Estimate	p-value	Estimate	p-value	Estimate	p-value
Soil moisture (S)	3,75	0.032	12,90	0.023	10,59	0.011
Distance (D)	not selected		0.06	0.199	0.19	<0.001
Field margin type (T)	not selected		not selected		not selected	
S x D	not selected		−0.29	0.097	not selected	
D x T	not selected		not selected		not selected	
S x T	not selected		not selected		not selected	
Variance expl.	47.7 %		47.2 %		49.6 %	

Arthropods, ground beetles and spiders emerged over the entire sampling period from March to June at constant or increasing rates over time (Appendix A: Fig. A.3). At all three investigated distances, emergence of the three taxa occurred (Appendix A: Fig. A.4). Between 644 and 2708 arthropods were caught per emergence trap over the sampling period. In total, 52,033 arthropods, with 11,399 in the pitfall traps (21.9 % of all individuals) were sampled. Emergence numbers of arthropods were positively related to soil moisture in the minimum adequate model (Table 1, Fig. 4) and all four alternative models within 2ΔAIC units (Appendix A: Table A.2).

In total, 1770 ground beetles, with 1355 in the pitfall traps (76.6 %), were sampled ranging from 8 to 254 individuals per emergence trap. Emergence numbers of ground beetles were positively related to soil moisture in the minimum adequate model (Table 1, Fig. 5A) and all four alternative models within 2ΔAIC units (Appendix A: Table A.2). Distance from a field margin as well as the interaction between distance and soil moisture were selected as predictors in the minimum adequate model, but both model terms did not affect the emergence numbers significantly (Table 1, Fig. 5B). At greater distances from a field margin, the positive influence of soil moisture became weaker, with no relationship at a distance of 40 m or greater. Distance decay of the emergence numbers was strongest at soil moisture higher than 0.27 m^3/m^3. At low soil moisture values (0.21–0.24 m^3/m^3) or a large distance from a margin (40 −50 m), emergence numbers of ground beetles were generally lower.

In total, 1500 spiders, with 1041 in the pitfall traps (69.4 %), were sampled ranging from 3 to 111 individuals per emergence trap. Emergence numbers of spiders were positively related to soil moisture in the minimum adequate model (Table 1, Fig. 6A) and the single alternative model within 2ΔAIC units (Appendix A: Table A.2). Distance from a field margin affected emergence numbers of spiders, with highest numbers at 20 m distance from a margin independent of field margin type (Table 1, Fig. 6B).

Discussion

We investigated the emergence of arthropods, ground beetles and spiders in winter wheat fields. Here we show that soil moisture positively influences the emergence numbers of all three taxa, but that the effect of distance from a field margin differs between taxa. Overall, emergence numbers suggest crop fields as relevant overwintering habitats.

Soil moisture

We expected soil moisture to be highest closest to the field margins of kettle holes and to show generic decreasing trends towards the field centre (Gerke et al., 2010). Soil moisture was indeed highest close to field margins, but independent of the field margin type (kettle hole or other semi-natural landscape element). Surprisingly, sampling points on the kettle hole transects showed no strong trend towards elevated soil moisture values compared to the transects from other field margins. The year 2020 was very dry, together with the proceeding years, with kettle holes falling dry or having a much smaller water body than in more average years (Pätzig & Düker, 2021). These drought conditions may be a reason for the lack of differences in soil moisture between the two field margin types. A second potential explanation may be that we measured soil moisture in the upper part of the soil which dries out first. We decided to sample soil moisture at this depth, because it is the most relevant layer for soil-living organisms in this study.

Soil moisture was the most important predictor of the emergence numbers of total arthropods as well as ground beetles and spiders, as numbers of all three taxa were higher at high soil moisture levels. This result confirms our hypothesis and underlines the relevance of soil

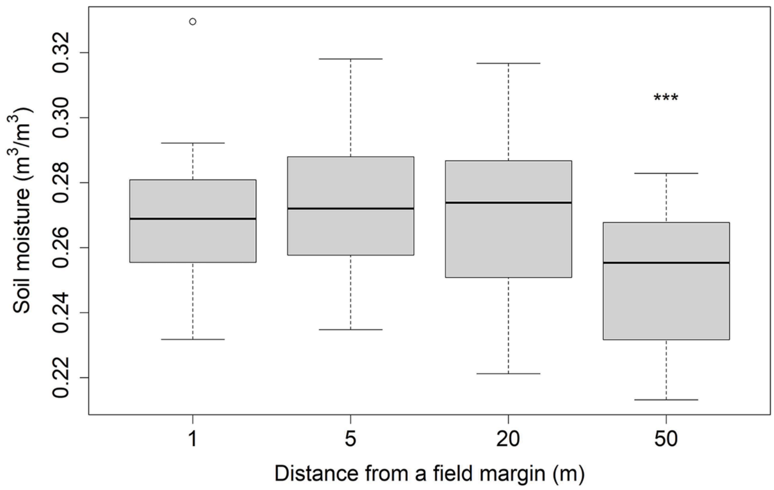


Fig. 3. Response of soil moisture to distance from a field margin (combined for transects from kettle holes and other semi-natural landscape elements). At the furthest distance of 50 m, soil moisture was significantly lower than near a field margin. The bold horizontal line inside the boxes represents the median, with the box ranging from the first to the third quantile. Whiskers mark 1.5 times the interquartile range from the top and bottom of the box and points are outliers.

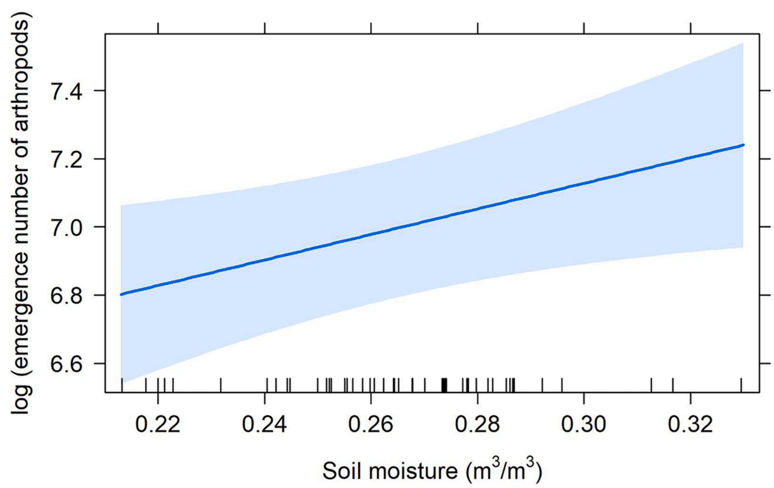


Fig. 4. Positive relationship between the emergence numbers of arthropods and soil moisture. The graph shows the prediction of the minimum adequate model using the “effects” package (Fox & Weisberg, 2019). Emergence numbers of arthropods are log-transformed.

moisture for arthropods. This is consistent with the finding that decreasing soil moisture leads to lower abundance of ground-dwelling arthropods (Frampton et al., 2000; Zaller et al., 2014). However, emergence is rarely studied in relation to soil moisture in the field. One exception is the study by Holland et al. (2007) who found emergence numbers in individual ground beetle species to respond positively to soil moisture in winter-sown cereals. Given the positive influence of soil moisture on total arthropod as well as ground beetle and spider emergence, the widespread decrease in soil moisture associated with anthropogenic climate change (Seneviratne et al., 2010) is worrying in light of the general decline in arthropod populations worldwide (Cardoso et al., 2020; Wagner, 2020).

Distance from field margins

In contrast to soil moisture, which had a positive effect on the emergence of all three taxonomic groups, the influence of the distance from a field margin differed between taxa: for spiders it was hump-shaped with peak numbers at 20 m (Fig. 6B), but for ground beetles it was negative or weak depending on soil moisture levels (Fig. 5B).

For ground beetle emergence, distance showed a negative trend, especially at high soil moisture levels, whereas at low soil moisture values, emergence numbers remained constant at all distances (Fig. 5B). The positive effect of soil moisture on the emergence numbers generally disappeared with increasing distances and soil moisture effects were even higher close to the edges of the fields (Fig. 5A). The potential for overwintering close to the field margin is probably higher for ground beetles and beneficial effects of soil moisture lead to higher emergence at these distances.

The influence of distance from a field margin on the emergence numbers of ground beetles and spiders is only partly reflected by previously observed activity-densities during the growing season in cereal fields (see Introduction). Accordingly, those findings cannot generally be transferred to emergence numbers.

Crop fields as overwintering habitat

Crop fields can be important habitats for the overwintering of generalist predators (Feng et al., 2021; Hanson et al., 2017; Holland et al., 2007). Especially winter-sown cereals as in this study can support overwintering predatory arthropods (Birkhofer et al., 2018; Sotherton, 1984) due to a less detrimental timing of soil tillage (Fadl et al., 1996; Purvis & Fadl, 1996). Based on the high numbers of spiders and ground beetles (and overall arthropods) caught in our study, we conclude that

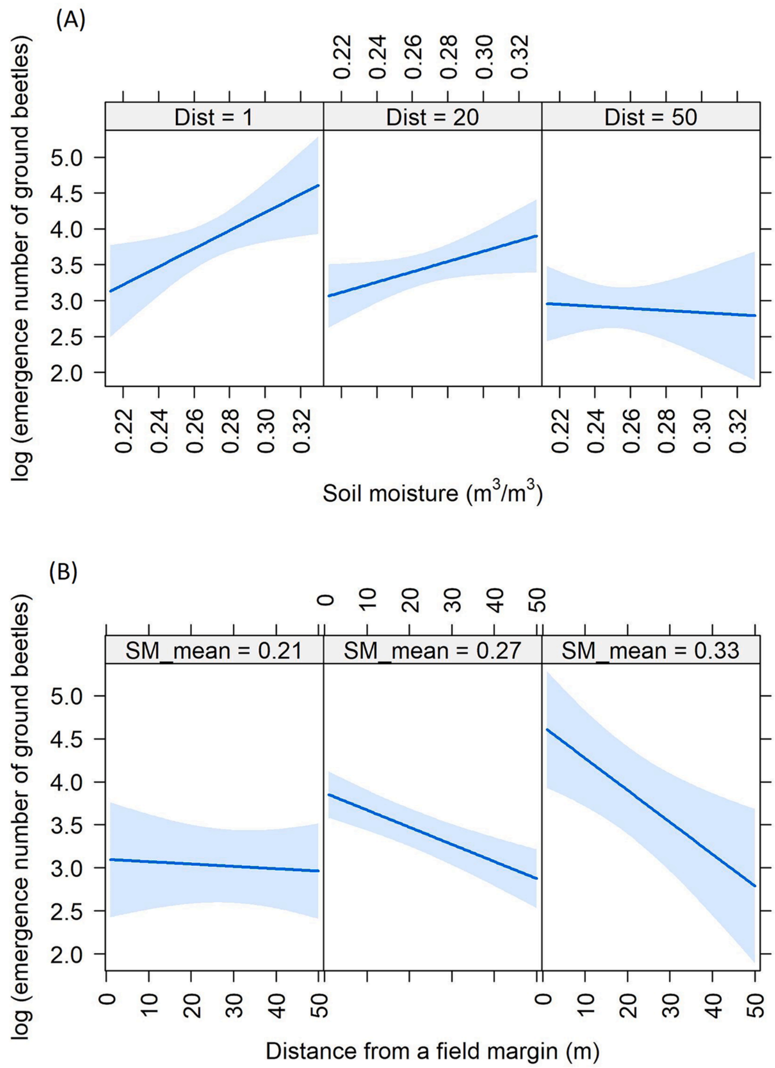


Fig. 5. Relationship between the emergence numbers of ground beetles and (A) soil moisture, depending on the distance from a field margin, (B) distance from a field margin, depending on soil moisture. The graphs show the prediction of the minimum adequate model using the "effects" package (Fox & Weisberg, 2019). Emergence numbers of ground beetles are log-transformed.

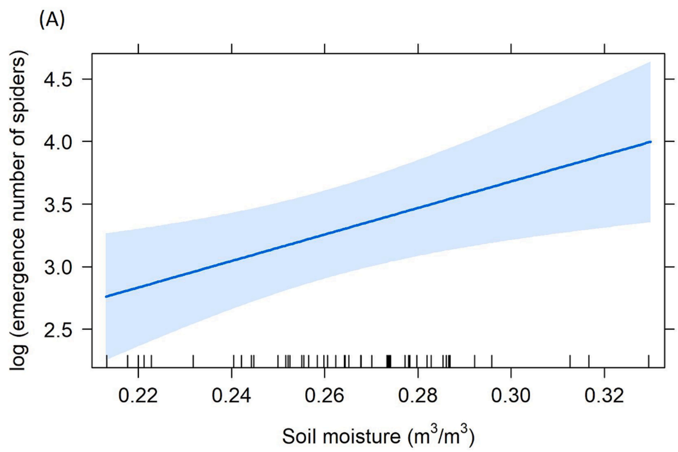
not only field margins are important, but soil management in-field also impacts arthropods. Consequently, we propose that efforts to maintain arthropod numbers should not be limited to the promotion of field margins and semi-natural habitats. Crop fields themselves deserve attention as important overwintering sites for arthropods. Soil management resulting in reduced disturbance during the overwintering period (Thorbek & Bilde, 2004) and higher soil water holding capacity (Birkhofer et al., 2021) may help to reduce arthropod mortality and can promote emergence numbers from crops fields.

This may result in enhanced pest control (Noordhuis et al., 2001) and early-season pest regulation (Athey et al., 2016) as within-field emerging arthropods can reduce the need for colonization of fields from surrounding habitats. The high number of individuals not being ground beetles or spiders leaves open whether such management adaptations would also favour the emergence of pest groups.

Furthermore, our findings are not only important for overwintering arthropods, since emergence traps captured an increasing number of arthropods in May-June (Appendix A: Fig. A.3). Potentially, these are not exclusively overwintering individuals. Several ground beetle species are burrowers that dig into the soil not only for overwintering (Thiele, 2012). Thus, our study highlights the general importance of agricultural soils and their adequate management as habitats for arthropods. Considering that agriculture is the most important land use type worldwide, covering 37 % of the terrestrial surface (Raschka & Carus, 2012) and 50.6 % in Germany (Bundesministerium für Ernährung und Landwirtschaft, 2022), our study confirms its great potential in promoting arthropods and halt their decline (Samways et al., 2020).

Emergence traps

Emergence traps are a valuable method to estimate numbers of emerging arthropods related to a location of fixed area size which is not possible using pitfall traps. Emergence traps allow to identify and characterise overwintering habitats of organisms that develop in the soil. However, mobile taxa may not stay at their overwintering location and emergence traps cannot provide estimates of locally active organisms. The technique can therefore not be used to derive conclusions about ecosystem services provided by the respective organism groups. Hence, for an ecological evaluation both sampling methods (pitfall traps and emergence traps) should ideally be used together (Birkhofer et al., 2018; Hanson et al., 2016). Given that one fourth of the ground beetles and even one-third-of the spiders were caught with the collecting bottles, it seems reasonable to use both, pitfall traps and collecting bottles, inside the tents when sampling ground-dwelling taxa with emergence



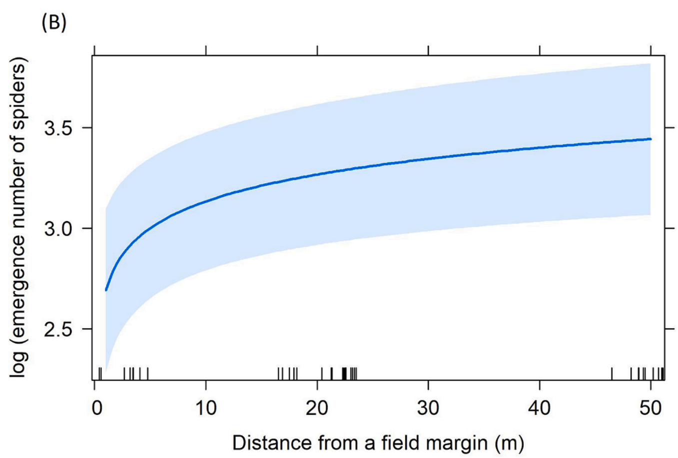


Fig. 6. Relationship between the emergence numbers of spiders and (A) soil moisture, (B) distance from a field margin. The graphs show the prediction of the minimum adequate model using the "effects" package (Fox & Weisberg, 2019). Emergence numbers of spiders are log-transformed.

traps.

Conclusion

Within-field soil conditions matter for arthropod communities. Soil moisture is an important property for the overwintering of ground-active arthropods. Consistent for all three studied taxa, emergence numbers were positively related to soil moisture. Ground beetle and spider emergence numbers showed the same relationship to soil moisture, but differed regarding their response to the distance from a field margin. Thus, management for higher soil water holding capacity is a promising option to conserve numbers of beneficial arthropods but management practices that solely focus on narrow edges of crop fields may miss an opportunity to conserve arthropod predators. Management adaptations would be especially effective where emergence is highest, i. e. where moisture is high and at distances of up to 20 metres to field margins. It is crucial to emphasize that emergence numbers inside the fields were high. We therefore conclude that crop fields should not be neglected as overwintering habitats of beneficial arthropods. Increasing numbers over time even highlight the general importance of agricultural soils for arthropods. Consequently, management adaptations in crop fields that minimize the mortality of soil-emerging arthropods should become key practices to halt the ongoing biodiversity loss.

Funding

This study is part of the project SWBTrans: "Smart Use of Heterogeneities of Agricultural Landscapes". It is subject of an internal project funding of the Leibniz Centre for Agricultural Landscape Research (ZALF) which is as institution financed in equal parts by the Federal Ministry of Food and Agriculture (BMEL) and the Ministry for Science, Research and Culture of the State of Brandenburg (MWFK).

CRediT authorship contribution statement

Klarissa Kober: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Klaus Birkhofer:** Writing – review & editing, Validation, Supervision. **Michael Glemnitz:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

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.

Acknowledgements

We thank all involved farmers for the permission to access their fields. We are grateful to Cornelia Fischer and Dorith Henning for their help in the field and lab. Thanks also to our colleagues from the experimental station in the AgroScapeLab Quillow for their support. We acknowledge the valuable comments of two anonymous reviewers on the manuscript.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.09.001.

References

AgroScapeLab Quillow. Retrieved 27.09.2023 from https://comm.zalf.de/sites/aslq/SitePages/Home.aspx.

Andersen, A. (1997). Densities of overwintering carabids and staphylinids (Col., Carabidae and Staphylinidae) in cereal and grass fields and their boundaries. *Journal of Applied Entomology, 121*(2), 77–80. https://doi.org/10.1111/j.1439-0418.1997.tb01374.x

Anjum-Zubair, M., Schmidt-Entling, M. H., Querner, P., & Frank, T. (2010). Influence of within-field position and adjoining habitat on carabid beetle assemblages in winter wheat. *Agricultural and Forest Entomology, 12*(3), 301–306. https://doi.org/10.1111/j.1461-9563.2010.00479.x

Athey, K. J., Dreyer, J., Kowles, K. A., Penn, H. J., Sitvarin, M. I., & Harwood, J. D. (2016). Spring forward: Molecular detection of early season predation in agroecosystems. *Food Webs, 9*, 25–31. https://doi.org/10.1016/j.fooweb.2016.06.001

Birkhofer, K., Entling, M. H., & Lubin, Y. (2013). Trait composition, spatial relationships, trophic interactions. In D. Penney (Ed.), *Spider research in the 21st century: Trends and perspectives* (Ed., pp. 200–229). Rochdale, United Kingdom: Siri Scientific Press.

Birkhofer, K., Fevrier, V., Heinrich, A. E., Rink, K., & Smith, H. G. (2018). The contribution of CAP greening measures to conservation biological control at two spatial scales. *Agriculture, Ecosystems and Environment, 255*, 84–94. https://doi.org/10.1016/j.agee.2017.12.026

Birkhofer, K., Fliessbach, A., Gavín-Centol, M. P., Hedlund, K., Ingimarsdóttir, M., Jørgensen, H. B., et al. (2021). Conventional agriculture and not drought alters relationships between soil biota and functions. *Scientific Reports, 11*(1), 23975. https://doi.org/10.1038/s41598-021-03276-x

Birkhofer, K., Wolters, V., & Diekötter, T. (2014). Grassy margins along organically managed cereal fields foster trait diversity and taxonomic distinctness of arthropod communities. *Insect Conservation and Diversity, 7*(3), 274–287. https://doi.org/10.1111/icad.12051

Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A. M., Rand, T. A., & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats [Review]. *Agriculture, Ecosystems and Environment, 146*(1), 34–43. https://doi.org/10.1016/j.agee.2011.09.005

Boetzl, F. A., Krimmer, E., Krauss, J., & Steffan-Dewenter, I. (2019). Agri-environmental schemes promote ground-dwelling predators in adjacent oilseed rape fields:

Diversity, species traits and distance-decay functions. *Journal of Applied Ecology, 56* (1), 10–20. https://doi.org/10.1111/1365-2664.13162

Boetzl, F. A., Schuele, M., Krauss, J., & Steffan-Dewenter, I. (2020). Pest control potential of adjacent agri-environment schemes varies with crop type and is shaped by landscape context and within-field position. *Journal of Applied Ecology, 57*(8), 1482–1493. https://doi.org/10.1111/1365-2664.13653

Boetzl, F. A., Sponsler, D., Albrecht, M., Batáry, P., Birkhofer, K., Knapp, M., et al. (2024). Distance functions of carabids in crop fields depend on functional traits, crop type and adjacent habitat: A synthesis. *Proceedings of the Royal Society B, 291*(2014), Article 20232383. https://doi.org/10.1098/rspb.2023.2383

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

Brühl, C. A., Bakanov, N., Köthe, S., Eichler, L., Sorg, M., Hörren, T., et al. (2021). Direct pesticide exposure of insects in nature conservation areas in Germany. *Scientific Reports, 11*(1), 24144. https://doi.org/10.1038/s41598-021-03366-w

Bundesministerium für Ernährung und Landwirtschaft. (2022). *Daten und fakten. land-, forst-und ernährungswirtschaft mit fischerei und wein-und gartenbau.* Germany: BMEL Berlin.

Bürki, H. M., & Hausammann, A. (1993). *Überwinterung von arthropoden im boden und an ackerkräutern künstlich angelegter ackerkrautstreifen.* Haupt.

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., et al. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation, 242*, Article 108426. https://doi.org/10.1016/j.biocon.2020.108426

Clem, C. S., & Harmon-Threatt, A. N. (2021). Field borders provide winter refuge for beneficial predators and parasitoids: A case study on organic farms. *Journal of Insect Science, 21*(3), 2. https://doi.org/10.1093/jisesa/ieab027

Coombes, D. S., & Sothertons, N. W. (1986). The dispersal and distribution of polyphagous predatory Coleoptera in cereals. *Annals of Applied Biology, 108*(3), 461–474. https://doi.org/10.1111/j.1744-7348.1986.tb01985.x

Culliney, T. W. (2013). Role of arthropods in maintaining soil fertility. *Agriculture (Switzerland), 3*(4), 629–659. https://doi.org/10.3390/agriculture3040629

Dennis, P., & Fry, G. L. A. (1992). Field margins: Can they enhance natural enemy population densities and general arthropod diversity on farmland? *Agriculture, Ecosystems and Environment, 40*(1–4), 95–115. https://doi.org/10.1016/0167-8809(92)90086-Q

Emergence trap. Retrieved 22.11.2023 from https://www.nhbs.com/soil-emergence-trap-ii.

Fadl, A., Purvis, G., & Towey, K. (1996). The effect of time of soil cultivation on the incidence of Pterostichus melanarius (Illig.)(Coleoptera: Carabidae) in arable land in Ireland. *Annales Zoologici Fennici, 33*, 207–214.

Feng, L., Arvidsson, F., Smith, H. G., & Birkhofer, K. (2021). Fallows and permanent grasslands conserve the species composition and functional diversity of carabid beetles and linyphiid spiders in agricultural landscapes. *Insect Conservation and Diversity, 14*(6), 825–836. https://doi.org/10.1111/icad.12520

Fox, J., & Weisberg, S. (2019). *An {R} companion to applied regression (Third ed.)*. Thousand Oaks CA: Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Frampton, G. K., Van Den Brink, P. J., & Gould, P. J. L (2000). Effects of spring drought and irrigation on farmland arthropods in southern Britain. *Journal of Applied Ecology, 37*(5), 865–883. https://doi.org/10.1046/j.1365-2664.2000.00541.x

Frank, T., & Reichhart, B. (2004). Staphylinidae and Carabidae overwintering in wheat and sown wildflower areas of different age. *Bulletin of Entomological Research, 94*(3), 209–217. https://doi.org/10.1079/BER2004301

Gabriel, D., Sait, S. M., Hodgson, J. A., Schmutz, U., Kunin, W. E., & Benton, T. G. (2010). Scale matters: The impact of organic farming on biodiversity at different spatial scales. *Ecology Letters, 13*(7), 858–869. https://doi.org/10.1111/j.1461-0248.2010.01481.x

Ganser, D., Knop, E., & Albrecht, M. (2019). Sown wildflower strips as overwintering habitat for arthropods: Effective measure or ecological trap? *Agriculture. Ecosystems and Environment, 275*, 123–131. https://doi.org/10.1016/j.agee.2019.02.010

Gerke, H. H., Koszinski, S., Kalettka, T., & Sommer, M. (2010). Structures and hydrologic function of soil landscapes with kettle holes using an integrated hydropedological approach. *Journal of Hydrology, 393*(1–2), 123–132. https://doi.org/10.1016/j.jhydrol.2009.12.047

Hanson, H. I., Birkhofer, K., Smith, H. G., Palmu, E., & Hedlund, K. (2017). Agricultural land use affects abundance and dispersal tendency of predatory arthropods. *Basic and Applied Ecology, 18*, 40–49. https://doi.org/10.1016/j.baae.2016.10.004

Hanson, H. I., Palmu, E., Birkhofer, K., Smith, H. G., & Hedlund, K. (2016). Agricultural land use determines the trait composition of ground beetle communities. *PloS one, 11* (1), Article e0146329. https://doi.org/10.1371/journal.pone.0146329

Hof, A. R., & Bright, P. W. (2010). The impact of grassy field margins on macro-invertebrate abundance in adjacent arable fields. *Agriculture, Ecosystems and Environment, 139*(1–2), 280–283. https://doi.org/10.1016/j.agee.2010.08.014

Holland, J. M., Thomas, C. F. G., Birkett, T., & Southway, S. (2007). Spatio-temporal distribution and emergence of beetles in arable fields in relation to soil moisture. *Bulletin of Entomological Research, 97*(1), 89–100. https://doi.org/10.1017/S0007485307004804

Kalettka, T., & Rudat, C. (2006). Hydrogeomorphic types of glacially created kettle holes in North-East Germany. *Limnologica, 36*(1), 54–64. https://doi.org/10.1016/j.limno.2005.11.001

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., et al. (2007). Importance of pollinators in changing landscapes for world crops [Review]. *Proceedings of the Royal Society B: Biological Sciences, 274*(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Knapp, M., Štrobl, M., Venturo, A., Seidl, M., Jakubíková, L., Tajovský, K., et al. (2022). Importance of grassy and forest non-crop habitat islands for overwintering of ground-dwelling arthropods in agricultural landscapes: A multi-taxa approach. *Biological Conservation, 275*, Article 109757. https://doi.org/10.1016/j.biocon.2022.109757

Kromp, B. (1999). Carabid beetles in sustainable agriculture: A review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment, 74*(1–3), 187–228. https://doi.org/10.1016/S0167-8809(99)00037-7

Landis, D. A., Wratten, 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

Michalko, R., Pekár, S., & Entling, M. H. (2019). An updated perspective on spiders as generalist predators in biological control [Review]. *Oecologia, 189*(1), 21–36. https://doi.org/10.1007/s00442-018-4313-1

Ng, K., Barton, P. S., Macfadyen, S., Lindenmayer, D. B., & Driscoll, D. A. (2018). Beetle's responses to edges in fragmented landscapes are driven by adjacent farmland use, season and cross-habitat movement. *Landscape Ecology, 33*(1), 109–125. https://doi.org/10.1007/s10980-017-0587-7

Noordhuis, R., Thomas, S. R., & Goulson, D. (2001). Overwintering populations of beetle larvae (Coleoptera) in cereal fields and their contribution to adult populations in the spring. *Pedobiologia, 45*(1), 84–95. https://doi.org/10.1078/0031-4056-00070

Pätzig, M., & Düker, E. (2021). Dynamic of dominant plant communities in kettle holes (northeast Germany) during a five-year period of extreme weather conditions. *Water (Switzerland), 13*(5), 688. https://doi.org/10.3390/w13050688

Pätzig, M., Kalettka, T., Glemnitz, M., & Berger, G. (2012). What governs macrophyte species richness in kettle hole types? A case study from Northeast Germany. *Limnologica, 42*(4), 340–354. https://doi.org/10.1016/j.limno.2012.07.004

Pfiffner, L., & Luka, H. (2000). Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agriculture, Ecosystems and Environment, 78*(3), 215–222. https://doi.org/10.1016/S0167-8809(99)00130-9

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2022). *_nlme: Linear and nonlinear mixed effects models_*. R package version 3.1-155. https://CRAN.R-project.org/package=nlme.

Pollier, A., Tricault, Y., Plantegenest, M., & Bischoff, A. (2019). Sowing of margin strips rich in floral resources improves herbivore control in adjacent crop fields. *Agricultural and Forest Entomology, 21*(1), 119–129. https://doi.org/10.1111/afe.12318

Purvis, G., & Fadl, A. (1996). Emergence of Carabidae (Coleoptera) from pupation: A technique for studying the'productivity'of carabid habitats. *Annales Zoologici Fennici, 33*, 215–223.

R Core Team (2022). *R: A language and environment for statistical computing*. In R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Raatz, L., Bacchi, N., Pirhofer Walzl, K., Glemnitz, M., Müller, M. E., Joshi, J., et al. (2019). How much do we really lose?—Yield losses in the proximity of natural landscape elements in agricultural landscapes. *Ecology and Evolution, 9*(13), 7838–7848. https://doi.org/10.1002/ece3.5370

Raschka, A., & Carus, M. (2012). *Industrial material use of biomass basic data for Germany, Europe and the world.* nova-Institute.

Samways, M. J., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., et al. (2020). Solutions for humanity on how to conserve insects. *Biological Conservation, 242*, Article 108427. https://doi.org/10.1016/j.biocon.2020.108427

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers [Review]. *Biological Conservation, 232*, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Schultz, A., Glemnitz, M., Stachow, U., & Schwierz, F. (2022). Changes in a bird community in an agricultural landscape in northeast Germany between 1999 and 2015. *Land, 11*(12), 2115. https://doi.org/10.3390/land11122115

Seneviratne, S. I., Corti, T., Davin, E. L., Hirschi, M., Jaeger, E. B., Lehner, I., et al. (2010). Investigating soil moisture-climate interactions in a changing climate: A review [Review]. *Earth-Science Reviews, 99*(3–4), 125–161. https://doi.org/10.1016/j.earscirev.2010.02.004

Sotherton, N. W. (1984). The distribution and abundance of predatory arthropods overwintering on farmland. *Annals of Applied Biology, 105*(3), 423–429. https://doi.org/10.1111/j.1744-7348.1984.tb03068.x

Symondson, W. O. C., Sunderland, K. D., & Greenstone, M. H. (2002). Can generalist predators be effective biocontrol agents? [Review]. *Annual review of entomology, 47*, 561–594. https://doi.org/10.1146/annurev.ento.47.091201.145240

Thiele, H. U. (2012). *Carabid beetles in their environments: A study on habitat selection by adaptations in physiology and behaviour, 10*. Springer Science & Business Media.

Thorbek, P., & Bilde, T. (2004). Reduced numbers of generalist arthropod predators after crop management. *Journal of Applied Ecology, 41*(3), 526–538. https://doi.org/10.1111/j.0021-8901.2004.00913.x

Ullmann, W., Fischer, C., Kramer-Schadt, S., Pirhofer-Walzl, K., Glemnitz, M., & Blaum, N. (2020). How do agricultural practices affect the movement behaviour of European brown hares (Lepus europaeus)? *Agriculture. Ecosystems & Environment, 292*, Article 106819. https://doi.org/10.1016/j.agee.2020.106819

Vasic, F., Paul, C., Strauss, V., & Helming, K. (2020). Ecosystem services of kettle holes in agricultural landscapes [Review]. *Agronomy, 10*(9), 1326. https://doi.org/10.3390/agronomy10091326

Wagner, D. L. (2020). Insect declines in the anthropocene [Review]. *Annual review of entomology, 65*, 457–480. https://doi.org/10.1146/annurev-ento-011019-025151

Wamser, S., Dauber, J., Birkhofer, K., & Wolters, V. (2011). Delayed colonisation of arable fields by spring breeding ground beetles (Coleoptera: Carabidae) in landscapes with a high availability of hibernation sites. *Agriculture, Ecosystems & Environment, 144*(1), 235–240. https://doi.org/10.1016/j.agee.2011.08.019

Zaller, J. G., Simmer, L., Santer, N., Tataw, J. T., Formayer, H., & Murer, E. (2014). Future rain fall variations reducea bundances of aboveground arthropods in model agroecosystems with different soil types. *Frontiers in Environmental Science, 2*(OCT), 44. https://doi.org/10.3389/fenvs.2014.00044