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Distribution of ground-dwelling arthropods across landscapes with intensive agriculture in temperate areas☆

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ARTICLE INFO

ABSTRACT

The idea that land use in the surroundings may affect the abundance of arthropods on a location plays an important role in the argument that agriculture is the prime cause of the recently discovered general decline of insects. We studied the abundance of ground-dwelling arthropods in agricultural fields along a gradient of increasing distance from (semi)natural areas and in relation to landscape complexity in both the North America (Illinois, USA) and Europe (The Netherlands) using pitfalls. Our results showed that the total abundance did not change with distance when we controlled for vegetation height and landscape complexity around the sample locations. Vegetation height affected abundance positively in crop land and negatively in grassland. Landscape complexity only affected abundance when it was measured in a 6000 m radius around sample location, not at lower levels of scale. We conclude that an effect of increasing landscape complexity may be expected when that is done on a large enough scale.

1. Introduction

In 2017, Hallmann et al. published a 75% decline of terrestrially flying insect biomass in 27 year in German nature conservation areas. The results of the study were communicated widely and shocked the world. (see for example https://www.bbc.com/news/science-environment-41670472; https://www.theguardian.com/environment/2017/oct/18/warning-of-ecological-armageddon-after-dramatic-plunge-in-insect-numbers; https://www.nytimes.com/2017/10/29/opinion/insect-armageddon-ecosystem-.html).

The publication of Hallmann et al. inspired many follow-up research (Wagner et al. 2021), and, based on 166 long-term surveys spanning the period 1925–2018, Van Klink et al. (2020a, 2020b) performed a meta-analysis showing a decline of terrestrial insect abundance by about 10.6% per decade and an increase of freshwater insect abundance by about 12.2% per decade.

However, it is important to notice that, when the insect samples of the meta-analysis were split into strata, viz. into insects from 'air', 'trees', 'herb layer', 'soil surface', 'below ground', and 'water', it turned out that the trends were not equal. *Air*, *herb layer*, and *soil surface* insects had negative trends in time, *trees* and *below-ground* insects showed no trend,

and the *water* insects increased as mentioned before (see Fig. S2 in Van Klink et al. 2020a, Supplementary material). The grouping of insects over strata was based on sample technique. A reason for making distinctions between strata could be that arthropods from different strata may have different dispersal capacity. For this reason, Marja et al. (2022) analyzed vegetation-dwelling and ground-dwelling arthropods separately, and they indeed found differences between the two groups of taxa. The flying insects of Hallmann et al. (2017) were sampled with malaise traps, which fall in the stratum *air* that showed only a weak decline in Van Klink et al.'s meta-analysis (2020a; $p_{one-sided\ test} = 0.952$). The difference between strata illustrates that it is of overall importance to take the sample technique and/or dispersal capacity into account when analyzing invertebrate trends over time and geographical space. It should also be noted that Hallmann et al. (2017) studied biomass, while Van Klink et al. (2020a) abundance. Of course, changes in biomass and abundance may be correlated, for example when the distribution of body size is constant, but this cannot always be assumed.

Increased agricultural intensity is one of the most often mentioned causes of the decrease in arthropods in reviews (e.g., Raven & Wagner 2021). Land use in the surroundings of the sample locations is thought to play an important role in the mechanisms that cause the decline of

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insects. For example, Hallmann et al. (2017) hypothesized that protected areas are "drained by the agricultural fields in the broader surroundings", although arable field decreased in 200 m surrounding their sample sites and they could not analyze the effects of changes in agricultural intensity. Van Klink et al. (2020a) found that the regional cover of cropland did not affect the trend of terrestrial insects, and that local cover of cropland had actually a positive effect on the trend. But a negative effect of arable lands within 1000 m radius around grassland sites on the trend of biomass and abundance of weak dispersing arthropods collected with sweeping nets was found by Seibold et al. (2019). So, we think that the effect of land use in the surroundings of a sample site on the abundance of arthropods of different strata on that site is still an issue worth studying.

We should keep in mind though, that changes in time are not the same as changes in space. Musters et al. (2021) found that flying insect abundance in agricultural fields did not change over a distance up to 600 m from (semi)natural areas. They defined flying insects as those that were sampled with sticky traps. Sticky boards as applied in Musters et al. (2021) seem to fall in Van Klink et al.'s *herb layer* (2017) that showed a clear decline in their meta-analysis ($p_{one-sided\ test}$ = 0.999), but we should resist the temptation to regard their result as contradicting the findings of Musters et al. (2021).

Taking sampling technique into consideration is undoubtedly needed in analyzing spatial distribution. For this reason, we want to analyze the spatial distribution of arthropods that were sampled with pitfalls and compare that with our earlier findings for sticky boards. Our research question is whether the abundance of these ground-dwelling arthropods is decreasing with increasing distance to (semi)natural areas. Pitfalls are the most common applied device for sampling arthropods (Mc Namara Manning and Bahlai 2021). Our null-hypothesis is that, like in flying insects, no change in abundance is to be expected in agricultural areas over a distance up to 600 m from (semi)natural areas. Insects and spiders are known to be good dispersers (Ashmole & Ashmole 1988; Peck 1994; Duelli et al. 1999; Bonte et al. 2003; De Bie et al. 2012; New 2015; but see Arribas et al. 2020 for soil arthropods). So, there is no *a priori* reason to expect that ground-dwellers have limited dispersing possibilities: many agricultural spiders are known to apply ballooning for dispersing (Weyman et al. 2002) and most carabids can fly, at least in part of their life cycle (Den Boer 1990). But Marja et al. (2022) found in their meta-analysis a difference between vegetation and ground-dwelling arthropods that they ascribe to a difference in dispersing capacity: abundance of vegetation-dwelling taxa was positively affected by the complexity of the landscape surrounding the sample sites, but this effect could not be detected in ground-dwelling taxa. Furthermore, body size may affect the relationship between abundance and distance to (semi)natural areas because of 1) larger arthropods may have a higher trapping probability (Lang 2000) and 2) larger arthropods may be better dispersers (Schweiger et al. 2005). The fact that Van Klink et al. (2020a) found a weak negative trend in *soil surface* insect abundance (Van Klink et al. 2020a, Supplementary material: $p_{one-sided\ test}$ = 0.947) and that Hallmann et al. (2020) found a yearly decline of 4% over 31 years of carabids caught in pitfalls on a location in the north-eastern part of the Netherlands (Wijster), cannot be regarded as results that reject our null-hypothesis, since these are changes in time, not over distances.

Ground-dwelling predators, such as ground and rove beetles (*Carabidae, resp. Staphylinidae*), and spiders (*Araneae*), are regarded as being important agents in the natural biocontrol of crop pests. In order to create possibilities to manage these arthropods, pitfall research has been done on their spatial distribution in agricultural fields and their margins for decades (Mc Namara Manning and Bahlai 2021). More specifically, the focus has often been on the abundance of these arthropods in (semi) natural elements, such as beetle banks, field margins, road verges, hedges, or woodlots, and in crop area adjacent to these elements (Dennis & Fry, 1992; Collins et al., 2002; Marshall & Moonen, 2002; Thomas et al. 2002; MacLeod et al, 2004; Kragten & de Snoo 2004; Noordijk et al 2010). The basic idea has been that natural elements provide winter

habitats and refuges, and that the predatory arthropods disperse from here into the crop fields in search for food (Geiger et al. 2009; Sarthou et al. 2014; Martin et al. 2019; Zamberletti et al. 2021). The distance over which the effect of the presence of the (semi)natural elements could be assessed, has often been the actual research question, but was usually supposed to be no more than 100 m (e.g. Collins et al. 2002; Saska et al. 2007; Holland et al. 2008; 2009; Knapp et al. 2018). As far as we know, one of the few studies that sampled at larger distances (up to 200 m) from the natural element, remnant woodland, was Ng et al. (2018). Studies that show how the abundance of soil surface-dwellers is distributed beyond the close neighborhood of (semi)natural elements seem rare, probably because field sizes are usually limited. However, the effect of land use in the surroundings of sample locations on arthropod abundance has been studied frequently, reporting the effect of landscape complexity at distances up to 6000 m (Tscharntke et al. 2012; Evans et al. 2016; Martin et al. 2019; Seibold et al. 2019; Marja et al. 2022).

We studied the effect of distance to (semi)natural areas on the abundance of ground-dwelling arthropods sampled with pitfalls in agricultural fields and their edges in both the USA, i.e., Illinois, and Europe, i.e., the Netherlands, taking body size into consideration. It should be noted that the studies in which these data were collected were not designed for answering our research question. As a consequence, we had limited information on factors that could confound our research question. Of the sampling locations, we knew the vegetation height, a variable that has been shown to be relevant for the abundance of insects (Evans et al. 2016; Musters et al. 2021). Also, the sample site within the sample location (field interior *versus* edge) was known. Information on landscape complexity was available and of the arthropods, we knew, along with their size class (small *versus* large), their taxonomic group.

2. Methods

Study area and management, sampling protocol, landscape complexity, and vegetation characteristics have been described in Musters et al. (2021) and completely reproduced in the Supplementary material, but are summarized here.

2.1. Study area and management

The Dutch data were collected in the Western Peat District of the Netherlands in the province of Zuid-Holland (Blomqvist et al. 2003). Data collection took place in two polders, viz. Krimpenerwaard and Vijfheerenlanden (Fig. S1 in Suppl. material), where 27 fields were sampled, 9 fields in nature conservation reserves and 18 fields on farmland neighboring these reserves (Wiggers et al. 2015, 2016). The fields were used for dairy farming and had permanent grassland. The conservation reserves studied were mostly managed with meadow bird Agri-Environmental Schemes (AES) and sometimes for botanical purposes. The adjacent fields on farmland had no specific AES.

The North-American data were collected in the Grand Prairie Region in the state of Illinois, USA (Schwegman 1973). Data collection took place in central Illinois in Cass, Christian and Sangamon counties (Fig. S1). Thirty agricultural fields were sampled with 10 fields in each of the three counties (Evans et al. 2016). The arable fields were mostly used for Roundup ready soy and maize, but there was also some hay growing.

The two study areas were similar in that both are flat or almost flat, open, large-scale, and human dominated landscapes, with large fields that are very intensely managed. Non-agricultural elements are rare and far apart (Fig. S2).

2.2. Sampling protocol

All Dutch fields were sampled in 2011 between July 1st, and August 2nd, for vegetation and invertebrates. Nine blocks were formed around 9 conservation reserves. In every block one nature reserve field was

sampled, together with one field directly next to the reserve and one field parallel to this second field.

On all 27 fields at every location, 2 plots of 1 m wide were sampled. The first plot was situated at 1.5 m from the ditch within the productive part of the field to represent the field margin. The second plot was located 10 m from the ditch and represented the field interior (Fig. S1). Within the reserve, sample locations were situated at 10, 50 and 100 m from the boundary of the reserve. Within the agricultural fields, sample locations were at 10, 50, 100, 200 and 300 m from respectively the boundary of the reserve or the boundary of the field parallel to the reserve. Thus, in the reserve fields 6 plots were sampled, providing us with 54 samples from reserves, and in both agricultural fields 10 plots were sampled, resulting in 180 samples. All plots within a field and all three fields within a block were always sampled at the same time. Distance to reserve was regarded as the distance to (semi)natural area.

The Illinois fields were sampled from May 25th, to June 15th, of 2011 and 2012. Per sampling location, three plots were sampled in the field interior and three outside the productive part of the field, in the boundary, 10 m apart and grouped equidistant from the ends of the field. This gave us 180 samples per year and 360 samples in total (Evans et al. 2016). Sampling plots in the field interior were ~ 10–15 m from the boundary, in the 2nd equipment row (Fig. S1).

2.3. Landscape complexity

In both the Dutch and the Illinois study, landscape complexity was determined using the method described in Musters et al. 2021. Complexity was defined as the proportion of non-agricultural land cover using nested circular areas with radii of 500, 1000, and 6000 m around the center of each sampling location. In the Dutch study, non-agricultural areas were defined as all non-agricultural area plus the area of nature conservation areas. In the Illinois study, we defined non-agricultural areas as those classified as upland forest, savannah, coniferous forest, wet meadow, marsh, seasonally flooded, floodplain forest, swamp, and shallow water, but the exact distribution and area of types of non-agricultural area per location was not recorded. Other classifications such as open water, clouds and cloud shadows were not included in calculating landscape complexity.

2.4. Vegetation characteristics

In the Dutch study, we determined vegetation height per plot with 3 measurements at 5-m intervals, using a 50-cm diameter disc pasture meter with a pressure of 0.178 g/cm^2 (Eijkelkamp, Giesbeek, The Netherlands). In the Illinois study, direct measurements included vegetation height (cm) for both field interiors and edges. Indirect measurements were made via GIS ArcView GIS 3.2 and ArcGIS Spatial Analyst (Environmental Systems Research Institute, Inc., Redlands, CA, USA) and included distance (m) to the nearest non-arable green space greater than 1 ha, which was here regarded as the distance to (semi)natural area.

2.5. Arthropods

In the Dutch study, pitfalls traps were 500 mL plastic cups with a diameter of 100 mm and placed into the ground so that the mouths were flush with the ground. Above each pitfall a clear plastic roof of 15 × 15 cm was placed to keep rain out of the pitfalls. Each trap was filled to ~ 6 cm with 4% formaldehyde and a few drops of dish soap added to break the surface tension of the liquid. Trapping was performed with 1 trap per plot during one week. 7 days after placement the pitfall traps were retrieved, the invertebrates were separated from the formaldehyde and placed in a labeled plastic jar containing 70% ethanol. In the lab, we sorted invertebrates into rove beetles (Staphylinidae), ground beetles (Carabidae), true weevils (Curculionidae), spiders (Araneae), springtails (Collembola) and other. We counted the invertebrates in these groups

and sorted them by size (body size classes 0–4 mm and >4 mm).

In Illinois, pitfall traps were 150 mL plastic cups with an aperture of 70 mm placed into the ground so that the mouths were flush with the ground. Each trap was filled to ~2.5 cm with a solution of water and vinegar and a few drops of dish soap added to break the surface tension of the water. Ethylene glycol was not used because it attracted mammals to the traps during a pilot study. Pitfall traps were retrieved seven days after placement and contents placed in a labeled clear Ziploc bag containing 70% isopropyl alcohol. Invertebrates were examined using a binocular microscope. Ten percent of the samples were examined a second time as quality control. An independent investigator adjudicated any conflicting identifications. Numbers of invertebrates smaller than 2 mm were estimated. Invertebrates larger than 2 mm were identified to lowest operational taxonomic unit (OTU), which in most cases was family, using all taxonomic keys and reference collections housed at the Illinois State Museum Research and Collections Center (ISM RCC). Some invertebrates were identified to orders rather than family due to rarity, dominance of one family, or difficulty of identification.

For the analysis of prey and predators, we defined Illinois arthropods smaller than 2 mm and Dutch arthropods smaller than 4 mm, plus all arthropods other than Staphylinidae, Carabidae, and Araneae, as prey and all Illinois Staphylinidae, Carabidae, and Araneae and all Dutch Staphylinidae, Carabidae, and Araneae larger than 4 mm as predators.

2.6. Statistical analyses

Only those variables that were present in both the dataset of Illinois and of the Netherlands were chosen for further analyses. These variables were abundance (number of arthropods), distance to a (semi)natural area (distance to >1 ha non-agricultural green area in Illinois and distance to reserve in the Netherlands), vegetation height, location of the sampling plot within the field (interior *versus* edge, i.e., boundary for Illinois and margin for the Netherlands), landscape complexity within 500, 1000 and 6000 m radius, year of sampling, field code, which included country, county within Illinois, and block number in the Netherlands, and sample code.

All statistical analyses were performed in R software version 4.0.3 (R Core Team 2020). The non-parametric *median_test()* and *Fligner_test()* of variance are permutation-based tests from the package *coin* (Hothorn et al. 2006). For the boxplot the default settings of the function *boxplot()* were used; for the scattergram the default settings of the function *scatterplot()* of the package *car* (Fox & Weisberg 2019), except that the plotting of the regression line was suppressed. The non-linear smoothed line is the loess-line with the *span* = 2/3. Its variance lines of are the mean smooth plus/minus the square root of the fit to the positive squared residuals. Mixed models were estimated with the *glmmTMB()* function of the *glmmTMB* package (Brooks et al. 2017). We always tested whether our data best fitted a zero-inflated or zero-altered model in case of zero inflation (Zuur et al. 2009). In all these cases, our data fitted the zero-altered negative binomial distribution best. For that, we set the model family to "*truncated_nbinom1*" with a log link in the *glmmTMB()*. In cases whit no zero inflation, we set the family to "*nbinom1*" with log link. Our dependent variable was in all these cases the number of arthropods; the independent, fixed-effect variables were the distance to a (semi)natural area, log-transformed vegetation height, location of plot within the field (interior *versus* edge), landscape complexity, and all their interactions. All independent variables, except location, were scaled before including in the models. Because we could not assume independence of samples within fields, within country or within year, the nested random-effect variable was field-code - field number within reserve-block within country – within year. In analyses where the samples of pitfalls were divided into taxonomic groups, small *versus* large body size, or prey *versus* predator, sample code was also included as random-effect variable. Only random effects of the intercept were taken into consideration because random effects of the slope resulted in singularity. Plots of the results of the model fitting were drawn with the

packages *emmeans* (Lenth 2021) and *ggplot2* (Wickham, 2019). Automatic model selection of all possible combinations of the main fixed variables and their interactions was performed by the *dredge()* function of the *MuMIn* package (Bartoń 2020). The best models, i.e., those with an AICc less than 4 higher than the model with the lowest AICc (Delta-AICc < 4; Anderson 2008), were fully averaged using *model.avg()* of the same package.

3. Results

The total number of arthropods caught in our pitfalls was 101,110. The average number of arthropods per pitfall was 170.2 (median = 134.5; n = 594). Illinois had higher numbers (mean = 188.6; median = 140; n = 360) than the Netherlands (mean = 141.9; median = 124; n = 234), and the variance in abundance was different between the two countries (Fig. 1).

At first sight, there seemed a decrease in abundance with increasing distance to (semi)natural area in Illinois (regr. coeff. = -0.002, p = 0.028), which was not present in the Netherlands (regr. coeff. = 0.001, p = 0.100), but when corrections for zero inflations were made, neither Illinois, nor the Netherlands showed a significant relationship between distance to (semi)natural areas and the abundance of arthropods, although a difference in the regression coefficient could be detected between the two countries in the significant interaction between distance and country (Table 1).

For further analyzing the relationship between the distance to (semi) natural areas and the abundance of arthropods, we selected data outside nature conservation areas only, which left 540 samples. We again assumed zero inflation and started with simple a model to see the effect of country and location within field (interior *versus* edge of the field) on the relationship between arthropod abundance and distance to (semi) natural area. This showed a small significant effect of country: in Illinois the insect abundance decreased with increasing distance from (semi) natural area, while that was not the case in the Netherlands, although the estimated variance of the four relationships strongly overlapped (Fig. 2A; Table 2). The effect of zero inflation was only present in the overall intercept, i.e., affecting the position of all lines in relation to the y-axis the same way, but not in differences between the positions of the lines, nor the regression coefficients. No effect of location within field could be detected (Fig. 2B) and therefore location within field will be ignored in all further analyses.

However, when a more complicated model was applied, in which the effect of country, vegetation height, landscape complexity, and all of their possible interactions on the relationship between arthropod

Table 1
The effect of distance to (semi)natural area and country on arthropod abundance. A zero altered negative binomial distribution was assumed (Zuur et al. 2009).

Conditional model					
	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	4.9256	0.1380	35.69	<0.001	***
Distance	0.0618	0.0528	1.17	0.241	
Country	0.0070	0.1672	0.04	0.967	
Distance: Country	−0.2875	0.1254	−2.29	0.022	*

Zero-inflation model					
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	−7.8624	2.7706	−2.84	0.005	**
Distance	−0.3039	1.0982	−0.28	0.782	
Country	2.0015	1.5499	1.29	0.197	
Distance:Country	0.1539	1.3054	0.12	0.906	

abundance and distance to (semi)natural area were included, no longer an effect of distance on abundance was found in the best models for all three levels of scales of landscape complexity, viz within a radius of 500 m, 1000 m, and 6000 m (Table 3). Note that the variance explained by the fixed variables, the marginal R^2, is highest at the landscape level of 6000 m.

This is also true for the averages of the Delta-AICc < 4 models, i.e., the models that differed less than 4 AICc from the best model that was selected (Table S1 in Suppl. material).

We also analyzed the difference between small and large arthropods and were surprised to find that in Illinois, small arthropods (<2 mm) were clearly decreasing in abundance with increasing distance to (semi) natural area, while in the Netherlands small arthropods (<4 mm) did not decrease with distance (Fig. 3; Table S3). This effect remained when controlling for vegetation height and landscape complexity (Fig. S4; Table S4).

Although these results from both the simple and complex models are enough for testing our null-hypothesis, we explored the data in order to find patterns that are connected to results of other authors. We analyzed the differences between taxonomic groups in their relationship between abundance and distance to (semi)natural area. In Illinois, spiders (Araneae) and springtails (Collembola) declined and carabids (Carabidae), rove beetles (Staphylinidae), and weevils (Curculionidae) increased, while in the Netherlands, rove beetles declined and carabids, spiders, springtails, and weevils increased with increasing distance to green areas (Fig. S3; Table S2). Further, assuming that small ground-dwelling
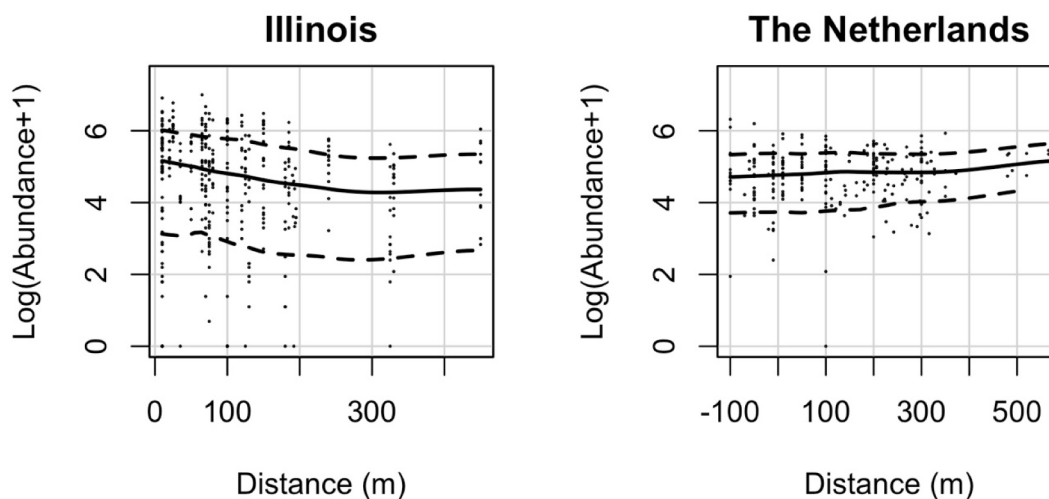

Fig. 1. Smoothed nonlinear regression line of the relationship between distance to (semi)natural area and abundance of ground-dwelling arthropods in Illinois and the Netherlands; dashed lines show the variance. Data from within (semi)natural areas only from the Netherlands.
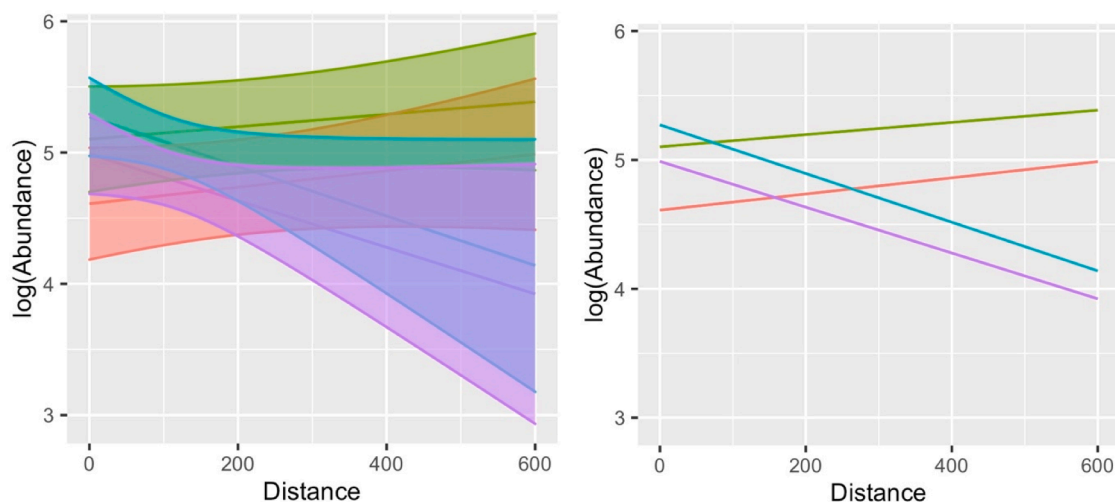
Fig. 2. Estimated effect of distance to (semi)natural area on the abundance of arthropods in the edges and interior agricultural fields of Illinois and the Netherlands. Right is the same as left, but without the estimated variance in abundance. Red: edge in the Netherlands; Green: interior in the Netherlands; Blue: edges in Illinois; Purple: interior in Illinois.

Table 2

Simple model of the effect of distance to (semi)natural area, country, and locations within fields on arthropod abundance. A zero altered negative binomial distribution was assumed (Zuur et al. 2009).

Conditional model					
	Estimate	SE	z value	Pr(>|z|)	
(Intercept)	5.0041	0.1076	46.52	<0.001	***
Distance	−0.2243	0.1167	−1.92	0.055	.
Interior.Illinois	−0.2677	0.0584	−4.59	<0.001	***
Edge.Netherlands	−0.3048	0.2151	−1.42	0.157	
Interior.Netherlands	0.1649	0.2113	0.78	0.435	
Distance:Interior.Illinois	0.0132	0.0661	0.20	0.842	
Distance:Edge. Netherlands	0.2989	0.1350	2.21	0.027	*
Distance:Interior. Netherlands	0.2806	0.1301	2.16	0.031	*

Zero-inflation model					
	Estimate	SE	z value	Pr(>|z|)	
(Intercept)	−7.2860	2.5450	−2.86	0.004	**
Distance	0.1550	0.9557	0.16	0.871	
Interior.Illinois	1.3700	0.8323	1.65	0.100	.
Edge.Netherlands	−0.0015	1.8960	0.00	0.999	
Interior.Netherlands	−14.6800	1447.0000	−0.01	0.992	
Distance:Interior.Illinois	−0.3841	0.9032	−0.43	0.671	
Distance:Edge. Netherlands	−0.8916	1.6840	−0.53	0.597	
Distance:Interior. Netherlands	−0.2584	1502.0000	0.00	1.000	

Table 3

Best models out of all possible models that model the effect of distance to (semi) natural area, country, vegetation height, and landscape complexity on arthropod abundance at three level of scale. Model selection according to Anderson (2008).

Complexity 500 m marginal R^2: 0.038; conditional R^2: 0.624					
	Estimate	SE	z-value	p-value	
(Intercept)	4.8231	0.1076	44.82	<0.001	***
Country	−0.2217	0.2449	−0.91	0.365	
Complexity 500 m	−0.0055	0.0795	−0.07	0.945	
log(Vegetation height)	0.1548	0.0384	4.03	<0.001	***
Country: log(Veg.height)	−0.5546	0.1296	−4.28	<0.001	***
Comp500m: log(Veg.height)	0.0917	0.0378	2.43	0.015	*

Complexity 1000 m marginal R^2: 0.051; conditional R^2: 0.602					
	Estimate	SE	z-value	p-value	
(Intercept)	4.7908	0.1041	46.03	<0.001	***
Country	−0.0800	0.2385	−0.34	0.738	
Complexity 1000 m	0.1476	0.0882	1.67	0.094	.
log(Vegetation height)	0.1763	0.0384	4.60	<0.001	***
Country: log(Veg.height)	−0.5869	0.1286	−4.56	<0.001	***

Complexity 6000 m marginal R^2: 0.154; conditional R^2: 0.614					
	Estimate	SE	z-value	p-value	
(Intercept)	4.7850	0.0964	49.65	<0.001	***
Country	−0.0724	0.2183	−0.33	0.740	
Complexity 6000 m	0.3497	0.0828	4.22	<0.001	***
log(Vegetation height)	0.1743	0.0380	4.58	<0.001	***
Country: log(Veg.height)	−0.5934	0.1271	−4.67	<0.001	***

arthropods are part of the prey of the larger ground-dwelling ground beetles, rove beetles, and spiders, we expected to find a difference in the effect of distance to (semi)natural area on abundance between prey and predators, a pattern that was indeed seen in Illinois (Fig. S5; Table S5).

4. Discussion

In agricultural fields, we did not find a relationship between the distance to (semi)natural areas and the total number of ground-dwelling arthropods trapped in pitfalls, when we controlled for vegetation height, landscape complexity, and country (Table 3; Table S1). So, we were not able to reject our null-hypothesis.

The effect of vegetation height on abundance was different in Illinois and the Netherlands, as is shown by a significant interaction between

vegetation height and country in Table 3. In Illinois, vegetation height had a positive effect on abundance, as might be expected due to the higher biomass and richer structure of higher vegetation (not tested due to lack of data; for information on the variance of vegetation height, see Fig. S6). In the Netherlands, vegetation height had a negative effect on abundance. This might be the result of the fact that the Dutch fields were grasslands, with relative low vegetation height (<35 cm) and a positive correlation between vegetation height and vegetation density (r = 0.154, p = 0.019, n = 233). High vegetation density may hinder arthropod activity and therefore arthropod sampling probability in pitfalls (Lang 2000).

Landscape complexity had no effect on abundance at the scale of 500 m and 1000 m, but it had a positive effect in case of 6000 m around the sampling location. So, in landscapes with more non-agricultural areas in
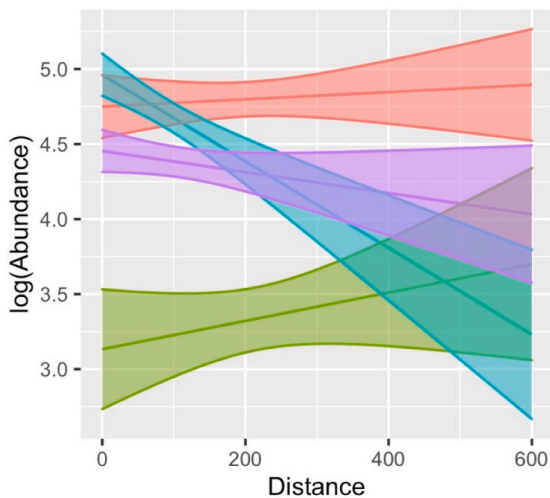
Fig. 3. Estimated effect of distance to (semi)natural area on the abundance of small and large arthropods in Illinois and the Netherlands. Red: small arthropods in the Netherlands; Green: large arthropods in the Netherlands; Blue: small arthropods in Illinois; Purple: large arthropods in Illinois.

an area with radius of 6000 m around the sampling location, higher numbers of ground-dwelling arthropods were trapped. The effect of landscape complexity on ground dwelling arthropod biomass or abundance has been studied extensively, showing both positive effects, negative effects and no effects. For example, a weak positive effect of the proportion of (semi)natural habitats within an area of 1 km around sampling locations on carabid abundance was found by Fusser et al. (2016). Hallmann et al. (2017) indicated that the presence of land use elements within 200 m radius might better predicted insect biomass than elements within 500 m and 1000 m radius. Seibold et al. (2019) found that biomass and abundance of weak dispersing arthropods of grasslands declined stronger when surrounded by more arable land in 1000 m and they state that other scales (radii of 250, 500, 1500 and 2000 m) showed very similar results. But Martin et al. (2019) found differences between landscape scales and the effects differed between trait groups based on dispersal mode, overwintering behavior, and diet. The negative effect of percentage arable land, which is the same as a positive effect of our landscape complexity, on the abundance of all arthropods was only significant at the largest scales, that of 2000 and 3000 m around the sampling site. A recent meta-analysis based on 29 European cropland studies showed no significant effect of landscape complexity on the abundance of ground-dwelling arthropods (n = 184; Marja et al. 2022). However, the definition of 'landscape complexity' was heterogeneous in this meta-analysis, while the effect of landscape complexity on arthropod abundance seems to depend on landscape scale. Our previous study showed that in case of flying insects, a negative effect of landscape complexity on abundance at 500 m and 1000 m was found, but not at 6000 m (Musters et al. 2021). More research on the effect of landscape complexity at different scales on abundance and biomass of arthropods of different strata is needed.

Remarkable was that the two countries had no significantly different intercepts in the complex models, although the latitude at which sampling took place and the trapping devices were different. We regard this as a coincidence.

How can our result of no effect of distance to (semi)natural area on ground-dwelling arthropods be understood in the light of the general accepted assumption that ground-dwelling arthropods are relatively weak dispersers (e.g., Marja et al. 2022) and winter habitats are needed for the survival of predators in agricultural areas (e.g., Zamberletti et al. 2021)?

Let us start with discussing the need for winter refuges. What exactly do arthropods need to be able to survive winter weather? Winter

survival has been related to the presence of perennial herbaceous vegetation in (semi)natural areas (Geiger et al. 2009). If such vegetation is crucial, arthropods in permanent grasslands would not need refuges, which could explain why no effect of distance is found in the Dutch grasslands. But this could not explain the found absence of an effect in the Illinois croplands. However, it should be taken in consideration that at least some ground-dwelling arthropods seem to prosper in non-forested, arable landscapes and may not depend on (semi)natural areas for overwintering (Geiger et al. 2009; Knapp et al. 2018; Martin et al., 2019). And even in arthropods that depend on overwintering areas, the distribution of abundance over fields may strongly change between early spring and full summer, with a peak in abundance around harvest time (Thorbek 2003). After all, how long will it take from the time that arthropods become active in spring to colonize fields over 600 m? Moreover, many arthropods show more than one generation per year, so that abundance may increase on crop fields by reproduction (Purvis and Fadl, 2002; Thorbek 2003). The temporal aspect of arthropod distribution has been rarely studied (but see Den Boer 1990; Holland et al. 2009; Knapp et al. 2018). Note that climate change might affect this process, because it could advance the time of arthropods becoming active after winter.

This brings us to the second issue of ground-dwellers being weak dispersers. It has been shown before that large ground-dwelling arthropods are better dispersers than small ones (Schweiger et al. 2005), which could well explain our results from Illinois, where we found a difference in effect of distance to (semi)natural areas between small and large arthropods. Only small Illinois arthropods showed a negative effect of distance on abundance (Fig. 3; Table S3). This was also true when we controlled for vegetation height and landscape complexity (analysis only applied at landscape scale of radius 6000 m; Fig. S5; Table S4). It is consistent with the fact that in Illinois also springtails showed a negative effect of distance (Fig. S3; Table S2).

Our results concern the total abundance of ground-dwelling arthropods. That this does not change with changing distance to (semi)natural areas does not mean that the species composition also does not change. Our own data show that the relative abundance depends on body size in Illinois and also that species groups differ over distance to (semi)natural areas in both countries (Fig. S3; Table S2). However, this latter result is difficult to judge, especially that of Illinois, because of strong effects of zero inflation, even to the point that it was not possible to estimate some of the effect in Illinois. This issue needs further study.

When we assume that small arthropods are part of the prey of large Staphylinidae, Carabidae, and Araneae, we see that the decrease of prey with increasing distance to (semi)natural areas did not affect the abundance of predators (Fig. S5; Table S5), so that the ratio between prey and predator numbers decreases clearly in Illinois. This could mean that, at least in Illinois, ground-dwelling predators do not depend on the abundance of ground-dwelling prey for keeping their abundance, either because of plentiful ground-dwelling prey, or because of the abundant presence of non-ground-dwelling prey, or both.

A conclusion that can be drawn from our findings is that spatial gradients in the abundance of arthropods that one expects based on literature may not be present and therefore need explicit checking. First, it is important to take ways of arthropod sampling into consideration, because trapping devices may sample different strata. Then, body size of the arthropods may be relevant in that the larger the arthropod, the better it is able to disperse. Further, it should be recognized that sampling results are affected by the landscape around the sampling sites and that the relevant radius of the area to take into consideration may be different for arthropods from different strata. Also, type of agriculture (annual crops *versus* permanent grassland) may be relevant. These kinds of issues have been acknowledged in numerous previous studies, but the research questions in these studies are usually different and results are presented differently. This make it hard to bring these results together and interpret (Martin et al. 2019). What we seem to need is general applicable null-model for the distribution of arthropods in space and

time, which cannot be constructed based on our results only. However, what our results suggest is that, due to the high dispersal capacity of arthropods, we may expect that the spatial distance over which the abundance of arthropods is equal, apart from fine scale clustering, is larger than we usually think.

For nature conservation, we may only expect an effect of increasing landscape complexity when that is done on a large enough scale (Martin et al. 2019; this study). Hence, for better biological control, farmers and other stakeholders should be stimulated to cooperate on a relatively large landscape scale.

Author contributions

CM and GdS conceived the ideas. CM performed the statistical analyses and wrote the first draft. Tracy Evans and JW collected and processed the data. All authors improved and sharpened the ideas, contributed critically to the drafts and gave final approval for publication. None of them had conflicts of interests.

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.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109042.

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