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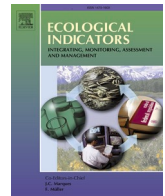
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Distribution of flying insects across landscapes with intensive agriculture in temperate areas

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ABSTRACT

The abundance of insects has been strongly decreasing over the last decades, at least in the temperate zones of North America and Europe. This decrease has generally been attributed to increased human activity, especially increased agricultural production. Therefore, one would expect that insect abundance is spatially distributed according to human land use, more specifically that the abundance of insects in agricultural fields should be affected by the distance to (semi)natural areas. We tested this expectation on an extensive dataset of flying insects from Illinois, USA, and the Netherlands, Europe. Flying insects were collected with yellow sticky boards in agricultural fields at distances up to 566 m from (semi)natural areas. We did not find any effect of distance to (semi)natural area on the abundance of flying insects, after correcting for the confounding variables 'landscape complexity', 'vegetation height' and 'plot locations' (interior vs edge of the field). One might prematurely infer from this that (semi)natural areas do not affect flying insect abundance. We argue that knowing that flying insects are highly mobile, both active and passive, although sticky boards sample local insect abundance, abundance may be homogenized over a relatively large area in open landscapes. Therefore, the study of the effect of nature conservation management on flying insects should be done on spatially large scales, e.g., the landscape level.

1. Introduction

Based on a recent *meta-analysis*, Van Klink et al. (2020a); (2020b); have shown a temporal decline of terrestrial insect abundance by about 10.6% per decade and an increase of freshwater insect abundance by about 12.2% per decade at the landscape level. Both patterns were largely driven by trends in the temperate zones of North America and Europe, from which most observations came. At the local level, Hallmann et al. (2017) described a temporal decrease of terrestrially sampled flying insect biomass by >75% over 27 years in nature conservation areas in Germany, while biomass and abundance in arthropods decreased 67%, respectively 78% between 2008 and 2017 in German grasslands (Seibold et al. 2019). Hallmann et al. suggested agricultural intensification as a plausible cause: "The reserves in which the traps

were placed are of limited size in this typical fragmented West-European landscape, and almost all locations (94%) are enclosed by agricultural fields. Part of the explanation could therefore be that the protected areas (serving as insect sources) are affected and drained by the agricultural fields in the broader surroundings (serving as sinks or even as ecological traps)". Van Klink et al. (2020a) found that trends in protected areas were slightly weaker than in non-protected areas. The hypothesis of Hallmann et al. about the impact of the surroundings on local observations together with the findings of Van Klink et al. suggest that the abundance distribution of flying insects over space may differ between nature conservation acreage and agricultural fields. Here, we will explore the validity of this hypothesis. Using two extensive datasets of flying insects caught with sticky traps, one from USA and one from Europe, we studied the distribution of these insects in agricultural fields

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¹ Our colleague and friend Tracy Evans has passed away during the revising period of this paper. Her enthusiasm and commitment are dearly missed.

along a gradient of increasing distance from (semi)natural areas, as was done previously by [Leng et al. \(2009\)](#); [\(2010\)](#) for plants. The results might show us whether there is a difference in abundance and, if so, at which distance the effect of the (semi)natural area on the abundance of the insects is still manifest in the agricultural fields. This again could show us the level of spatial scale we should take into consideration when interpreting results like those of [Hallmann et al.](#), as well as the size of sampling plot we best would choose in future research.

A complicating factor in this type of research is the effect of landscape complexity ([Boutin et al., 2009](#); [Tschamtkke et al., 2012](#)). However, most of the research in this field has presently been focused on the confounding effect of landscape complexity on the results of conservation management on *insect species diversity*, not *insect abundance*. An exception is [Ekroos et al. \(2013\)](#) who studied the abundance of butterflies, bumblebees, and hoverflies. As far as we know, our study will be one of the first that takes differences in landscape complexity into consideration when studying the distribution of all flying insect abundance across agricultural landscapes.

We used datasets of the Netherlands and of Illinois, USA, and tested the hypothesis that the abundance of flying insects is higher in (semi) natural areas than in agricultural areas, and that in agricultural areas it decreases with the distance to the (semi)natural areas. This spatial gradient in abundance will be affected by vegetation height, location within the fields (interior vs edge), landscape complexity, or any of the interactions between these variables.

2. Methods

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](#)). In this area, situated below sea level, dairy farming is the main form of agriculture and most farmland is grassland with peat or clay on peat soils, sown with a mixture of mainly *Lolium perenne*. Pastures are long (0.2–1 km) and narrow (30–60 m), with 1–4 m wide ditches between the fields and sloped ditch banks of 0.5–1.5 m width. Ditches are cleaned every year and water tables are artificially controlled by the water board, usually fluctuating 10–15 cm over the year on a level between 0 and 40 cm below the surface of the field ([Blomqvist et al. 2003](#)). Data collection took place in two polders, viz. Krimpenerwaard and Vijfheerenlanden ([Fig. 1](#)), where 27 fields were sampled, 9 fields in nature conservation reserves and 18 fields on farmland neighboring these reserves. 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](#)). Historically, this area was predominantly tall-grass prairie with fertile soils developed from glacial till, lakebed sediments and varying depths of loess. The topography is slightly rolling to level and modified for high yield arable agriculture (mostly genetically modified corn and soybeans). Drainage

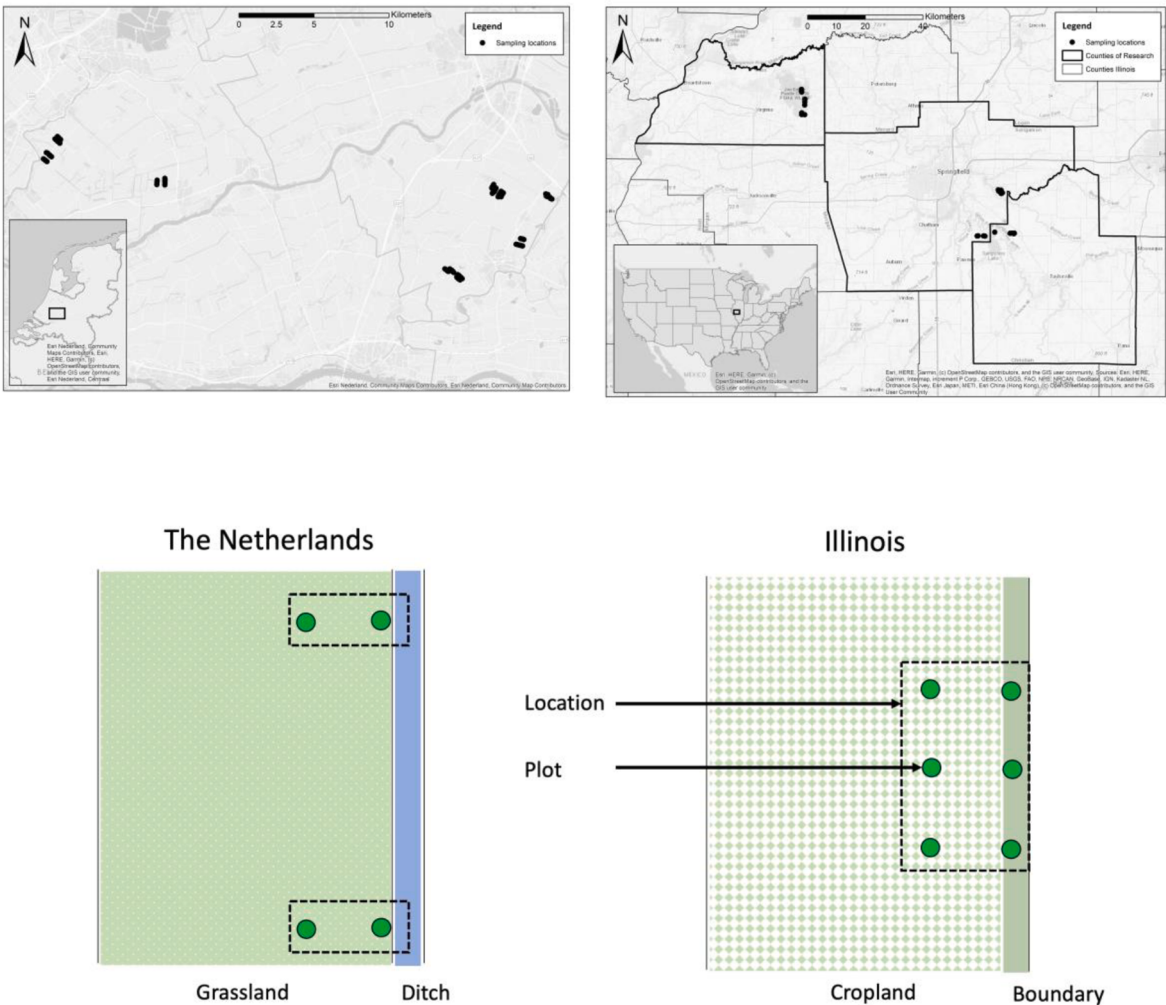


Fig. 1. Sampling sites in the Netherlands (left) and Illinois (right). All plots within a location have the same latitude and longitude.

has been modified with tiles and ditches. Interspersed with agricultural fields are areas enrolled in the Conservation Reserve Program. This program along with state and local programs are targeted at conserving soil, water, and wildlife resources by removing highly erodible and environmentally sensitive lands from agricultural production and installing resource-conserving practices. Data collection took place in central Illinois in Cass, Christian and Sangamon counties (Fig. 1). Thirty agricultural fields were sampled with 10 fields in each of the three counties (Evans et al., 2016a, 2016b).

The two study areas were similar in that both were flat or almost flat, open, large-scale, and human dominated landscapes, with large fields that were very intensely managed. Non-agricultural elements are rare and far apart (Fig. 1).

2.2. Sampling protocol

All Dutch fields were sampled in 2011 between July 1st, and August 2nd, for vegetation characteristics 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. 1). 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 of which one was lost. All plots within a field and all three fields within a block were always sampled at the same time.

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. Sampling plots in the field interior were ~ 10–15 m from the boundary, in the 2nd equipment row (Fig. 1).

2.3. Landscape complexity

In both the Dutch and the Illinois study, landscape complexity was determined using ArcView GIS 3.2 and ArcGIS Spatial Analyst (Environmental Systems Research Institute, Inc., Redlands, CA, USA.). 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, Bestand Bodemgebruik (CBS 2015) and Nature Network Netherlands 2019 were used for assessing landscape complexity. Non-agricultural areas were defined as all non-agricultural area plus the area of nature conservation areas. In the Illinois study, digital landcover maps (Luman et al., 2009) were used for the assessment of landscape complexity. Here, 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. 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/cm² (Eijkelkamp, Giesbeek, The

Netherlands). We determined vegetation biomass by cutting a plot of 30 × 30 cm at ground level. We then determined dry weight by placing the sample in a stove for 48 h at 70 °C. We also determined when the vegetation had been cut or grazed for the first time in 2011 by interviewing the farmer. Of the 27 fields measured, 21 had been mown, 4 had been grazed and 2 were unmown and not grazed before we took our measurements.

In the Illinois study, direct measurements included crop type and vegetation height (cm) for both fields and boundaries. 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 space > 1 ha, width of the field boundary (m), length of the field boundary (m) and the area of field interior (ha).

2.5. Insects

In the Dutch study, aerial insects were captured using yellow sticky traps of 25 × 10 cm (Koppert, Berkel en Rodenrijs, The Netherlands) that were placed with the bottom edge at ground level. We used 1 sticky trap per sampling plot for 72 h. We cut short an area of 30 × 30 cm at ground level around each trap to prevent vegetation from sticking to the traps. In the lab, we counted insects and sorted them by size.

In Illinois, aerial insects were also sampled with yellow sticky traps (Sensor ~ 13 cm × 6 cm Yellow Monitoring Cards, GrowSmart) attached to a wire and placed with a minimum of ½ of the board placed above the vegetation for 48 h. In the lab we counted insects and identified to family.

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 insects), distance to a (semi)natural area, vegetation height, location of the sampling plot within the field (interior vs edge, i.e., boundary for Illinois and margin for the Netherlands), landscape complexity within 500, 1000 and 6000 m radius, year of sampling and field code, which included country, county within Illinois, and block number in the Netherlands.

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*. The boxplots used the default settings of the function *boxplot()*; the scattergrams the default settings of the function *scatterplot()* of the package *car*, 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 *lme()* of the *nlme* package. Method was set to Maximum Likelihood to enable model selection based on AICc (Anderson 2008). The dependent variable was always the log-transformed number of insects plus one; the independent, fixed-effect variables were the distance to a (semi)natural area, log-transformed vegetation height, location of plot within the field (interior vs edge) and 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. 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* and *ggplot2*. 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. The best models, i.e., those with an AICc < 4 higher than the model with the lowest AICc (Delta-AICc < 4),

were fully averaged using *model.avg()* of the same package.

3. Results

3.1. General results

In total, 169,252 individual insects were caught with the sticky traps, 87,003 in Illinois and 82,249 in the Netherlands. On average, 285.4 insects were caught per trap (Illinois: 241.7, $n = 360$; Netherlands: 353.0; $n = 233$), but the distribution of numbers per trap was highly skewed to the low numbers (Fig. 2). For this reason, we worked only with the natural logarithm of the abundance per trap plus one in all our statistics (Fig. 2). The median number was 256 per trap. The maximum number caught was 1694 in Illinois. In only three cases, zero insects were caught. In Illinois, most insects were small Diptera (mostly gnats, but also many other species), followed by Hemiptera (mostly aphids and leafhoppers), and Hymenoptera (mostly braconid wasps). In the Netherlands, most insects were also small ($\pm 75\% < 4\text{mm}$) Diptera (mostly gnats, but also many other species), followed by insects sized 4–8 mm and some insects > 8 mm.

3.2. Difference in abundance between conservation reserves and agricultural fields in the Netherlands

Data on the abundance of flying insects both of nature conservation reserves and of agricultural field were only available from the Netherlands. Here, no difference was found in the abundance (t -test: $t = 0.791$, $p = 0.430$; median test $z = 1.7515$, $p = 0.080$; $n = 233$; Fig. 3). In the following analyses, data from the Dutch nature reserves were excluded.

3.3. Distance to (semi)natural areas in both Illinois and the Netherlands

A positive correlation between the distance to (semi)natural areas and the abundance of flying insects in the agricultural fields was found in the raw data (Pearson $r = 0.170$, $p < 0.001$; Spearman test: $z = 4.215$, $p < 0.001$; $n = 539$; Fig. 4).

As for the confounding variables, we found that in our study, that landscape complexity seemed to be negatively related to insect abundance. The correlation between complexity at 500 m and 1000 m, as well as between 1000 m and 6000 m, was high ($r = 0.85$ resp. 0.80 , $p < 0.001$, $n = 593$), but less so between 500 m and 6000 m ($r = 0.58$, $p < 0.001$, $n = 593$). For this reason, we did separate analyses for the three distances. We found a significant negative relationship to vegetation height ($r = -0.180$, $p < 0.001$) and also location of sample plot within the field seemed to affect the abundance of flying insects (interior vs

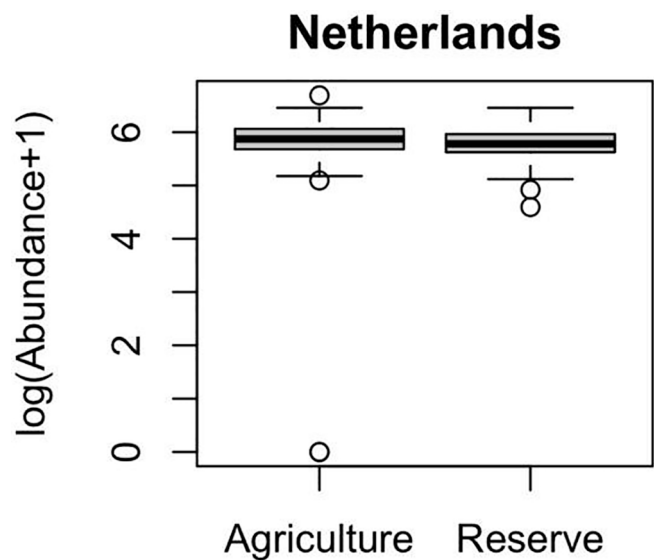
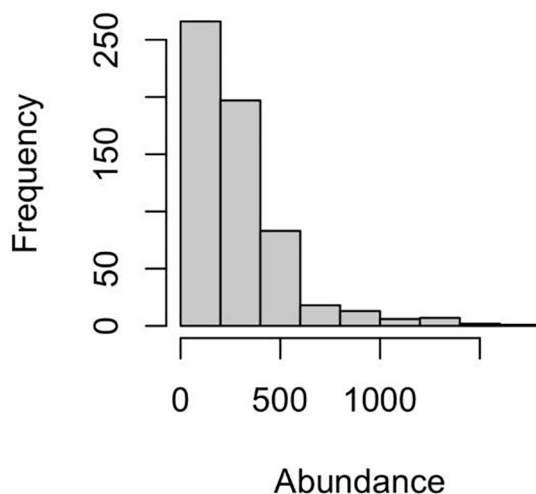


Fig. 3. Difference in flying insect abundance between conservation reserves and agricultural fields in the Netherlands only ($n = 233$).

edge, median test: $z = 4.691$, $p < 0.001$; Fligner test of variance: $z = 1.945$, $p = 0.052$).

For this reason, we performed a model selection procedure in which the models differed in the inclusion of confounding variables, viz. landscape complexity, vegetation height and location within the field, and their interactions. The results of averaging the best LMM-models ($\Delta \text{AICc} < 4$) are given in Table 1.

The positive effect of distance to the reserves on abundance of flying insects disappeared by the inclusion of confounding variables. Only landscape complexity within 500 and 1000 m, vegetation height, the location of the plot within the field (interior vs edge), and some of their interaction had significant effects on the abundance of the flying insects (Table 1). Complexity within 500 and 1000 m had a negative effect on abundance (Fig. 5), while interiors have lower abundance and variance than edges (Table 1; Fig. 6). More insects are caught when the vegetation is high, but the interaction showed that the positive relationship between the abundance of flying insects and vegetation height is stronger in the edges of the fields (Table 1; Fig. 6).

The best model of the 1000 m radius seems to be the best fitting model (lowest AICc), although the differences between the best models of 500 and 1000 m radii are small. The conditional R^2 showed good fit of

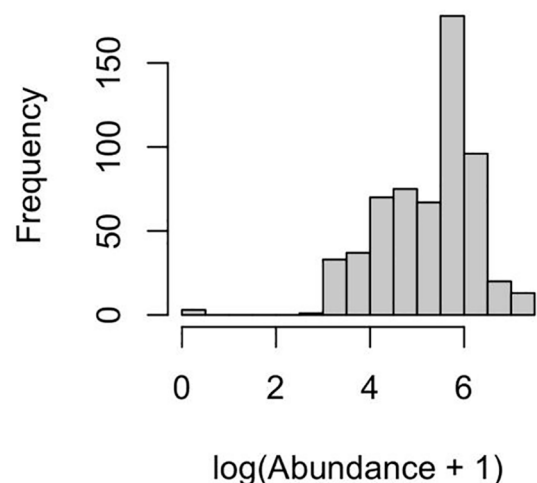


Fig. 2. The distribution of the number of flying insects per sticky trap, raw data (left) and natural logarithmic transformed data (right, $n = 593$).

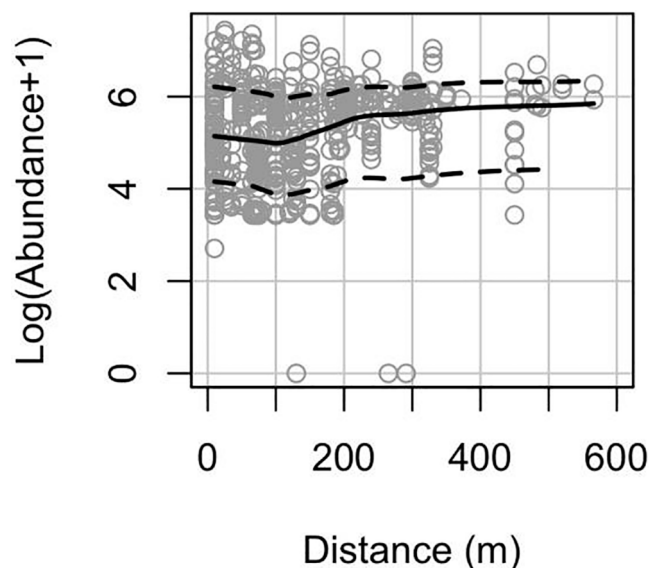


Fig. 4. Smoothed nonlinear regression line of the relationship between distance to (semi)natural area and abundance of flying insects; dashed lines show the variance. All data combined ($n = 539$).

the complete models (0.677 in the best 1000 m model), but the fixed variables explain little of the variance in the observations (marginal $R^2 = 0.097$ in the best 1000 m model). Analysis of the separated datasets of Illinois and the Netherlands did not give a different result of the effect of distance to the (semi)natural area on the abundance of flying insects (see [Supplementary Information](#)).

4. Discussion

Our results could not show that in temperate agricultural areas of the USA and Europe, the abundance of flying insects is affected by the distance to (semi)natural areas up to at least 500 m. This was true after correcting for landscape complexity, sample plot (interior vs edge), and vegetation height.

This indicates that the abundance of flying insects may not be affected by the presence of nature conservation reserves in the form of (semi)natural areas at the spatial scale we studied. However, this does not mean that (semi)natural areas are not effective at all. Rather we think that if they are effective, these effects might become manifest at higher spatial scales.

Why is that? After all, our results give no reason to doubt the ability of our sampling method to assess local difference in abundance since fields and boundaries showed clearly a different abundance. We think that we should take into consideration that the abundance of flying insects in agricultural fields may not only be affected by the presence of (semi)natural areas, but also by other factors, such as active, as well as passive dispersal of insects. It may well be possible that the abundance of flying insects is quickly homogenized over a relatively large, open area like an agricultural field by this dispersal so that a temporary gradient in abundance over the distance to the (semi)natural area is quickly lost within the 500 m we studied.

The yellow traps are known to attract flying insects by their color ([Hoback et al. 1999](#)). Extensive studies of agricultural pests indicate that even weak flying insects may fly a local distance of 10 km ([Byrne, 1999](#); [Loxdale et al., 1993](#); [Leitch et al., 2021](#)). Moreover, it is well known that flying insect abundance is strongly affected by daily weather conditions, including the wind ([Wiktelius, 1981](#); [Pasek, 1988](#); [Grüebler et al., 2008](#); [Leitch et al., 2021](#)). The combination of potential attraction over large distances and the easy distribution of flying insects over the landscape by wind could mean that sticky traps actually sample relatively large

Table 1

The average model per radius area. Only the models that had an AICc that differed <4 from the model with the smallest AICc were included in the averaging. In all cases, the number of samples was 539. P-value 0.000 indicate $p < 0.001$.

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)	
500 m radius						
Best model: marg. $R^2 = 0.082$; cond. $R^2 = 0.665$; AICc = 1223.2						
Number of models averaged = 11						
(Intercept)	5.20402	0.10545	0.10573	49.221	0.000	***
Distance to (semi) natural area	-0.01431	0.05287	0.05299	0.270	0.787	
Complexity within 500 m	-0.27662	0.09820	0.09846	2.810	0.005	**
Interior	-0.22678	0.06540	0.06558	3.458	0.001	***
Vegetation height	0.18543	0.06377	0.06392	2.901	0.004	**
Distance:Veg. height	-0.00724	0.02726	0.02729	0.265	0.791	
Complex: Distance	0.00101	0.01491	0.01495	0.067	0.946	
Complex:Veg. height	0.00031	0.01629	0.01633	0.019	0.985	
Complex: Interior	0.00048	0.02176	0.02181	0.022	0.982	
Interior:Veg. height	-0.14376	0.07836	0.07852	1.831	0.067	.
Interior: Distance	-0.00707	0.03056	0.03060	0.231	0.817	
1000 m radius						
Best model: marg. $R^2 = 0.097$; cond. $R^2 = 0.677$; AICc = 1221.7						
Number of models averaged = 12						
(Intercept)	5.19093	0.10657	0.10685	48.579	0.000	***
Distance to (semi) natural area	0.01254	0.04354	0.04364	0.287	0.774	
Complexity within 1000 m	-0.27803	0.10147	0.10174	2.733	0.006	**
Interior	-0.23354	0.06562	0.06579	3.550	0.000	***
Vegetation height	0.17156	0.06419	0.06435	2.666	0.008	**
Distance:Veg. height	-0.00394	0.02199	0.02202	0.179	0.858	
Complex: Distance	-0.00021	0.01252	0.01255	0.017	0.986	
Complex:Veg. height	0.09225	0.06392	0.06403	1.441	0.150	
Complex: Interior	0.00052	0.01569	0.01573	0.033	0.974	
Interior:Veg. height	-0.16406	0.07864	0.07881	2.082	0.037	*
Interior: Distance	-0.01072	0.03635	0.03638	0.295	0.768	
Complex2: Interior:Veg. height	0.00052	0.01569	0.01573	0.033	0.974	
6000 m radius						
Best model: marg. $R^2 = 0.052$; cond. $R^2 = 0.676$; AICc = 1226.4						
Number of models averaged = 19						
(Intercept)	5.17476	0.10954	0.10984	47.114	0.000	***
Distance to (semi) natural area	0.06628	0.06606	0.06617	1.002	0.317	
Complexity within 6000 m	-0.11007	0.10971	0.10997	1.001	0.317	
Interior	-0.24192	0.06599	0.06617	3.656	0.000	***
Vegetation height	0.18398	0.06212	0.06228	2.954	0.003	**
Distance:Veg. height	-0.00409	0.02393	0.02397	0.171	0.865	
Complex: Distance	0.00146	0.01926	0.01931	0.076	0.940	
Complex: Interior	0.13761	0.06644	0.06656	2.067	0.039	*

(continued on next page)

Table 1 (continued)

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)	
Complex:Veg. height						
Complex:	0.04148	0.06705	0.06715	0.618	0.537	
Interior:						
Interior:Veg. height	-0.21547	0.07784	0.07803	2.762	0.006	**
Interior:						
Distance	-0.01543	0.04108	0.04114	0.375	0.708	
Complex:						
Interior:Veg. height	0.00228	0.02518	0.02525	0.090	0.928	

areas, when these areas are open. Our results suggest that this area may have a diameter of at least 500 m in agriculture areas.

Since there seems to be no reason why this not also should be true for other techniques that sample both passive and active movements of flying insects, such as Malaise traps (but see [Steinke et al. 2020](#)), this would mean that the decrease in flying insects over time measured in conservation areas by [Hallmann et al. \(2017\)](#) is indeed indicative for the decrease of these insects in the landscape around the conservation areas.

Is there a contradiction between the obvious ability to assess local difference in abundance in fields and edges and the idea that sticky traps sample large areas? We think not, because this observation could be the result of passive accumulation of flying insects in high vegetation under windy conditions, as was shown by [Grüebler et al. \(2008\)](#). However, there also could be other reasons for the fact that the abundance of insects is usually higher in high than in low vegetation, such as the higher presence of resources or a higher structural diversity of the vegetation.

Another striking result was that in our raw data we found a negative

relationship between abundance and vegetation height, while our models showed in all cases a non-negative relationship ([Tables 1, Fig. 6](#)). This can be explained by the fact that the Dutch fields were all grassland with short vegetation as compared to the vegetation heights in the croplands of Illinois. At the same time, the sticky traps of the Netherlands collected relatively large numbers of insects ([Suppl. Inf. Fig. S4](#)). Our models corrected for this unbalance in our data with the random-effect variables.

We think that our results indicate that when insects are monitored with sticky traps, we should not consider the actual sampling plot as the research unit, but the area around the sampling location. The fact that no difference in abundance is found up to 500 m from (semi)natural areas suggests that the research unit should at least be an area of a circle with a diameter of 500 m, i.e., an area of at least 19.6 ha. The mixture of management within such an area should probably be regarded as the independent variable affecting the abundance of flying insects at the center of the area.

Some studies have previously shown the importance of taking the spatial scale of sampling units into consideration when studying arthropods. [Chust et al. \(2004\)](#) have shown that Homoptera and Diptera, as well as functional groups within the Diptera, differ in the optimal scale to relate species richness assessed by net-sweeping to landscape variables. [Schmidt et al. \(2007\)](#) collected spiders in pit fall traps and showed that species differed in their optimal scale to relate abundance to landscape complexity. And [Marini et al. \(2012\)](#) have shown at different scales that β -diversity of Orthoptera in hay meadows is strongly affected by the mobility of the species.

The difference in results between Illinois and the Netherlands is small. Only the effect of the location of sampling plot (interior vs boundary, resp. margin) is clear: there seems no such effect in the Netherlands, while it is present in Illinois. Furthermore, only an

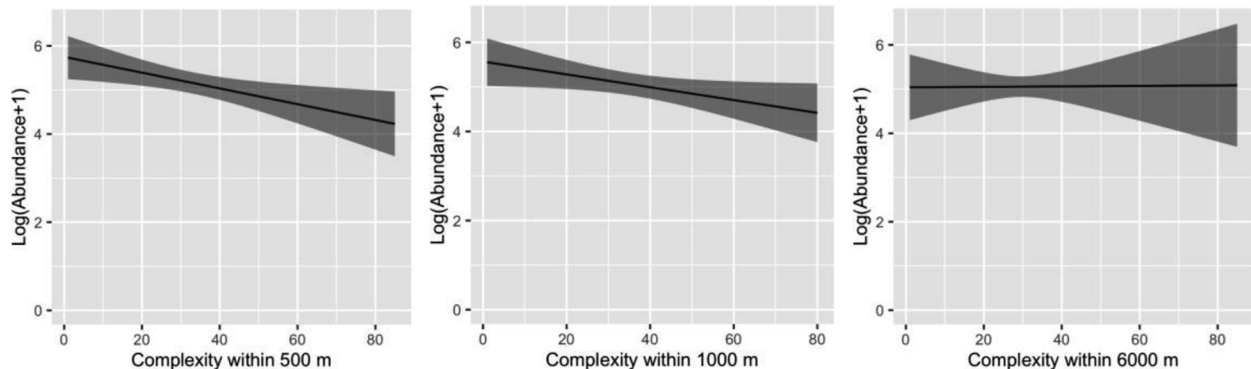


Fig. 5. The relationship between landscape complexity (percentage of non-agricultural area) and abundance of flying insect as fitted by the complete LMM models ($n = 539$). The grey area is the Confidential Interval area.

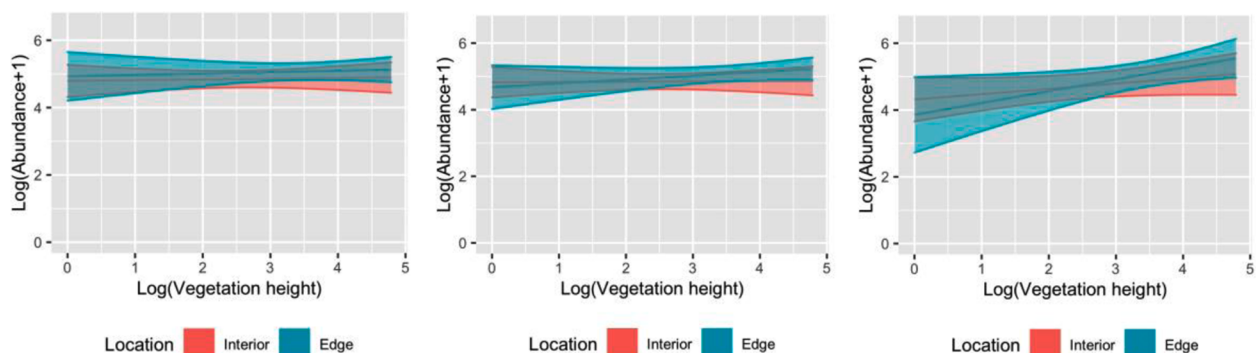


Fig. 6. Effect of vegetation height and location within field on the abundance of flying insects as fitted by the complete LMM models, with landscape complexity at 500 m (left), 1000 m (middle), and 6000 m (right) ($n = 539$). The colored area is the Confidential Interval area.

indication of a positive effect of vegetation height is present in the Netherlands, while it is absent in Illinois. This is probably due to the difference in agricultural landscape between the two countries: dairy farming in the Netherlands and arable farming in Illinois. Consequently, the difference in vegetation structure between interior and field margin in the Netherlands is always small, while it may be much larger between interior and field boundary in Illinois, so that the accumulating effect of wind may be much stronger in Illinois (Figs. S2, S3 and S5). Although this may be the case, previous research in the same Dutch landscape showed a significant difference in larger flying insect (>4 mm) abundance between the field margin and the interior of the field (Wiggers et al., 2015, 2016). However, in these studies, the management of the margins was such that relatively high vegetation is to be expected.

Previous research on the effects of landscape complexity, defined as the percentage of natural elements of the km² sampling grids, showed a positive relationship between insect species richness and complexity (Cormont et al. 2016), while Evans et al. (2016a) showed that increased complexity, defined as the percentage of non-agricultural area in circles of resp. 500, 1000, and 6000 m radius around sampling locations, decreased the invertebrate species richness and diversity in agricultural fields and increased the richness and diversity in field boundaries. Extensive research of the effect of landscape on conservation management in agricultural fields in Europe has shown that landscape complexity may be an important factor in the success of such management, even to the point that the effect of local management on species diversity might be zero in either very simple or very complex landscapes (see Tschamntke et al. 2012 for an overview). That we did find a negative effect of complexity on flying insects may be because we studied abundance, not species diversity. The same pattern was found in a study of flying insect biomass in Denmark and Germany (Svenningsen et al., 2020). Abundance of insects may be affected by nutrient dilution in non-agricultural vegetation due to climate change (Welti et al. 2020). Ekroos et al. (2013) found that the abundance of bumble bees and butterflies in linear, uncultivated landscape elements decreased with increasing distance to semi-natural grassland, but not the abundance of hoverflies. Geslin et al. (2016) found that, when the mango trees were flowering, the abundance of flying insects in mango orchards of South Africa decreased with increasing distance to natural habitats, but no effect of distance was found outside the flowering season, when higher abundance was detected using pan traps. Much more research on the effects of management and disturbance on the abundance of insects is needed.

As a matter of fact, we think that we should conclude from our study that if one needs to study the effect of human activities on flying insects and one uses trapping devices, such as sticky traps, one should realize that effects may only be measurable at sampling units that are relatively large and that results may depend on weather and the presence of wind, which is affected by three-dimensional structures such as trees and buildings. This should also be taken into consideration when interpreting past research, including meta-analyses as that of Van Klink et al. (2020a). Therefore, the study of the effect of nature conservation management on flying insects should be done on spatial large scales, e. g., the landscape level (Seibold et al. 2019), and include the confounding effects of the three-dimensional structure of the landscape (Davies & Asner 2014).

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107889>.

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