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Research Paper

Local landscape elements enhance flying insect biomass in a complex agricultural landscape

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ABSTRACT

A current response to counteract insect biomass decline is to create landscape elements like hedgerows and flower strips in agricultural landscapes to provide habitat for insects. However, little is known about the additive effects of such landscape elements on biomass of flying insects, especially in a landscape that has already been partly restored. Our study area has a relatively high landscape complexity due to past conservation efforts. Here, we determined the impact of hedgerows and flower strips on flying insect biomass using 3 years of Malaise trap data from 24 field edges with either a hedgerow, flower strip or field boundaries without such landscape element present. To accurately compare biomass of the collected samples, we used a Bayesian model with hourly biomass as a latent variable, including temperature anomaly and Julian day to correct for the influences of weather and seasonal patterns on insect biomass. This model was expanded with information on local vegetation and land management, proportionalized land use, total length of hedgerows, and edge density to assess the wider impacts of landscape complexity and configuration on insect biomass. Hedgerows had a significantly positive effect on mean hourly biomass: 0.231 g/h compared to the control locations (0.105 g/h), whereas flower strips had an intermediate estimate (0.150 g/h). As one of the few additional landscape parameters having an effect, the percentage of protected natural area in the surroundings contributed significantly to insect biomass. Our results show that local natural elements, particularly hedgerows, can add to insect recovery even in highly complex landscapes. The exact land use and landscape configuration in its vicinity contribute little, except for protected natural areas dispersed in the landscape.

Introduction

Insect decline has become a growing concern recently, since Hallmann et al. (2017) found drastic declines in insect biomass in protected areas in Germany over a thirty-year period. Meanwhile, a multitude of studies have confirmed that insect decline is a widespread phenomenon (Didham et al., 2020; van Klink et al., 2020; Janzen & Hallwachs, 2021; Dalton et al., 2023). What makes these declines in insect biomass even more concerning, is that they do not just affect rare species, as also common species are decreasing in abundance (Hallmann et al., 2021; Barendregt et al., 2022; van Klink et al., 2024). Studies aimed at identifying possible causes of insect decline point at multiple interacting pressures, including land-use change, agriculture, introduced species, eutrophication and pollution (Wagner et al., 2021; Harvey et al., 2023; Grevé et al., 2024). Worldwide 44 % of the land is used for agriculture (Ritchie & Roser, 2019), and this is as high as 66 % in the Netherlands (CLO, 2024). While changing conventional agricultural practices have contributed to the current insect decline, transforming agricultural landscapes from hostile environments to habitat for insects might be key to restoring insect abundance. In the present study we investigate how insect biomass in an agricultural landscape, that already contains landscape elements to support insects, responds to the establishment of hedgerows and flower strips. Additionally, we explore the relation between insect biomass and the landscape characteristics in its immediate

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vicinity.

Studies on biomass of flying insects often yield contrasting results concerning effects of landscape composition. While many studies emphasize negative impacts of agriculture on insect biodiversity (Wagner et al., 2021), some fail to detect clear biomass differences between semi-natural and agricultural landscapes (Hallmann et al., 2017; Uhler et al., 2021; Svenningsen et al., 2024). A German study over nine years reported insect biomass declines of 41 % in forests and 67 % in grasslands, with steeper declines in areas with higher percentages of arable land (Seibold et al., 2019). Conversely, a Swiss study over 32 years reported insect biomass increases in agricultural regions, potentially due to improved habitat quality from agri-environmental schemes (Fürst et al., 2023; Gebert et al., 2024). These findings highlight persistent uncertainty about the exact influence of land use on insect biomass at landscape scales. Local measures, like reintroducing hedgerows and flower strips, can provide vital resources for pollinators and natural enemies, supporting ecosystem services such as pollination and pest control (Albrecht et al., 2020; Garratt et al., 2017; Martin et al., 2019; Morandin et al., 2011; Sutter et al., 2018). Most studies on local measures that promote insects, also focus on ecosystem service providers, however, they do not elucidate how the total community of insects responds to the reintroduction of landscape elements. The majority of insects play different roles in ecosystems, and these make up the bulk of insect biomass. Therefore, it remains an open question whether the beneficial effects of new landscape elements on pollinators and natural enemies also promote the insect community as a whole.

We used insect biomass as an indicator for insect abundance, rather than as a direct measure insect diversity, although total biomass and insect species richness can be positively correlated in some cases (Hallmann et al., 2021; Sinclair et al., 2024). Here, we investigate insect biomass responses to local and landscape-level drivers in an agricultural area, where significant efforts have been made to increase landscape heterogeneity and complexity through reintroduced hedges and flower strips, with the goal of improving local biodiversity. Using spatial variation across the study area, we quantified the contribution of hedgerows and flower strips to the biomass of flying insects and how these effects were modified by surrounding land use and landscape characteristics. To achieve our aims we factored the influence of weather conditions and seasonal fluctuations in insect populations into our analyses, which strongly impact insect trapping results (Wolda, 1988; Gutiérrez & Wilson, 2021; Welti et al., 2022).

Materials and methods

Study system

This study was performed in an agricultural area in former floodplains of the river Waal, the main distributary branch of the Rhine river in the Netherlands. The area is situated on fertile river clay, and characterized by relatively small-scale agricultural grasslands for dairy production, arable fields for crop cultivation, and patches of (semi-) natural grasslands. Local agriculture varies from conventional, intensive practices to organic. The landscape has been partially restored with the aim of enhancing biodiversity and restoring historical characteristics of the Dutch agricultural landscape. The reintroduction of landscape elements such as hedgerows, flower strips, but also pools, natural ditch banks and tree rows has resulted in a patchwork of connected and more isolated landscape elements within an agricultural landscape interspersed with (protected) natural and forested areas.

Malaise traps

We collected insect samples from 24 agricultural field edges of which 9 had a hedgerow, 8 a flower strip, while 7 field edges did not have a natural element (Fig. 1). Flying insects were caught using Malaise traps (British Museum type, SKU: 10.501). The highest point of these traps was 1.75 m at the front, sloping down to 0.95 m at the back. The width was 1.12 m and depth was 1.70 m. Collection jars were filled with 96 %

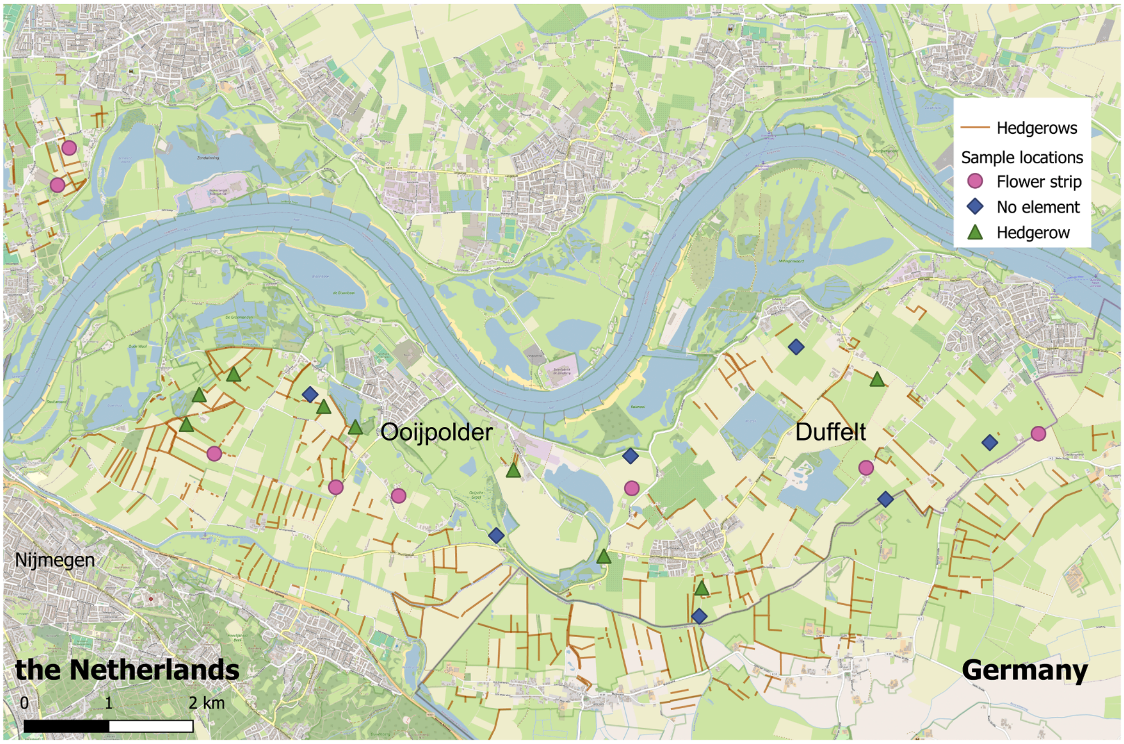

Fig. 1. Map of the study area. The Western area is known as the Ooijpolder, the Eastern area is known as the Duffelt. All 24 sample locations are marked: green triangles represent hedgerow locations, pink dots represent flower strip locations and blue diamonds represent locations without a landscape element. The orange lines represent all hedgerows in a 1000 m radius from our sample locations.

ethanol as a preservative fluid. The research was carried out over three consecutive years (2021 – 2023). Each of the 24 locations was sampled 8 times, with one exception being sampled only 6 times. In 2021 locations were sampled in June, July, August and September. From 2022 onwards the sampling scheme was adjusted to sampling efforts in May, June, July and August until a total of 8 samples per location was achieved. A detailed overview of the sampling locations, years and dates can be found in Table A1.

We placed the traps at field edges, either with or without a landscape element. To ensure standardized trapping, a few precautions were taken during trap installation (Ssymank et al., 2018). Traps were placed as close to the field edge as possible. In 82 % of cases the trap was directly adjacent to the landscape element (no distance), in the other 34 cases the mean distance was 4.22 m (sd = 2.14 m). The traps were set up tautly, so the opening to the collection jar was accessible. In addition, any gaps at the bottom were prevented. The vegetation underneath the traps was cleared to standardize the lateral accessibility, and all traps were set perpendicular to the field edge or landscape element. The exact time of trap placement, as well as collection, was recorded. The sampling period lasted a week (6–8 days) at a time. The sample biomass was weighed using the protocol of Schwan et al. (1993).

Environmental data

In our modelling approach we incorporated effects of weather conditions on flying insect biomass, as they are known to impact the sampling results of Malaise traps (Hallmann et al., 2017; Welti et al., 2022). Hourly weather data for our sampling instances were derived from the KNMI (Royal Netherlands Meteorological Institute) weather station closest to the sampling locations (375 Volkel). Since temperature and seasonality are correlated, we also calculated temperature anomalies: the deviation from the mean temperature of the past 30 years. For a given day and hour combination in our study we calculated these deviations (1990–2020 for 2021, 1991–2021 for 2022, 1992–2022 for 2023).

Local covariates

We investigated the effects of local factors in the form of vegetation characteristics and farming practices on flying insect biomass. Vegetation height was measured directly around the Malaise traps and in the adjacent agricultural field. At the time of placement, all flowering plant species in a 10 m radius of the Malaise trap were recorded. The vegetation cover and composition of the agricultural fields and flower strips was determined by vegetation surveys (Braun-Blanquet, 1951). The species diversity of hedgerows was captured in linear surveys (100 m). Linear surveys consisted of scoring all plant species in the hedge and its undergrowth at 5-meter intervals for the 100 m survey length. Ultimately, we used vegetation heights, both next to the trap and in the adjacent agricultural field, total plant diversity and diversity of non woody species as local vegetation covariates. For local management practice covariates, we consider whether the field is used for livestock or crop cultivation, fertilized with manure or chemicals, and whether pest control is applied. We retrieved this information from questionnaires filled in by all cooperating farmers and landowners.

Landscape covariates

As landscape context plays an important role in determining the possibilities for insect populations to inhabit an area (Kleijn et al., 2011; Martin et al., 2019), we quantified landscape scale data at different scales (radii 50 m, 250 m and 500 m) using landcover maps (Top10NL; het Kadaster, 2021 and Natuurnetwerk Nederland - Provincies; Nationaal Georegister, 2022). While there is some overlap at larger radii, the circles around locations are largely independent at 250 m with a mean of 90.9 % independent area on average (sd = 14 %). At 500 m there is more overlap, with a mean independent area of 57.7 % (sd = 26 %) (Figures B2–4).

We determined percentages of arable cropland, arable grassland, forest and protected natural area. These four land cover types provide close to 100 % cover of the areas surrounding the traps (only roads and settlements are excluded). To prevent overlap between land-cover types, we excluded forest patches from the protected natural area cover. Protected natural areas in this study region consist of flood plains, semi-natural grasslands and several water bodies with their associated vegetation.

As a measure for landscape heterogeneity and configuration, we used edge density: landscapes with small fields and patches of natural area have a higher density of edges than landscapes with large fields (Martin et al., 2019). We quantified edge density as the total length of edges per area (m/m^2) at all radii for each sampling location (Martin et al., 2019). Furthermore, an extensive map of all hedgerows surrounding the sampling locations (radius of 1000 m) was hand drawn using a combination of satellite images and height maps in QGIS version 3.22.5 (Google Earth, 2024; Nationaal Georegister, 2023; PDOK, 2023). We calculated the total hedge length (m) for all radii. Spatial calculations were performed in R (version 4.2.2) using the sf package (Pebesma & Bivand, 2023).

Analyses

We developed a JAGS model to quantify effect sizes for a selection of weather, vegetation and landcover variables (Su & Yajima, 2008). The JAGS model was utilized for Bayesian inference and uses Markov chain Monte Carlo (MCMC) simulations. Our stepwise model selection strategy was to first arrive at a basic model including landscape element (our focal interest), seasonal patterns, site nested in region, and weather variables. Variable selection and model validation is detailed in Appendix B. This analysis enabled us to uniquely investigate the effects of landscape elements and other environmental variables on insect biomass while correcting for weather and seasonal patterns. Our second aim was to extend the base model with a range of local and landscape covariates (Fig. 2).

Our sampling scheme had weekly sampling intervals of different hourly lengths (119.7–219.2 h). To overcome discrepancies in temporal resolution between variables and to account for differences in collection intervals, we modelled the expected biomass per hour, a latent variable. First, we included different hourly weather variables until the most accurate predictor for hourly biomass was found (details on the selection and performances of different weather variables can be found in Appendix B - Supplementary methods). The cumulative biomass $M_{j,s,r}$ of sample j, collected at site s in region r, was assumed to be normally distributed around the sum of the latent expected hourly biomass z with sample specific variance σ_j^2

$$M_{j,s,r} = N\left(\mu_{j,s,r},\ \sigma_j^2\right) \tag{1}$$

Where the cumulative latent expected biomass is defined as

$$\mu_{j,s,r} = \sum_{t=\tau 1\ (j)}^{\tau 2\ (j)} z_{t,s,r} \tag{2}$$

with $\tau_1$and τ_2 represent the collection interval (in hours) for sample j, and t the hourly timestep. Expected latent hourly biomass $z_{t,s,r}$was considered log-normally distributed and therefore modelled as

$$z_{t,s,r} = e^{y_{t,s,r}} \tag{3}$$

$$y_{t,s,r} = \beta_e + \beta_t T_{anomaly} + \beta_{J1}\ J + (\beta_{J2}\ J)^2 + u_s \tag{4}$$

where β_e is the intercept for landscape element (where the first element, i.e. no landscape element, was set to 0), β_t the coefficient for tempera-

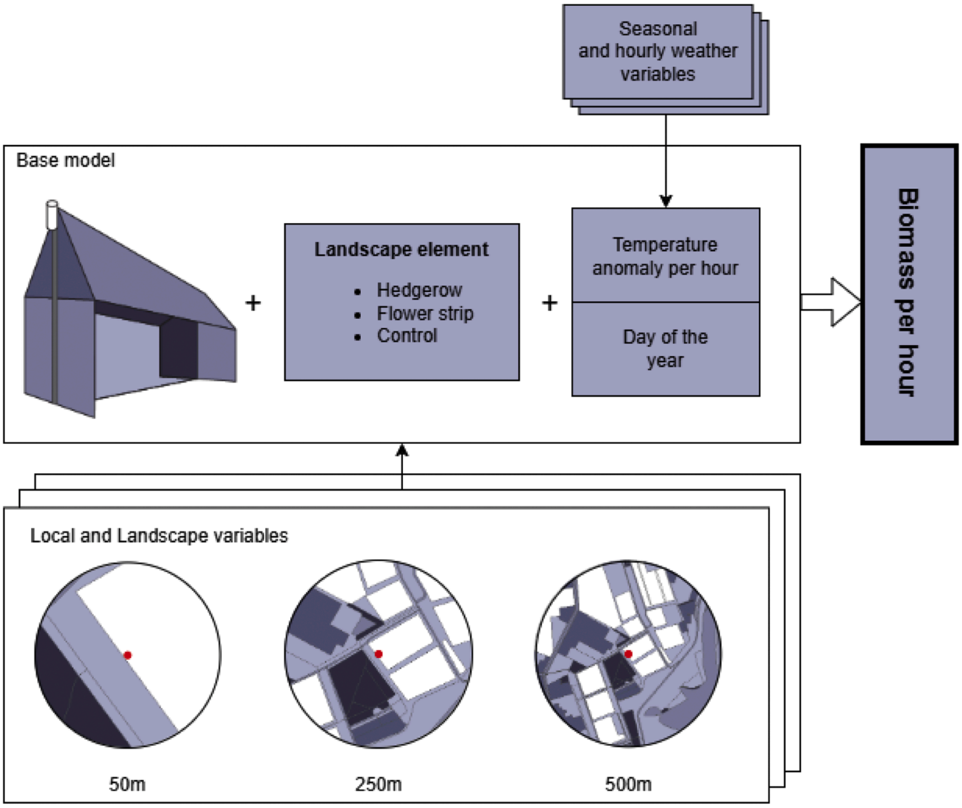

Fig. 2. Schematic overview of the developed model of insect biomass. The base model started out with insect biomass (from Malaise traps, and thus indicated) and the landscape elements, our focal interest. We then identified the seasonal and hourly weather variables that had the most predictive power for our observed biomass out of a list of traditionally recorded weather variables. The base model calculates biomass per hour and can estimate the relative effects of hedgerows, flower strips and control locations. In the final step we added local and landscape variables (land use and landscape configuration variables at 50 m, 250 m and 500 m radii) to assess their impact on the predicted insect biomass per hour.

ture anomaly $T_{anomaly}$, and β_{J1} and β_{J2} the coefficients for Julian day J and Julian day squared (respectively). Non-informative normal priors were assigned to fixed-effect coefficients (0.001, 0.001) and a uniform prior (0–5) to the residual standard deviation.

u_s was included as hierarchical random intercepts for site nested within four regions (Fig. B2). Region was modelled as normally distributed with $u_r \sim N(0, \sigma_r^2)$. Site effects were modelled as normally distributed around their corresponding region effect $u_s \sim N(u_r, \sigma_s^2)$. Precision parameters $\left(\sigma_s^2\right)$ for both levels were assigned non-informative gamma priors. The base model (as described above) was further expanded by the addition of 32 covariates (Table A3). These were added to the base model one by one, because of the number of sampling locations (24). This means that we were not able to quantify potential interactive effects of multiple landscape variables.

Results

Our initial model selection resulted in a base model with the following variables: temperature anomaly, Julian day, Julian day squared, landscape element, and as a random factor location nested within region (detailed model summary is provided in Table A2). All model parameters (except for the effect size of flower strip) were significantly different from 0 and converged (R-hat ≤ 1.01). At locations without a landscape element, the base model predicted a biomass of 0.105 (95 % CI: 0.066 – 0.163) gram per hour for an average temperature at peak summer (Fig. 3). Near flower strips, the hourly biomass was higher with a mean of 0.150 g/h (CI: 0.101 – 0.224). The posterior distribution of the effect of flower strips, as compared to no landscape element, included positive estimates in 94.2 % of the iterations. Hedgerows significantly increased the hourly biomass of flying insects, with a predicted hourly biomass of 0.231 g/h (CI: 0.161 – 0.337). The model predictions for hourly biomass were consistent with patterns in weighed Malaise trap samples (Fig. A1).

Locally, only vegetation height next to the trap had a significantly negative impact on insect biomass (Table 1, effect size in the model: −0.111). Few of the covariates related to the studied landscape impacted insect biomass significantly, and only one covariate produced significant results at two different radii (Table 2). Percentage forested area in a 50 m radius had a significant negative effect (−0.187). At a 500 m radius, percentage crop area also had a significant negative effect (−0.157). At both a 50 m and 500 m radius, the percentage of protected natural area had a significantly positive effect on insect biomass (effect size 0.252 at 50 m and 0.327 at 500 m) (Fig. 4). At the 250 m radius effects of natural area were not significant, however they were positive for 77.8 % of iterations. In total, there were 32 covariates added to the base model one by one and an overview of model summaries can be found in the supplementary material (Table A3). Interaction models between significant local/landscape variables and landscape elements were tested but did not produce significant effects. The effect of local hedgerows was significant in all models. While flower strips had positive effect sizes in all models, they were mostly non-significant (like in the base model) but were significant in 9 of the 32 models with additional covariates (Table A3). The impact of flower strips on biomass of flying insects was thus less consistent than the impact of hedgerows.

Discussion

Our results show that hedgerows and flower strips contribute positively to biomass of flying insects. After correction for weather effects on insect activity and catching efficiency using Malaise traps, locations

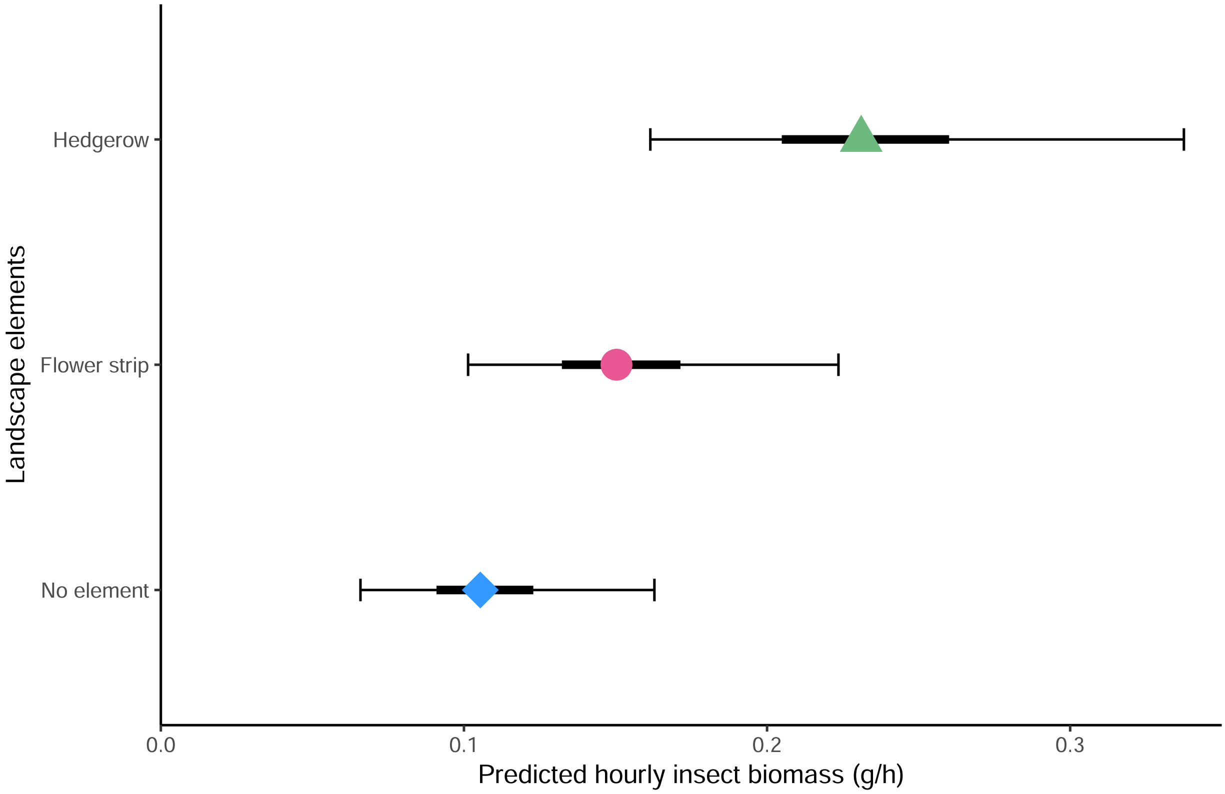

Fig. 3. The predicted hourly biomass (g/h) for locations without a landscape element, locations with flower strips and locations with hedgerows. The graph shows the predicted intercept for each category (diamonds), the 95 % confidence interval (thin black line) and the 50 % confidence interval (thick black line). The results were calculated for the mean temperature anomaly (+1.195 °C) and the mean day of the year (191.4 or 9th of July) of our sample period.

Table 1
Results of the local variables added to the base model. Variables with an effect size in bold had a significant effect on hourly biomass of flying insects.

Class	Local variables Name	Effect sizes
Vegetation height	Vegetation height next to trap	**−0.111**
	Vegetation height field	0.035
Plant diversity	Number of flowering species	0.011
	Total plant species	0.025
	Non woody plant species	0.029
Management	Fertiliser use	0.022
	Manure use	−0.127
	Crop protection use	0.114
	Grassland or crop field	0.024

Table 2
Results of the landscape variables, at different radii, added to the base model. Variables with an effect size in bold had a significant effect on hourly insect biomass.

Covariate name		Effect sizes	
	50m	250m	500m
Crop area (%)	−0.004	−0.107	**−0.157**
Agricultural grassland area (%)	0.092	0.096	0.169
Forest area (%)	**−0.187**	0.06	0.082
Protected natural area (%)	**0.252**	0.104	**0.327**
Edge density (m/m^2)	−0.117	−0.23	−0.131
Hedge length (m)	0.069	0.152	0.102

with hedgerows yielded more than twice as much biomass of flying insects than locations without landscape elements. Flower strips also tended to have a positive effect on biomass of flying insects, although this effect was not significantly different from the controls. Interestingly, the effects of hedgerows were hardly modified by the structure and composition of the surrounding landscape, showing that hedgerows may promote insects even in a landscape that already has considerable complexity.

High effect of hedgerow presence, irrespective of local field management

Our results demonstrate that hedgerows enhance biomass of flying insects in an area where there are already landscape elements present in the landscape. While flower strips tended to yield more insect biomass than conventional field margins, the effect was not statistically significant due to strong variation within each landscape element. An explanation could be that half (4) of flower strips in our study area were annually tilled and resown (refer to Table A4 for an overview of flower strip sowing details and species composition). Because of this, some Malaise traps at flower strips yielded relatively low and inconsistent insect biomass early in the season (May), when the flower strips as a food source for flying insects were yet to develop. As a result, insect species that hibernate or develop in the soil or in remnant vegetation cannot complete their life cycles (Unterweger et al., 2018). Litovska et al. (2025) studied arthropods in agricultural landscapes and found that the time since the last cultivation determined arthropod abundance. Apparently, the yearly overhaul of the plant community and its related resources, makes some of the annual flower strips unable to support insects year-round (also see discussions on flower strip age in Haaland et al. (2011) and Albrecht et al. (2021)). Hedgerows, on the other hand, remain largely undisturbed throughout the year. Arguably, this is part of the valuable contribution of long-term perennial landscape elements to insect populations in agricultural landscapes (Slikboer & Zeegers, 2020).

Unexpectedly, none of the effects of local factors related to management practices and local vegetation characteristics had a significant impact on hourly biomass, except for vegetation height surrounding the

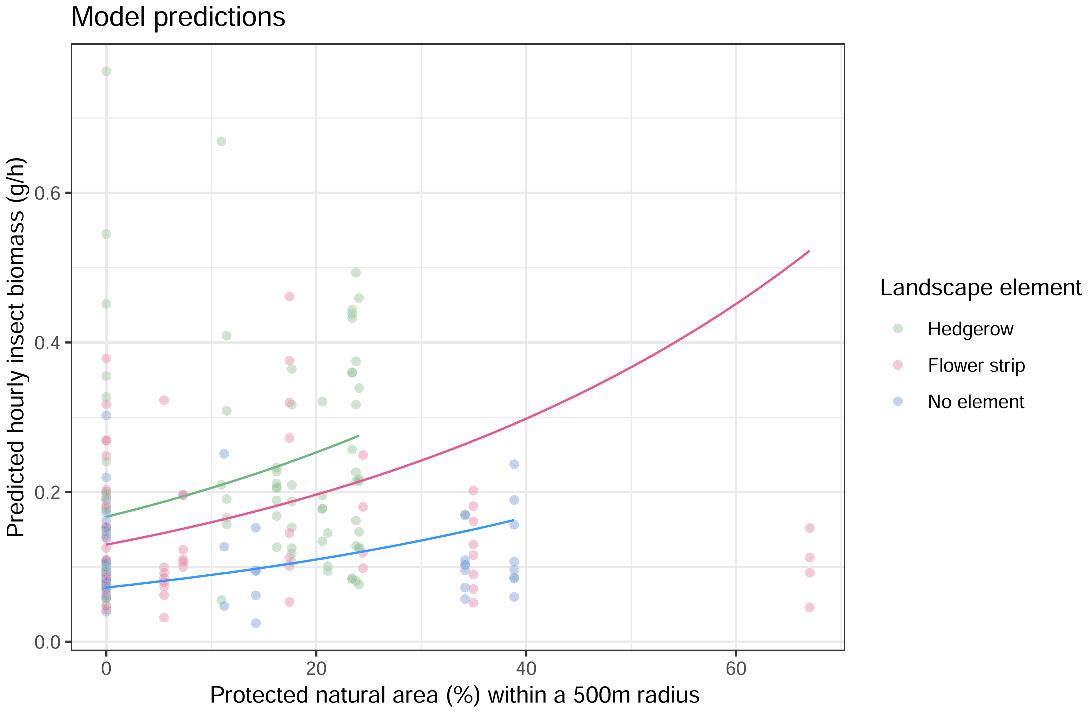

Fig. 4. Model predictions for different landscape variables. The background dots in the graph represent the insect biomass in our samples divided by the hours that a Malaise trap was in the field. Lines represent the predicted hourly insect biomass (g/h) when including protected natural area at a radius of 500 m in the model.

Malaise traps. Potentially, vegetation height can impact trapping efficiency directly. None of the variables that represented management practices of the field where the trap was located (e.g. application of manure and chemical fertilizer, and pesticides use) affected insect biomass. Some studies on arthropod abundance and diversity have shown a similar lack of response to agricultural management variables (Litovska et al., 2025). In our study, the management variables we included were confined to the field directly next to the sampling location. In a relatively small-scale agricultural landscape, such as our study area, management practices of neighboring fields may have obscured the influence of adjacent field management on flying insect biomass.

Landscape-scale variables hardly contribute to local insect biomass

Where numerous insect studies have proposed that (semi-)natural areas and heterogeneity in a landscape enhance insect abundance and diversity (Duelli & Obrist, 2003; Kleijn et al., 2011; Martin et al., 2019; Haan et al., 2021; Kratschmer et al., 2024), we found only a few significant effects of landscape features surrounding the trap locations (i.e. the percentages crop area and protected natural area), although we did not investigate potential interactions between different landscape variables due to the limited number (24) of sampling locations. Proportion of crop area within a 500 m radius was the only agricultural land use covariate that had a significant negative impact on insect biomass. Smaller radii and the proportion of agricultural grasslands did not have significant effects. The impact we demonstrate here has also been covered in other studies, such as Seibold et al. (2019) who found stronger declines of insect biomass, abundance and species richness at sample sites with a higher cover of agricultural land.

The percentage of protected natural area had a significant positive effect on biomass of flying insects at different radii around our trapping locations. This result is in line with numerous studies on insect abundance, species richness and specific taxonomic groups, such as butterflies (Duelli & Obrist, 2003; Hendrickx et al., 2007; van Strien et al., 2019). Insect biomass studies in relation to the landscape often report less conclusive effects of natural areas; insect biomass does not show distinctive differences between agricultural and (semi-)natural areas (Hallmann et al., 2017; Uhler et al., 2021; Svenningsen et al., 2024). We suspect that the strong effects of local surroundings on biomass catches are often not taken into account in these large-scale studies (Ssymank et al., 2018). We demonstrate first of all, that hedgerows consistently determine the amount of insect biomass caught. Secondly, that including these local impacts in an analysis allows for more accurate evaluation of insect biomass as determined by the surrounding landscape.

The structural complexity of a given landscape will matter greatly for the effectiveness of biodiversity-enhancing measures; effects are dependent on context. For example, cleared landscapes that lack any complexity will lack the source populations for biodiversity enhancement to have any effect. Therefore, in simple landscapes a measure that significantly improves the landscape complexity for insects may be highly effective, provided that insects can reach that element. However, in complex landscapes adding new structural elements to the existing complexity will lead to a relatively moderate biodiversity enhancement, as vital habitat and resources are already present (Kleijn et al., 2011). The specific agricultural landscape in which our study was carried out harbors a sizable level of complexity due to past conservation efforts and the reintroduction of landscape elements. Still, we found a substantial difference in insect biomass between locations with hedgerows and control locations. Our results highlight that every additional meter of hedgerow enhances the biomass of the flying insect community in the landscape, regardless of the landscape characteristics in its vicinity.

Conclusions

Our results show the effectiveness of establishing hedgerows for enhancing biomass of flying insects in an agricultural landscape that already contains a variety of landscape elements. Biomass increases were local, especially near hedgerows. Flower strips at most yielded a non-significant positive trend on flying insect biomass. While insect biomass could be a proxy for insect species richness and abundance (Hallmann et al., 2021; Sinclair et al., 2024), future studies need to further test this assumption by dissecting biomass into diversity-based data. As one of the first studies focusing on insect biomass in relation to landscape elements, the implications for biodiversity restoration in agricultural settings is evident. Enhanced insect biomass may already have substantial positive effects on higher trophic level species as these may benefit from the availability of overall insect abundance as a food source.

Our results show that even in a landscape with high complexity levels, the establishment of hedgerows has a positive effect on biomass of flying insects. Exactly where they are placed, connected or not to other hedgerows hardly matters. Our study also indicates that naturally protected areas dispersed in the landscape promote insect abundance. Our results are thus an encouragement for further improving landscape complexity as local natural elements, particularly hedgerows, contribute to insect recovery. Therefore, we conclude that understanding the contribution of new landscape elements in supporting insect biomass helps to further enhance insects, leading to (cost-)effective insect conservation in a wide variety of agricultural landscapes.

Data availability

All research data and corresponding model code can be found in Lexmond et al. (2026).

CRediT authorship contribution statement

Robin E. Lexmond: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Eelke Jongejans:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis, Conceptualization. **Theo Zeegers:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Joshua D. Climo:** Writing – review & editing, Investigation, Formal analysis. **Wim H. van der Putten:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Hans de Kroon:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of Interest Statement

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2026.03.004.

References

Albrecht, M., Kleijn, D., Williams, N. M., Tschumi, M., Blaauw, B. R., Bommarco, R., Campbell, A. J., Dainese, M., Drummond, F. A., Entling, M. H., Ganser, D., de Groot, G. A., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., … Sutter, L. (2020). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecology Letters, 23*(10), 1488–1498. https://doi.org/10.1111/ele.13576

Albrecht, M., Knecht, A., Riesen, M., Rutz, T., & Ganser, D. (2021). Time since establishment drives bee and hoverfly diversity, abundance of crop-pollinating bees and aphidophagous hoverflies in perennial wildflower strips. *Basic and Applied Ecology, 57*, 102–114. https://doi.org/10.1016/j.baae.2021.10.003

Barendregt, A., Zeegers, T., van Steenis, W., & Jongejans, E. (2022). Forest hoverfly community collapse: Abundance and species richness drop over four decades. *Insect Conservation and Diversity, 15*(5), 510–521. https://doi.org/10.1111/icad.12577

Braun-Blanquet, J. (1951). *Pflanzensoziologie: Grundzüge der vegetationskunde*. Springer-Verlag.

CLO. (2024). *Land- en tuinbouw: Ruimtelijke spreiding, grondgebruik en aantal bedrijven, 1980-2023 | compendium voor de Leefomgeving*. https://www.clo.nl/indicatoren/nl211913-land-en-tuinbouw-ruimtelijke-spreiding-grondgebruik-en-aantal-bedrijven-1980-2023.

Dalton, R. M., Underwood, N. C., Inouye, D. W., Soulé, M. E., & Inouye, B. D. (2023). Long-term declines in insect abundance and biomass in a subalpine habitat. *Ecosphere (Washington, D.C), 14*(8), e4620. https://doi.org/10.1002/ecs2.4620

Didham, R. K., Basset, Y., Collins, C. M., Leather, S. R., Littlewood, N. A., Menz, M. H. M., Müller, J., Packer, L., Saunders, M. E., Schönrogge, K., Stewart, A. J. A., Yanoviak, S. P., & Hassall, C. (2020). Interpreting insect declines: Seven challenges and a way forward. *Insect Conservation and Diversity, 13*(2), 103–114. https://doi.org/10.1111/icad.12408

Duelli, P., & Obrist, M. K. (2003). Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat islands. *Basic and Applied Ecology, 4*(2), 129–138. https://doi.org/10.1078/1439-1791-00140

Fürst, J., Bollmann, K., Gossner, M. M., Duelli, P., & Obrist, M. K. (2023). Increased arthropod biomass, abundance and species richness in an agricultural landscape after 32 years. *Journal of Insect Conservation, 27*(2), 219–232. https://doi.org/10.1007/s10841-022-00445-9

Garratt, M. P. D., Senapathi, D., Coston, D. J., Mortimer, S. R., & Potts, S. G. (2017). The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. *Agriculture. Ecosystems & Environment, 247*, 363–370. https://doi.org/10.1016/j.agee.2017.06.048

Gebert, F., Bollmann, K., Schuwirth, N., Duelli, P., Weber, D., & Obrist, M. K. (2024). Similar temporal patterns in insect richness, abundance and biomass across major habitat types. *Insect Conservation and Diversity, 17*(1), 139–154. https://doi.org/10.1111/icad.12700

Google Earth. (2024). *Satellite Images Google Earth* [Map]. earth.google.com/web/@51.85386704,5.96649439,12.53242914a,11687.15576969d,35y,0h,0t,0r/data=CgRCAggBOgMKATBCAggASg0I________ARAA.

Grevé, M. E., Marx, M. T., Eilmus, S., Ernst, M., Herrmann, J. D., Baden, C. U., & Maus, C. (2024). Insect decline—Evaluation of potential drivers of a complex phenomenon. *Insects, 15*(12), Article 12. https://doi.org/10.3390/insects15121021

Gutiérrez, D., & Wilson, R. J. (2021). Intra- and interspecific variation in the responses of insect phenology to climate. *Journal of Animal Ecology, 90*(1), 248–259. https://doi.org/10.1111/1365-2656.13348

Haaland, C., Naisbit, R. E., & Bersier, L.-F. (2011). Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity, 4*(1), 60–80. https://doi.org/10.1111/j.1752-4598.2010.00098.x

Haan, N. L., Iuliano, B. G., Gratton, C., & Landis, D. A. (2021). Designing agricultural landscapes for arthropod-based ecosystem services in North America. In *Advances in ecological research, 64* pp. 191–250). Elsevier. https://doi.org/10.1016/bs.aecr.2021.01.003

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE, 12*(10), Article e0185809. https://doi.org/10.1371/journal.pone.0185809

Hallmann, C. A., Ssymank, A., Sorg, M., de Kroon, H., & Jongejans, E. (2021). Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. *Proceedings of the National Academy of Sciences of the USA, 118*, Article e2002554117. https://doi.org/10.1073/pnas.2002554117

Harvey, J. A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P. K., Basset, Y., Berg, M., Boggs, C., Brodeur, J., Cardoso, P., de Boer, J. G., de Snoo, G. R., Deacon, C., Dell, J. E., Desneux, N., Dillon, M. E., Duffy, G. A., Dyer, L. A., … Chown, S. L. (2023). Scientists' warning on climate change and insects. *Ecological Monographs, 93*(1), e1553. https://doi.org/10.1002/ecm.1553

Hendrickx, F., Maelfait, J.-P., Wingerden, W. V., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V., & Bugter, R. (2007). How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology, 44*(2), 340–351. https://doi.org/10.1111/j.1365-2664.2006.01270.x

het Kadaster. (2021). *Top10NL* [Map]. het Kadaster. https://www.kadaster.nl/zakelijk/producten/geo-informatie/topnl.

Janzen, D. H., & Hallwachs, W. (2021). To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. *Proceedings of the National Academy of Sciences of the USA, 118*, Article e2002546117. https://doi.org/10.1073/pnas.2002546117

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G., & Tscharntke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution, 26*(9), 474–481. https://doi.org/10.1016/j.tree.2011.05.009

Kratschmer, S., Hauer, J., Zaller, J. G., Dürr, A., & Weninger, T. (2024). Hedgerow structural diversity is key to promoting biodiversity and ecosystem services: A systematic review of Central European studies. *Basic and Applied Ecology, 78*, 28–38. https://doi.org/10.1016/j.baae.2024.04.010

Lexmond, R. E., Jongejans, E., Zeegers, T., Climo, J. D., van der Putten, W. H., & de Kroon, H. (2026). *Data and code from Local landscape elements enhance flying insect biomass in a complex agricultural landscape. Zenodo*. https://doi.org/10.5281/zenodo.19053484.

Litovska, I., van der Plas, F., & Kleijn, D. (2025). Arthropod abundance is most strongly driven by crop and semi-natural habitat type rather than management in an intensive agricultural landscape in the Netherlands. *Agriculture, Ecosystems & Environment, 378*, Article 109298. https://doi.org/10.1016/j.agee.2024.109298

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Al Hassan, D., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., … Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters, 22*, 1083–1094. https://doi.org/10.1111/ele.13265

Morandin, L., Long, R. F., Pease, C., & Kremen, C. (2011). Hedgerows enhance beneficial insects on farms in California's Central Valley. *California Agriculture, 65*(4). https://escholarship.org/uc/item/1rh197qj.

Nationaal Georegister. (2022). *Natuurnetwerk Nederland—Provincies* [Map]. Nationaal Georegister. https://www.nationaalgeoregister.nl/geonetwork/srv/dut/catalog.search#/metadata/a6341e75-0dff-4948-9317-433324ab483b.

Nationaal Georegister. (2023). *Actueel hoogtebestand Nederland (AHN) DTM* [Map]. https://www.nationaalgeoregister.nl/geonetwork/srv/dut/catalog.search#/metadata/41daef8b-155e-4608-b49c-c87ea45d931c.

PDOK. (2023). *Luchtfoto 2023 Ortho 8cm RGB* [Map]. https://www.pdok.nl/introductie/-/article/pdok-luchtfoto-rgb-open-.

Pebesma, E., & Bivand, R. (2023). *Spatial Data science: With applications in R*. Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016.

Ritchie, H., & Roser, M. (2019). Half of the world's habitable land is used for agriculture. *Our World in Data*. https://ourworldindata.org/global-land-for-agriculture.

Schwan, H., Sorg, M., & Stenmans, W. (1993). Naturkundliche untersuchungen zum naturschutzgebiet "Die Spey" (Stadt Krefeld, kreis Neuss)—I. Untersuchungsstandorte und methoden. *Natur am Niederrhein (NF), 8*(1), 1–13.

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature, 574*(7780), 671–674. https://doi.org/10.1038/s41586-019-1684-3

Sinclair, J. S., Buchner, D., Gessner, M. O., Müller, J., Pauls, S. U., Stoll, S., Welti, E. A. R., Bässler, C., Buse, J., Dziock, F., Enss, J., Hörren, T., Künast, R., Li, Y., Marten, A., Morkel, C., Richter, R., Seibold, S., Sorg, M., … Haase, P. (2024). Effects of land cover and protected areas on flying insect diversity. *Conservation Biology, 39*, Article e14425. https://doi.org/10.1111/cobi.14425. n/a.

Slikboer, L., & Zeegers, T. (2020). *Insecten in de Zegenpolder te Rhoon in 2020* (Nos. EIS2020-26; p. 36). EIS kenniscentrum insecten. https://kenniscentruminsecten.nl/publicaties/insecten-in-de-zegenpolder-te-rhoon-in-2020/.

Ssymank, A., Sorg, M., Doczkal, D., Rulik, B., Merkel-Wallner, G., & Vischer-Leopold, M. (2018). Praktische hinweise und empfehlungen zur anwendung von malaisefallen für insekten in der biodiversitätserfassung und im monitoring. *Series Naturalis, 1*, 1–12.

Su, Y.-S., & Yajima, M. (2008). *R2jags: Using R to run "JAGS"* (p. 0.8-9) [Dataset]. https://doi.org/10.32614/CRAN.package.R2jags.

Sutter, L., Albrecht, M., & Jeanneret, P. (2018). Landscape greening and local creation of wildflower strips and hedgerows promote multiple ecosystem services. *Journal of Applied Ecology, 55*(2), 612–620. https://doi.org/10.1111/1365-2664.12977

Svenningsen, C. S., Peters, B., Bowler, D. E., Dunn, R. R., Bonn, A., & Tøttrup, A. P. (2024). Insect biomass shows a stronger decrease than species richness along urban gradients. *Insect Conservation and Diversity, 17*(2), 182–188. https://doi.org/10.1111/icad.12694

Uhler, J., Redlich, S., Zhang, J., Hothorn, T., Tobisch, C., Ewald, J., Thorn, S., Seibold, S., Mitesser, O., Morinière, J., Bozicevic, V., Benjamin, C. S., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebl, R., Rojas-Botero, S., Rummler, T., … Müller, J. (2021). Relationship of insect biomass and richness with land use along a climate gradient. *Nature Communications, 12*(1), 5946. https://doi.org/10.1038/s41467-021-26181-3

Unterweger, P. A., Klammer, J., Unger, M., & Betz, O. (2018). Insect hibernation on urban green land: A winter-adapted mowing regime as a management tool for insect conservation. *BioRisk, 13*, 1–29. https://doi.org/10.3897/biorisk.13.22316

van Klink, R., Bowler, D. E., Gongalsky, K. B., Shen, M., Swengel, S. R., & Chase, J. M. (2024). Disproportionate declines of formerly abundant species underlie insect loss. *Nature, 628*(8007), 359–364. https://doi.org/10.1038/s41586-023-06861-4

van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., & Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science (New York, N.Y.), 368*(6489), 417–420. https://doi.org/10.1126/science.aax9931

van Strien, A. J., van Swaay, C. A. M., van Strien-van Liempt, W. T. F. H., Poot, M. J. M., & WallisDeVries, M. F. (2019). Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biological Conservation, 234*, 116–122. https://doi.org/10.1016/j.biocon.2019.03.023

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences of the USA, 118*, Article e2023989118. https://doi.org/10.1073/pnas.2023989118

Welti, E. A. R., Zajicek, P., Frenzel, M., Ayasse, M., Bornholdt, T., Buse, J., Classen, A., Dziock, F., Engelmann, R. A., Englmeier, J., Fellendorf, M., Förschler, M. I., Fricke, U., Ganuza, C., Hippke, M., Hoenselaar, G., Kaus-Thiel, A., Kerner, J., Kilian, D., … Haase, P. (2022). Temperature drives variation in flying insect biomass across a German malaise trap network. *Insect Conservation and Diversity, 15*(2), 168–180. https://doi.org/10.1111/icad.12555

Wolda, H. (1988). Insect seasonality: Why? *Annual Review of Ecology and Systematics, 19*, 1–18.