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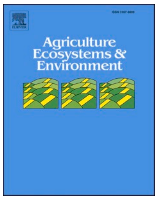

Reducing ploughing promotes ground-nesting flying insects

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ABSTRACT

Many flying insects, such as bees, wasps, and hoverflies, live aboveground, but depend on soil for nesting, development, and overwintering. In agricultural landscapes, soil is managed for production and therefore frequently subjected to disturbances such as ploughing, potentially influencing flying insects during their belowground life stages. To investigate the effects of ploughing on ground-nesting flying insects, we conducted a two-year field experiment in twelve wildflower strips. All strips were ploughed and sown during establishment and were 0, 1, 2 or 3 years old at the start of the experiment. Within wildflower strips, we compared unploughed control plots with adjacent treatment plots that were ploughed between the two sampling years. This design allowed us to assess the ploughing effect across different ages and whether time since establishment influenced insects. We used emergence traps to sample insects emerging from the soil and measured insect biomass, abundance, and body size. We found that ploughing substantially reduced ground-nesting flying insect biomass. When wildflower strips were left unploughed, biomass increased rapidly, particularly during the first years after their establishment. Ploughing consistently reduced insect biomass to equally low levels regardless of how long the wildflower strips had been established. This was driven primarily by declines in the abundance of large insects. Our findings highlight that even moderate reductions in ploughing frequency - for example, only every second year - can benefit ground-nesting flying insects and point to the potential for incorporating reduced ploughing frequencies into agricultural management and agri-environmental schemes.

1. Introduction

Insects are integral to the productivity of global agricultural systems. By providing a multitude of ecosystem services - such as pollination, nutrient cycling or pest control - they contribute directly to agro-economical output and are essential for safeguarding global food security (Dainese et al., 2019; Klein et al., 2007; Losey and Vaughan, 2006; Requier et al., 2022). At the same time, some insects act as important agricultural pests, reducing crop yields worldwide (Deutsch et al., 2018). Conserving insect diversity, abundance, and their beneficial ecological interactions, is therefore not just an ecological priority, but a requirement for sustainable agricultural production. Meeting this requirement depends on managing agricultural landscapes with viable and diverse habitats that provide foraging, nesting, and overwintering resources for insects (Gebert et al., 2024; Pimentel et al., 1992).

Agricultural land is often shaped by management practices such as ploughing, which is carried out to turn over the soil to prepare the seedbed for new cultures or to manage weeds (Soane et al., 2012). While conventional ploughing is usually conducted annually, or sometimes more than once per year, it may be reduced in frequency, or fully abandoned, under different soil management strategies such as short-term, occasional or conservation tillage (Blanco-Canqui and

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Wortmann, 2020; Renton and Flower, 2015). In any case, each ploughing event interrupts the natural succession of plants and alters the structure and layering of the soil (Morris et al., 2010; Pagliai et al., 2004). Ploughing is relevant to the management of wildflower strips, which are often established on agricultural land as part of agri-environmental schemes. After the subsidy period ends, ploughing the wildflower strips is usually required to prepare the soil for subsequent crops. Strips may be ploughed after one flowering season (annual wildflower strips) or left undisturbed for several years before being ploughed again (perennial wildflower strips) (Haaland et al., 2011). Wildflower strips provide habitat for many insects for which soil plays an important role in their life cycle, serving as a habitat for reproduction (i.e., nesting), overwintering (i.e., diapause), and larval development (Boetzl et al., 2022; Lavelle and Spain, 2005; Williams et al., 2024). Ploughing wildflower strips could therefore have detrimental effects on ground-dwelling insects, with effects varying by taxon and body size (Ganser et al., 2019; Kladivko, 2001; Pfiffner and Luka, 2000).

Current knowledge about the effects of disturbance on soil fauna is mostly limited to specific taxa due to the employed sampling method (Moreno-García et al., 2024; Rowen et al., 2020). Soil cores or pitfall traps predominantly target epigean and soil-dwelling taxa of the meso-and macrofauna, such as springtails, nematodes, earthworms or carabid beetles (Müller et al., 2022; Wardle, 1995; but see Pfiffner and Luka, 2000). Most of these species cannot fly and are limited in their capacity to actively disperse and colonize new areas. Using other sampling methods such as sweep netting or pan trapping to sample flying taxa (e.g., Hymenoptera, Coleoptera or Orthoptera) can only detect indirect effects of soil disturbance, for example, those mediated through changes in soil litter structure or weed density and diversity (Stinner and House, 1990). They do not allow a direct assessment of emergence from soil and whether sampled insects are using a particular habitat for nesting (Revilla-Martin et al., 2025; but see Ullmann et al., 2016).

In the present study, we used emergence traps ('e-traps') in a replicated field experiment to investigate the direct effects of spring ploughing and the frequency of ploughing on the biomass of ground-nesting and ground-overwintering flying insects in perennial wildflower strips. We further study how ploughing affects insect abundance and body size and whether changes in abundance or body size predominantly drive the corresponding changes in insect biomass. Insect biomass can be a suitable proxy for the state of an insect community and its capacity to provide ecosystem services, because it reflects abundance, and to a limited extent also species richness (Hallmann et al., 2021; Marini et al., 2025; Winfree et al., 2025). The taxa we targeted spend only parts of their life cycle below ground but disperse, feed, and mate aboveground, typically by means of flying. Because of their increased mobility, they play a key role in ensuring the provision of above-ground ecosystem services such as pollination and pest control (Kremen et al., 2007), the quick recolonization of disturbed habitats (Lundberg and Moberg, 2003) and, as a consequence, the ecological resilience in agricultural landscapes (Tscharntke et al., 2005).

The goal of our research was to assess the impact of a) ploughing, and b) ploughing frequency in wildflower strips, on ground-nesting and ground-overwintering flying insect biomass, and whether these changes are driven by insect abundance and body size.

Based on previous findings that ploughing negatively affects many soil-dwelling arthropod taxa (Müller et al., 2022; Wardle, 1995), we hypothesized that (a) ploughing reduces the biomass and abundance of ground-nesting and ground-overwintering flying insects, with disproportionate effects on larger-bodied species than compared to smaller species (Andrén and Lagerlöf, 1983; Kladivko, 2001). (b) We further hypothesized that insect biomass increases when reducing ploughing frequency, i.e. time since last ploughing (Boetzl et al., 2022). We assumed that insect biomass increases mostly in the first year after ploughing, with a decreasing rate thereafter, reflecting saturating community recovery (Schwerk and Szyszko, 2011) through the continuous provision of undisturbed nesting and overwintering habitat.

2. Materials and methods

2.1. Study area

The study was conducted in 2023 and 2024 in the Upper Rhine Valley, Baden-Württemberg, Germany. The study region (~200 m altitude) includes the flat Rhine plain with deep gravel soils and the hilly Tuniberg and Kaiserstuhl, shaped by loess deposits on volcanic bedrock. It has a sub-Atlantic climate influenced by maritime and continental air masses. With a mean annual temperature of ~10 ℃, it is among Central Europe's warmest regions; monthly maxima often exceed 30 ℃ in summer. Annual precipitation ranges between 600 and 700 mm, with up to 70 frost days. Land use is dominated by intensive arable farming (e.g., maize, sugar beet, cereals, rapeseed) and various specialty or permanent crops (e.g., asparagus, strawberries, tobacco, vineyards, stone fruits, hops); grasslands are of minor importance.

2.2. Experimental design

We established our experiment in early spring 2023 on three conventional farms. We used 12 wildflower strips covering areas ranging from 0.13 to 0.55 ha (mean = 0.25, SD = 0.12) and located 0.03–17.23 km apart (mean = 8.77, SD = 7.09) (see Figure S1 for wildflower strip locations). Seven of the 12 wildflower strips had already been managed as wildflower strips for up to three years, whereas the other five were newly established on land that had previously been under arable production (corn and wheat). At the end of March 2023, these new wildflower strips were established in the same way as the existing strips, i.e., the soil was ploughed to a depth of 20–25 cm using a conventional mouldboard plough and then sown with a perennial wildflower seed mix using a power-harrow seed drill. Each of the 12 wildflower strips was then divided into a control plot and an adjacent treatment plot. In 2023, all plots were treated identically and left unploughed to establish the baseline ("before") condition of a before–after–control–impact (BACI) design. In January and February 2024, the treatment plots in the wildflower strips were ploughed while the control plots remained unploughed, constituting the "after" condition of the BACI design. Two exceptions occurred: Treatment plots on wildflower strips 11 and 12, which were already three years old at the start of the experiment, were ploughed in May 2023. In addition, wildflower strip 3 was not ploughed due to miscommunication with the farmer and therefore served only as a control plot in 2024 (see Table S2b). Ploughing of treatment plots was carried out in the same way as for wildflower strip establishment, i.e., to a depth of 20–25 cm using a conventional mouldboard plough. The only difference was that the ploughed treatment plots were then left fallow, i.e., not resown, as we assumed that sowing would not affect already in-the-ground overwintering insects and their emergence into our traps. Treatment plots were thus ploughed after one, two, or three years after wildflower strip establishment (see Table S2a for an overview and the number of replicates). Control plots remained unploughed for one to five years, thus representing the full five-year cycle of perennial wildflower schemes typical of the study region. By comparing control and treatment plots and accounting for the time since wildflower strip establishment, we were able to study the impact of a) ploughing, and b) ploughing frequency. Our variable 'time since (wildflower strip) establishment' counts the number of years that have passed since the wildflower strips were established and is therefore '0 years' in the year of establishment. Different ploughing frequencies were then analysed by comparing the effects of ploughing after one, two or three years since wildflower strip establishment.

2.3. Insect sampling

Insect sampling took place in 2023 and 2024. We used custom-built emergence traps (e-traps) to sample ground-nesting insects on control and treatment plots. E-traps are a suitable passive method for non-specific sampling of insects at their place of nesting or overwintering. Here, we use the term ‘ground-nesting’ synonymous to ‘overwintering’ but acknowledge that collected individuals may have emerged from an overwintering place that is not necessarily a nest *sensu stricto* (i.e., the place of reproduction; see, e.g., Westrich, 2018). Typically, the method is biased towards flying taxa due to the elevated position of the collection unit (Hellerich et al., 2025). While e-traps have been used for a variety of research questions related to arthropod nesting and overwintering (Boetzl et al., 2022), e-trap studies on ploughing effects are rare (Funderburk et al., 1983; Ganser et al., 2019; Hanson et al., 2015; Holland and Reynolds, 2003; Thorbek and Bilde, 2004).

E-traps consisted of conventional hiking tents from which the ground floor was removed and which covered ca. 2.2 m^2 of ground per trap. Collection units were installed on top of the traps, each filled with 100 ml of a preservative solution (40% Ethanol, 10% Glycerine, odour-free dish soap) to kill and preserve specimens while minimizing evaporation loss (see Hellerich et al., 2025 for a full description of the e-trap method).

In each plot, we placed two transects, each with four e-traps, for a total of eight e-traps per plot. Transects were oriented along the plot length and centred laterally, with a 6 m separation between them. Each transect spanned the full length of the plot, except for 3 m at each end to maintain the same edge distance. As transect lengths varied between wildflower strips, we divided each transect into three sub-transects of equal length, with their ends marking the trap positions (see Fig. 1). In 2023, 160 e-traps were installed between April and May and remained at the same place for an average of 99 days (SD = 19 days). In 2024, 208 e-traps were installed in March and were in place for an average of 128 days (SD = 1 day). In that year, traps were positioned 2 m laterally to the right of their previous positions to avoid resampling ground areas covered by traps during the previous season. E-traps in the control and treatment plots were always installed on the same day and remained active for the same duration within each wildflower strip, except at the two strips that were partly ploughed in 2023. At these strips, traps were installed in April on the control plots, whereas installation on the treatment plots occurred in May, immediately after ploughing. The number of traps varied between the two years because two wildflower strips were only sampled in 2024 due to miscommunication with the farmer and logistical constraints, four additional control plots were newly created by splitting four existing control plots, and the two treatment plots that were ploughed in 2023 were discontinued (see Table S2b). For e-trap installation, the ground was cleared of vegetation and plant litter using an electric hedge mower and a rake, and the vegetation inside the e-traps was regularly trimmed throughout the season. E-traps were emptied every second week (14.2 days, SD = 1.5 days) by replacing the collection unit liquid.

2.4. Insect biomass assessment

Biomass of sampled insects was measured in a moist state to preserve samples for future analyses, following a standardized protocol (Hallmann et al., 2017). First, sampled insects were emptied into a stainless-steel sieve (1 mm mesh size). The contents of the sieve were shaken out onto a paper towel and spread out to remove any adhering liquid. Any non-arthropod species (e.g., Gastropods) were removed from the sample. Subsequently, the still-moist sample was weighed to the nearest 1 mg using an analytical precision scale (Kern ADJ 200–4) and then stored in Scheerpelz solution (70% Ethanol, 5% acetic acid). To standardize for sampling effort, insect biomass data were divided by the number of days in each sampling round.

We observed episodic mass-occurrence samples dominated by a single species, typically clustered ant nuptial flights in July. Because these events represent short-term dispersal swarms rather than local ground-nesting insect dynamics, we treated them as a distinct ‘outbreak’ process. Outbreaks were defined as > 100 individuals < 5 mm or > 50 individuals ≥ 5 mm of a single species; such cases were visually obvious outliers, with abundances orders of magnitude above typical samples. In

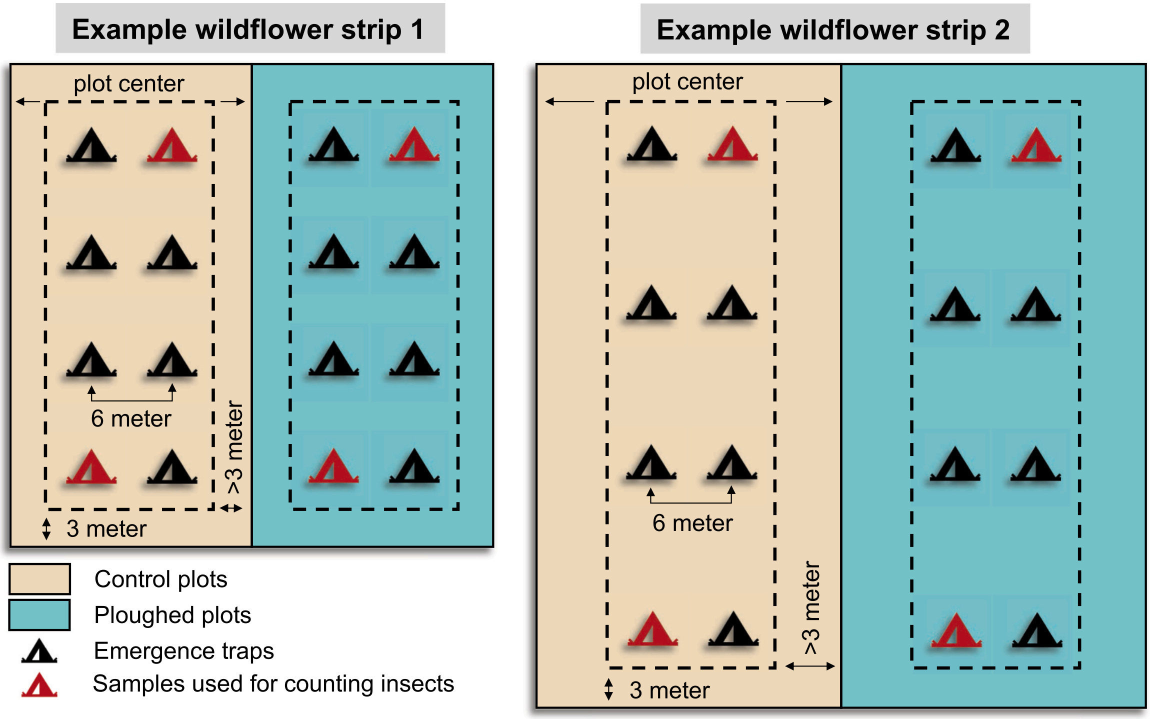

Fig. 1. Schematic figure illustrating e-trap placement (symbols) in control and ploughed plots on two example wildflower strips (1 and 2) of different size. Each plot contained two transects with four e-traps each (eight traps per plot). Transects started at an edge distance of 3 m and were divided into three equal sub-transects, with trap positions located at their four endpoints, to account for variation in site length. In 2024, traps were installed 2 m laterally to the right to their positions in the previous year. For the 2024 measuring and counting of insects, we selected the samples of two of the eight e-traps per plot (red symbols).

total, 144 samples met this criterion and were excluded prior to modelling (retained n = 2847). For transparency, we provide the models including all samples in the supplementary material (Table S3b, Table S3c2); treatment effects remained qualitatively similar, but variance-related tests became significant due to the influence of a few extreme values.

2.5. *Insect abundance and body size assessment*

To analyse the effects of ploughing on insect abundance and body size, individuals of a subset of samples in 2024 were categorized by body size (small <5 mm or large ≥5 mm) using millimetre paper and counted separately. Body size was measured without antennae and ovipositors. For each sampling round, we measured and counted all individuals collected in the first e-trap of the left transect and the last e-trap of the right transect, in each plot (n = 336; see Fig. 1). Ten of these samples were excluded prior to the analysis due to mass-occurrences (see above). To standardize for sampling effort and to align with the insect biomass data, insect abundance data were divided by the number of days in each sampling round. Due to the expected high numbers of individuals, no systematic taxonomic assessments were performed, but the most abundant taxonomic groups were noted qualitatively to provide an overview of the sampled arthropods. These included taxa from various insect families, with only minor contributions from non-insect taxa like Araneae and Acari. Among the larger insects, ground-nesting or ground-overwintering Hymenoptera (e.g., Vespoidea, Apoidea, Ichneumonidae), Diptera (e.g., Limoniidae, Tipulidae, and various Brachycera), and Lepidoptera as well as several families of Coleoptera (e.g., Cantharidae, Curculionidae, Carabidae, Oedemeridae), Orthoptera, and Dermaptera were observed. For the smaller species, various above- and belowground nesting families of Diptera (e.g., Sciaridae, Drosophilidae), Hemiptera (mainly Sternorrhyncha such as Aphididae, and Auchenorrhyncha), and small Coleoptera and Hymenoptera were observed.

2.6. *Statistical analysis*

All analyses were performed using R 4.4.1 (Core Team. 2024). The effects of ploughing and of reduced ploughing frequency on ground-nesting insect biomass were assessed using a generalized linear mixed model (hereafter called ‘insect biomass model’) in the ‘glmmTMB’ package (Brooks et al., 2017). To assess how ploughing affected insect biomass indirectly via changes in insect abundance and body size, a structural equation model (SEM) was fitted in the ‘piecewiseSEM’ package (Lefcheck, 2016) on a subset of data where individuals were counted.

2.6.1. *Insect biomass model*

The insect biomass model included daily insect biomass as the response variable (see Suppl. 3a for the model term and diagnostics). Predictors (fixed effects) were the time since wildflower strip establishment (in years), ploughing, sampling year, and Julian day. ‘Trap’ nested within (wildflower) ‘strip’ were included as nested random factors. The insect biomass model was fitted using a Gamma-distribution with a log-link. The best model was selected using residual diagnostics of the ‘DHARMa’ package (Hartig, 2024), Akaikes information criterion (AIC) and likelihood-ratio-tests of the ‘stats’ package (Core Team. 2024). Model performance was assessed using the root-mean square error (lower RMSE indicated better accuracy) and marginal and conditional R^2 in the ‘performance’ package (Lüdecke et al., 2021). Based on our hypothesis of a saturating recovery with time since establishment, we modelled this predictor using an inverse function (1 / time since establishment). While inclusion of the inverse function did not significantly improve model performance (Δ RMSE < 0.001), residual diagnostics indicated better model fit: the model without the inverse function for time since establishment showed significant deviation from residual uniformity (DHARMa KS test), whereas the model with the inverse function did not. Similarly, because seasonal dynamics often exhibit unimodal patterns (Forrest and Miller-Rushing, 2010), we modelled Julian day as a quadratic polynomial term, which significantly improved model fit (‘Chisq’-test: $p < 0.001$) compared to linear alternatives. Including wildflower strip patch size as a fixed effect did not improve model fit (Δ AIC < 2, ‘Chisq’-test: $p = 0.72$) and showed no significant effect on insect biomass (estimate = 0.03, ±0.09 SE, $p = 0.72$), and was therefore excluded to maintain model parsimony. We also tested the inclusion of wildflower strip-level random slopes for Julian day to allow seasonal biomass trends to vary among wildflower strips. These random slopes were not retained because they produced near-singular correlations among random effects (r = -0.96), indicating model overparameterization. Importantly, their inclusion did not change the direction and significance of fixed effects.

2.6.2. *Post-hoc analysis for the insect biomass model*

For the post-hoc analysis following fitting of the insect biomass model, we computed pairwise contrasts using the ‘emmeans’ package (Lenth, 2017), allowing estimation of percentage changes between control and ploughed plots and across different times since wildflower strip establishment. To illustrate insect biomass accumulation across the season (Fig. 4), we used the fitted model to predict marginal means for daily insect biomass per each Julian day (93−216) and treatment, and calculated the cumulative sum of these predictions.

2.6.3. *Structural equation model (SEM)*

The SEM model followed a bottom-up pathway with ‘ploughing’, ‘Julian day’ and ‘time since establishment’ influencing the top response ‘daily insect biomass’ directly and indirectly through their effects on the two mediating variables ‘daily abundance of small insects’ and ‘daily abundance of large insects’. The SEM comprised three component models: two separate models for each mediating variable and a third model for the top response variable (see Suppl. 3c for R model terms). To account for both direct and indirect effects, the top model included all upstream predictors and mediators as explanatory variables, except for ‘time since establishment’, which was dropped from the main model to avoid overparameterization (i.e., a saturated model with zero degrees of freedom). Its effects were captured through the mediator models. All component models included ‘trap’ nested in (wildflower) ‘strip‘ as random effects. The top response model (daily insect biomass) was fitted using a gaussian distribution on the log-transformed response; due to the presence of zeroes, the two response variables for the small and large insect abundance models were transformed using ln(1+x) ('log1p') to fit a gaussian distribution in each model. All numeric variables were centred around their mean at zero (‘scale’-function of the R ‘base’ package) to ensure interpretability of parameter estimates; the factorial ploughing variable (0 = unploughed, 1 = ploughed) was transformed to numeric values to enable inclusion in the SEM but left unscaled to preserve its categorical interpretation and maintain reference-level meaning. A covariance path between daily large and small insect abundance was added to the SEM to account for their non-independence.

3. Results

We analysed a total of 2847 e-trap biomass samples taken during the two study years. Standardized daily insect biomass ranged between 0.07 and 365.22 mg (mean = 32.48, SD = 39.71). In 2024, we counted 63507 individuals in a subset of samples (n = 326), of which 59007 (92.91%) belonged to the small group and 4500 (7.09%) to the large group. Standardized daily insect counts ranged from 0.07 to 145 insects (mean = 13.70, SD = 19.30).

3.1. *Effects of ploughing*

3.1.1. *Insect biomass*

Ploughing negatively affected biomass of ground-nesting flying insects (insect biomass model: estimate = −1.21, ±0.16 SE, $p < 0.001$; $R^2_{marginal} = 0.37$). Daily insect biomass was on average 62.52% (±9.99% SE) lower on ploughed plots (i.e., 37.48% of the daily insect biomass on control plots) than on unploughed plots regardless of time elapsed since the establishment of the wildflower strips and the Julian day, which reflects the season (see Fig. 2b and Table S3a).

3.1.2. Abundance and body size

The abundance of small and large insects had an approximately equal share in the total insect biomass (SEM biomass model: small insects: std. estimate = 0.45, ±0.03 SE, $p < 0.001$; large insects: std. estimate = 0.47, ±0.03 SE, $p < 0.001$; $R^2_{marginal} = 0.78$; see Fig. 3 and Table S3c1). The observed reduction of daily insect biomass after ploughing was only mediated by the significant reduction in the daily number of large insects (SEM large insects count model: std. estimate = −0.44, ±0.12 SE, $p < 0.001$; $R^2_{marginal} = 0.33$; see Fig. 3). The model did not indicate an effect of ploughing on small individuals (SEM small insects count model: std. estimate = −0.15, ±0.16 SE, $p = 0.06$; $R^2_{marginal} = 0.14$), but ploughing had a direct negative effect on daily insect biomass (SEM biomass model: std. estimate = −0.09, ±0.08 SE, $p = 0.02$).

3.1.3. Variation by season (Julian day)

The effect of ploughing on the daily biomass of ground-nesting flying insects significantly varied by Julian day and increased over the season (insect biomass model: estimate (quadratic term) = 11.72, ±1.83 SE, $p < 0.001$). Insect biomass accumulated more quickly on control plots than on ploughed plots (see Fig. 4), highlighting the effect of spring ploughing throughout the season, resulting in a larger difference of biomass between ploughed and unploughed plots later in the season than earlier. Both the abundance of large and small insects increased with Julian day (SEM large insects count model: std. estimate = 0.35, ±0.04 SE, $p < 0.001$; SEM small insects count model: std. estimate = 0.34, ±0.04 SE, $p < 0.001$; see Fig. 3).

3.2. Effects of ploughing frequency

3.2.1. Insect biomass

Daily insect biomass increased progressively on unploughed control plots with increasing time since wildflower strip establishment (insect biomass model, modelled as 1/time since establishment: estimate = −1.86, ±0.50 SE, $p < 0.001$). However, the increase was strongest in the first years (year 1: +55.69%, ±31.19% SE; year 2: +15.90%, ±10.40% SE) and is expected to reach a plateau with no further increase after more than four years without ploughing (see Fig. 2a; see Figure S4 for variability between wildflower strips). Due to the significant positive interaction with sampling year (estimate = 1.96, ±0.56 SE, $p < 0.001$), the effect of time since establishment was largely offset in 2024. In this year, overall insect biomass was significantly lower than in 2023 (estimate = −1.04, ±0.16 SE, $p < 0.001$).

3.2.2. Ploughing effect

While insect biomass increased with time since wildflower strip establishment, it was reduced to a consistently low level once wildflower strips were ploughed, which was indicated by the significant interaction between ploughing and the inverse function of time since establishment (estimate = 1.26, ±0.38 SE, $p < 0.001$). As a result, ploughing had a greater effect on insect biomass on older wildflower strips (year 3: −67.42%, ±8.22% SE) compared to younger wildflower strips (year 1: −55.33%, ±7.24% SE, see Fig. 2a). Ploughing always ‘reset’ insect biomass to the same low level compared to control plots left unploughed, and the ploughed curve (Fig. 2a) thus resembles the circumstances in intensive agricultural fields which are ploughed annually (i.e., once every year).

3.2.3. Abundance and body size

Time since establishment did not affect the daily abundance of either small or large insects in 2024 (SEM small insect count model: z = 0.38, $p = 0.71$; SEM large insect count model: z = 1.12, $p = 0.26$).

4. Discussion

Conventional mouldboard spring ploughing consistently resets ground-nesting flying insect emergence in wildflower strips, regardless of how many years have passed since the previous spring ploughing event. Larger insects (≥5 mm) are most strongly affected. A reduction in spring ploughing frequency increases insect emergence, particularly later in the season. To enhance insect abundance and support ecosystem service provision, ploughing should be minimised, and where ploughing is necessary, reducing its frequency to once every two years (biennial ploughing) can already largely mitigate its negative effects.

Our findings provide novel insights into the ground nesting and overwintering dynamics of flying insects. For this study, we deployed a

Fig. 2. a) Emerging insect biomass increases after wildflower strip establishment (Control plots), but is reduced by ploughing of one-, two- or three-year old wildflower strips (Ploughed plots). Model predictions (lines), standard errors of the mean (ribbons) and raw data (points) are shown. **b)** Overall effect of ploughing on insect biomass, pooling data across years. Predictions for means of control plots (circle) and ploughed plots (triangles) and standard errors of the means (error bars) are given; points show raw data. For both figures, the y-axis values were transformed using an inverse hyperbolic sine (‘asinh’) to improve interpretability.

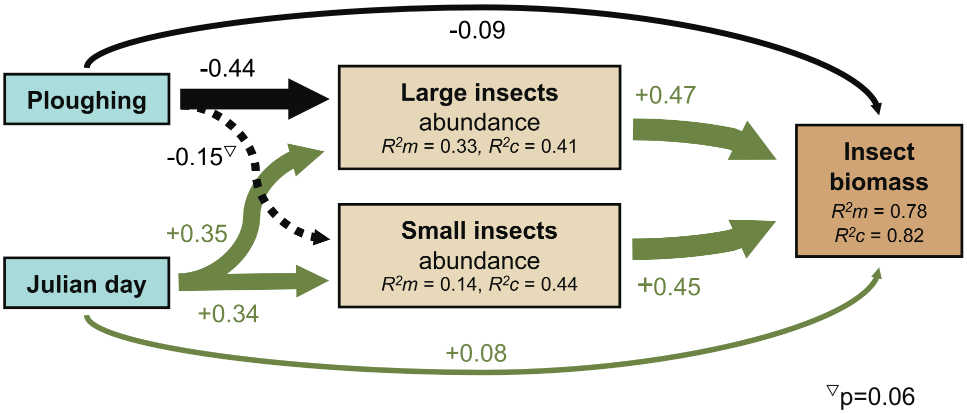

Fig. 3. Structural equation model (SEM) results. The arrows show positive (green) direct and indirect effects of Julian day via large and small insect abundance on insect biomass and negative (black) direct and indirect effects of ploughing on insect biomass. Ploughing reduced large insect abundance which indirectly reduced insect biomass. Only significant effects are shown, except for the non-significant effect of ploughing on small insect abundance (dashed line). The amount of variation explained by each model is indicated by the R^2m (Marginal R^2) and $R2c$ (Conditional R^2) values. The width of the arrows corresponds to the effect strength.

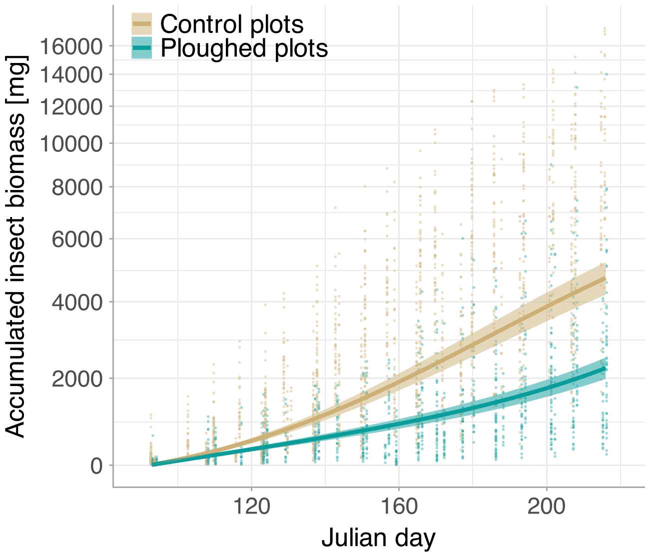

Fig. 4. Accumulation of insect biomass over the season on control plots and ploughed plots. Model predictions (lines) and standard errors of the mean (ribbons). The y-axis values were transformed using an inverse hyperbolic sine (‘asinh’) to improve interpretability.

low-cost and highly replicable type of emergence trap, which generated high-quality data allowing us to directly link collected individuals to their ground nesting and overwintering habitat. Because most of the sampled taxa are highly mobile, such direct links cannot typically be established with other flying insects sampling methods. We therefore encourage future ecological field studies to make use of this approach.

4.1. Effects of ploughing on insect biomass, abundance, and body size

Ploughing of wildflower strips effectively resets the biomass of ground-nesting flying insects to equally low baseline levels at any time, even after several years without ploughing. Our results therefore highlight the profound negative direct effect of ploughing on flying insects that were present in the soil in adult or preimaginal stage during ploughing. Previous studies have shown that ploughing negatively affects organisms adapted to living entirely in or on the ground, such as earthworms or carabid beetles (Wardle, 1995). Our findings demonstrate that insects with both below-ground and flying life stages, such as bees, flies, wasps, and moths, are similarly impacted, underscoring that ploughing can disrupt a wide range of insect functional groups beyond exclusively soil-dwelling taxa. Our observed reduction in insect biomass following annual (i.e., after one year) ploughing (-55%) also closely matches previous findings by Ganser et al. (2019), who reported a similar reduction in overwintering epigeous and flying arthropod abundance after ploughing of annual wildflower strips (-59%). As we have also found a link between insect abundance and biomass, the close similarity between findings reinforces evidence for the negative impact of ploughing on ground-nesting insects and suggests that insect biomass is a suitable proxy for insect abundance (Gebert et al., 2024; Vereecken et al., 2021).

At initial wildflower strip establishment - with site ploughing to prepare the seedbed - insect biomass showed higher variance compared to plots that were ploughed after one, two or three years of establishment. This contradicts the idea that ploughing always ‘resets’ insect biomass to the same level but indicates that previous land use and management and the resulting species assemblages may have influenced the effect of ploughing (Hendrix et al., 1986; House and Alzugaray, 1989). A potential explanation was given by the SEM, which showed that both small and large insect abundance contributed equally to insect biomass on wildflower strips that had remained unploughed for more than one year. Annually ploughed wildflower strips however may host a larger abundance of smaller species at lower trophic levels that are adapted to the level of disturbance generated by ploughing (Andrén and Lagerlöf, 1983; House and Alzugaray, 1989; Kennedy et al., 2013). Life history traits such as short generation times or resistant resting stages may make them less vulnerable to - or even benefit from the disturbance (Andrén and Lagerlöf, 1983; Wardle, 1995). Our results also show the importance of larger insects on older wildflower strips by showing that the negative effect of ploughing on insect biomass was mediated through reduced abundance of large insects, also supporting previous findings that larger species are more vulnerable to ploughing (Kladivko, 2001; Müller et al., 2022; Wardle, 1995). In addition, our results revealed a direct effect of ploughing on insect biomass independent of insect abundance, indicating that ploughing also lowered the mean body weight of remaining individuals. Ploughed plots therefore may have contained proportionally more smaller insects, a size shift that was not captured by our broad size categories.

4.2. Insect responses to reduced ploughing frequency

Many studies have examined the immediate effects of ploughing, or its effects several years later (Boetzl et al., 2022; Ganser et al., 2019; Wardle, 1995), yet little is known about the dynamics of soil fauna development in the years after ploughing. We observed the strongest increases in insect biomass particularly within the first few years of wildflower strip establishment. Our results indicate that even a moderate reduction in ploughing frequency by just 1–2 years can promote the rapid recovery of insect communities. Extending previous findings on how temporal continuity of habitats can influence ground-nesting, overwintering and succession of arthropods (Boetzl et al., 2022; Schwerk and Szyszko, 2011), our study shows in particular that these effects may be non-linear and saturating, i.e. initially increasing after disturbance but then plateauing over time.

Besides the direct effect of ploughing through mechanical intervention, indirect effects may have contributed to the observed non-linear development of insect biomass. Ploughing can alter soil environmental conditions by relocating and reducing biomass, interrupting litter accumulation and access to food resources (Andersen, 2003; Andrén and Lagerlöf, 1983; Müller et al., 2022) or changing soil microclimate leading to drying out of the soil (House and Alzugaray, 1989). It can also cause alteration to soil and aboveground food webs, for example by affecting slugs and earthworm abundance that serve as prey for predator species (Kennedy et al., 2013; Pelosi et al., 2009). Such consequences may be only present immediately after ploughing (e.g., bare soil) or diminish quickly within the following years (e.g., prey availability). In contrast, indirect effects may have also contributed to the rapid increase of insect biomass in the first year after ploughing by promoting influx and establishment of more mobile species, which can colonize bare ground areas from adjacent areas rapidly, while the establishment of less mobile species, such as many epigean and soil-dwelling taxa, may be delayed (House and Stinner, 1983). As time since establishment increases, shifts in the composition and abundance of natural enemies may have increased food web complexity, with variable effects on insect biomass development (Boetzl et al., 2022; Finke and Denno, 2004; Jachowicz and Sigsgaard, 2025).

The increasing magnitude of the ploughing effect over time, along with the strong influence of large insects on the ploughing effect, suggests that older wildflower strips hosted comparatively larger, more plough-sensitive species. This pattern implies that both time since establishment and ploughing shape insect abundance as well as species composition (Kennedy et al., 2013). However, we did not find significant temporal changes in the abundance of either small or large insects. The strongest increase in insect biomass was observed during the first year after wildflower strip establishment, but no new wildflower strips were established in 2024; thus, this effect was not represented in the data. Moreover, interannual variation in spring weather, particularly higher precipitation during peak emergence in April and May, likely contributed to annual variability in insect emergence. Together, the absence of first-year wildflower strip effects and the influence of weather conditions, which may be strong drivers of insect biomass fluctuations (Müller et al., 2024), help explain the lack of temporal changes in insect abundance and the significantly lower overall biomass in 2024.

4.3. Ecosystem service provision may benefit from reduced ploughing frequency across management types

The higher insect biomass observed on older wildflower strips, along with the strong negative effect of ploughing on biomass and abundance of large insects may be linked to changes in the provision of important aboveground ecosystem services, such as pollination, pest control or genetic dispersion (Kremen et al., 2007; Winfree et al., 2025). Most sampled taxa belonged to highly mobile groups such as Hymenoptera, Diptera, Lepidoptera or flying Coleoptera, which provide such services due to their dependency on aboveground food resources such as nectar and pollen of flowers, seeds, fruits or other insects (for predators and parasitoids). Various studies indeed suggest that reduced soil management can increase the numbers of pollinators and natural enemies (Appenfeller et al., 2022; Shuler et al., 2005; Stinner and House, 1990), whereas the number of arthropod pests has not been shown to increase under reduced soil management (Rowen et al., 2020). Our findings thus indicate that annual ploughing not only suppresses insect biomass, but may also diminish the delivery of ecosystem services across agricultural landscapes.

We could show that spring ploughing has fundamental negative effects on ground-nesting flying insects, while reducing ploughing frequency can promote rapid, non-linear increases in insect emergence. Ploughing is often an important part of farm management; decisions about when to work the soil depend on agronomic, economic and environmental conditions and may not always align with the requirements for agri-environmental schemes such as wildflower strips. Yet, we show that even small adjustments in the soil management of wildflower strips may have disproportionally large ecological benefits. Based on our findings, ploughing wildflower strips only after two flowering seasons (biennial wildflower strips) rather than after a single season (annual wildflower strips) would already substantially increase flying insect soil emergence in the second year. Moreover, strategical placement of wildflower strips within the landscape and alternation of the year of ploughing among adjacent wildflower strips may not only help enhance the dispersal of emerging flying insects, supporting their populations over time by providing undisturbed nesting ground (Häussler et al., 2017; Williams et al., 2024), but may also improve ecosystem service provision and yield (Albrecht et al., 2020; Poveda et al., 2025). However, it remains unclear to what extend the availability of suitable nesting habitats is limiting flying insect populations (Baden-Böhm et al., 2023).

Because insect occurrence is influenced by crop cover, agrochemical inputs, and management strategies (Appenfeller et al., 2022; Betancur-Corredor et al., 2022; Tschanz et al., 2023), the extent of the effects of ploughing and ploughing frequency may vary between wildflower strips and arable fields. Nevertheless, our findings suggest that the underlying direct and indirect mechanisms of ploughing remain consistent across management systems. As a result, similar ecological responses emerge even when site-specific conditions differ (Pfiffner and Luka, 2000). Besides underscoring the importance of maintaining undisturbed habitats within agricultural landscapes to support ground-nesting insects and associated ecosystem services, our findings highlight the ecological benefits of even short-term ploughing abatement (1–2 years), emphasizing the potential of short-term, flexible and still effective measures in agri-environmental policy and management.

CRediT authorship contribution statement

Michael Garratt: Writing – review & editing, Conceptualization. **Alexandra-Maria Klein:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **Christopher Hellerich:** Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Felix Fornoff:** Writing – review & editing, Validation, Project administration, Methodology, Conceptualization. **Anne-Christine Mupepele:** Writing – review & editing, Validation, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT (OpenAI) in order to improve the language, grammar, spelling and overall readability. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110399.

Data availability

I have shared the link to my data/code at the Attach file step Data and R-Code for the Publication (Figshare)

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