Agriculture, Ecosystems and Environment 378 (2025) 109298

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Arthropod abundance is most strongly driven by crop and semi-natural habitat type rather than management in an intensive agricultural landscape in the Netherlands

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ARTICLE INFO

Keywords:
Arthropods
Agriculture
Semi-natural habitats
Management

ABSTRACT

The intensification of agriculture has been identified as one of the main causes of arthropod declines. To halt the decline of arthropods, changes in farming practices and management of surrounding habitats may therefore be needed. A key challenge is to identify which changes in management approaches are most effective in restoring biodiversity. Therefore, this study examines arthropod abundance and diversity in different agricultural and semi-natural habitats, and among different management types. Arthropods were sampled three times in spring and summer of 2022 and 2023 with emergence traps in 128 unique sites in an intensively farmed area in Western Netherlands. These sites included a variety of crops as well as semi-natural habitats. Our study showed that on average the abundance and diversity of arthropods of several taxa was lower in crop habitats compared to semi-natural habitats. However, these effects strongly varied among crop species. For instance, alfalfa, spelt, spring and winter wheat fields (that often had a high plant cover) supported similar arthropod diversity and abundance levels as semi-natural habitats. Interestingly, in crop fields most variables related to field management, such as herbicide applications or amount of nitrogen fertilizers, did not show any significant relationship with arthropod abundances or diversity. The number of days after cultivation was an exception, and was positively related to total arthropod abundance, Hymenoptera and Collembola abundances, and Coleoptera family diversity. Within semi-natural habitats, number of days after mowing was positively related to total arthropod abundance, Diptera, Hemiptera and Hymenoptera abundances, and Hemiptera family diversity. Additionally, plant cover was positively related to total arthropod abundance. Overall, our findings suggest that crop species and management practices that increase plant cover in spring and early summer are increasing arthropod abundance and, to a lesser extent, higher-taxa diversity in intensively farmed agricultural landscapes.

1. Introduction

During the last decades there has been a major decrease of biodiversity worldwide (Butchart et al., 2004; Hoffmann et al., 2011; van Klink et al., 2020). This decline is also very apparent in the abundances and diversity of insects and other arthropods (Hallmann et al., 2017; Lister and Garcia, 2018; Seibold et al., 2019). However, only in recent years this group of animals has been receiving more academic attention (Wagner, 2020). It is generally implied that one of the major drivers responsible for the decline of insects is the intensification of agriculture (Seibold et al., 2019; van Klink et al., 2020), which comprises the use of synthetic pesticides, fertilizers, intensive monocultures, increased field size and reduction of semi-natural areas, which leads to landscape simplification (Dudley and Alexander, 2017; Sánchez-Bayo and Wyckhuys, 2019). This is of a great concern because arthropods play a pivotal role in the food chain. Specifically, yield of insect-pollinated crops relies at least partially on pollination by wild insects (Garibaldi et al., 2013), and natural enemies predate or parasitize crop pests, often preventing crop damage without the use of costly and environmentally harmful pesticides (Bianchi et al., 2006).

In agricultural landscapes there are two classes of land-use and both affect insect communities in different ways. Semi-natural habitats are areas that were generally used for agriculture in the past, but were transformed or maintained in conditions similar to those found in purely

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https://doi.org/10.1016/j.agee.2024.109298
Received 4 June 2024; Received in revised form 13 August 2024; Accepted 10 September 2024

natural ecosystems, thus currently are primarily biodiversity-promoting and non-commercial. Such habitats are green the whole-year round for several consecutive years without intensive management such as ploughing. Therefore, semi-natural habitats provide perennial habitat, more diverse plant communities and hence resources throughout the entire year (Sarthou et al., 2014; Álvarez et al., 2019; Guo et al., 2022) and are generally found to have a positive impact on arthropods regardless of the type of semi-natural habitat (Fijen et al., 2024). Crop fields can be defined as intensively managed fields, where a crop is grown generally for commercial purposes. Typically these fields are ploughed at least annually and other management practices may be carried out, such as fertilizer or herbicide applications. These fields are inhospitable to most arthropods during parts of the year, yet they do provide a lot of resources during specific periods and many arthropod species capitalize on them by colonizing crop fields from nearby non-productive landscape elements after cultivation (Ryszkowski and Karg, 2007).

Crop fields as well as most semi-natural habitats within agricultural landscapes, are managed in ways that may strongly drive the diversity and abundances of arthropods. Within semi-natural habitats, management practices generally comprise different cutting or mowing regimes of the herbaceous or woody vegetation. Mowing often has an immediate negative effect through direct mortality of arthropods that live in the vegetation (Humbert et al., 2010), as well as longer-term negative effects on certain taxa like Hemiptera, Orthoptera and Lepidoptera, since it removes shelter and food sources (Valtonen et al., 2006; Proske et al., 2022; Steidle et al., 2022). Meanwhile, other taxa might not be strongly impacted by mowing, like Diptera (Proske et al., 2022). On arable land, arthropods could be affected by a variety of practices, like tillage, fertilizer or agro-chemical applications or harvesting. For instance, fertilizer applications in winter wheat can have significant positive effects on rove beetles, negative effects on wolf spiders and no effect on carabid beetles (Gagic et al., 2017), while reductions of agro-chemical usage can allow the re-establishment of natural enemies that provide natural pest control (Roubos et al., 2014). While these management activities have been shown to affect the abundances or diversity of certain arthropod groups (Holzschuh et al., 2007; Gagic et al., 2017), it remains largely unclear what is the relative strength by which these management activities affect arthropod diversity, and how this varies among different arthropod groups.

Agri-environment schemes represent the main instrument to counter the decline of insects and other fauna in European agricultural landscapes and they target both productive and non-productive land. Some agri-environment schemes prescribe measures that aim to strengthen the semi-natural components of agroecosystems (Science for Environment Policy, 2017) by, for instance, converting arable land into extensive grasslands, hedges or grass or wildflower strips. The establishment of grass and wildflower strips on crop fields has been shown to almost invariably positively influence the abundance of wild pollinators (Scheper et al., 2013). Agri-environment schemes that target productive land generally prescribe reducing management intensity, for example by restricting fertilizer and pesticide inputs, delaying the first agricultural activities, or prescribing organic farming. There is mixed evidence for positive effects of such agri-environment schemes (Kleijn et al., 2006), although schemes on non-productive land seem to be more effective than on productive land (Batáry et al., 2015).

To get a better understanding of how agricultural land-use affects arthropods, and what this means for agri-environment scheme design, there is a need to analyse how the entire agroecosystem affects arthropods. Such an approach should consider semi-natural habitats as well as productive land and include management practices in the analyses (Hole et al., 2005; Steingröver et al., 2010). Previous studies have primarily focused on specific taxa, such as spiders and beetles, as well as particular crops and habitats, like oilseed rape fields and grassy field margins (Labruyere et al., 2016; Li et al., 2018). This limited scope has left the impact of management practices on other arthropod groups largely unexplored, so that we have limited understanding on whether optimal management for one taxonomic group is also beneficial for other groups. Furthermore, while some research has examined various agricultural habitats, it often targets specific groups of arthropod (Holzschuh et al., 2007; Hanson et al., 2017), restricting our understanding of overall biodiversity. Consequently, the effects of agricultural practices, such as fertilizer and herbicide use, on a wide range of arthropods remain unclear. Understanding these impacts is essential for developing effective biodiversity conservation and restoration practices in farmland systems (Hole et al., 2005).

In this study we examine the relative importance of semi-natural and farmed habitats for maintaining abundant arthropod populations and analyse whether management practices can explain these differences. First, we studied the relative importance of crop fields in general and specific crop types compared to semi-natural habitats for arthropod diversity and abundance, within a landscape with nature-based management. Second, we tested how management explains variation in arthropod biodiversity and abundances in crop fields. Third, we tested how management explains variation in arthropod biodiversity and abundances in semi-natural habitats. We hypothesised that semi-natural habitats overall would show higher arthropod abundance and diversity compared to crop fields. Additionally, different groups of arthropods will respond differently to the different crop types. Regarding management in crop fields, we expected that this response might be caused not by type of crop, but by management practices. More specifically we expect that fertilizers will increase the overall abundance of arthropods (Birkhofer et al., 2008; Kleijn et al., 2010); however, on fields where fungicides and/or herbicides were used such effects of fertilizer might be suppressed. Additionally, lands with a short time after their last cultivation will show lower numbers of carabids and spiders (Thorbek and Bilde, 2004; Shearin et al., 2014). At last, similarly to what was described by Proske et al. (2022), we hypothesised that mowing of semi-natural habitats will decrease the abundance of Hemiptera, Orthoptera and Lepidoptera, while other taxa will not be affected by it.

2. Methods

2.1. Study area

Our study was carried out in the polder area Buijtenland van Rhoon (Fig. 1), south of Rotterdam (Netherlands), in 2022 and 2023. Since 2018, land-use in this area has been transitioning from conventional towards a so-called nature-inclusive farming system. Nature-inclusive farming is an approach where farmers integrate biodiversity-enhancing practices into their farm management to make optimal use of ecosystem services and maintain and promote wildlife. In our study area, the main practices that the stakeholders aim to achieve are: (1) increasing the percentage of non-productive, high-diversity landscape elements and fields to 40 %, (2) extending the crop rotation by increasing the number of cultivated crops and reducing the proportion of root crops to a maximum of 33 % and (3) reducing, and ideally ultimately ceasing, the use of pesticides as long as this does not significantly reduce yield and income. Although the transition towards nature-inclusive management has not been finalized yet, significant progress had been made during the years of study (e.g. in 2022 a total of 25 different crops were cultivated in the area and semi-natural habitat cover was 24 %). Despite such changes, many crop fields remain heavily managed, for instance in 2022 total number of fungicide applications per field ranged from 0 to 23, total number of herbicide applications ranged from 0 to 18 and total nitrogen (N) fertilizer applied to crop fields ranged from 0 kg ha^{-1} to 469.5 kg ha^{-1}. As an indication of the productivity of the two most widely cultivated crops, the potato yield in 2022 was on average 51 ton ha^{-1} and that of winter wheat was 10 ton ha^{-1}. Compared to most other countries in the world, the agricultural fields in this area can therefore still be considered high-yielding and very intensively managed. For instance, in France in 2022 the potato yield on

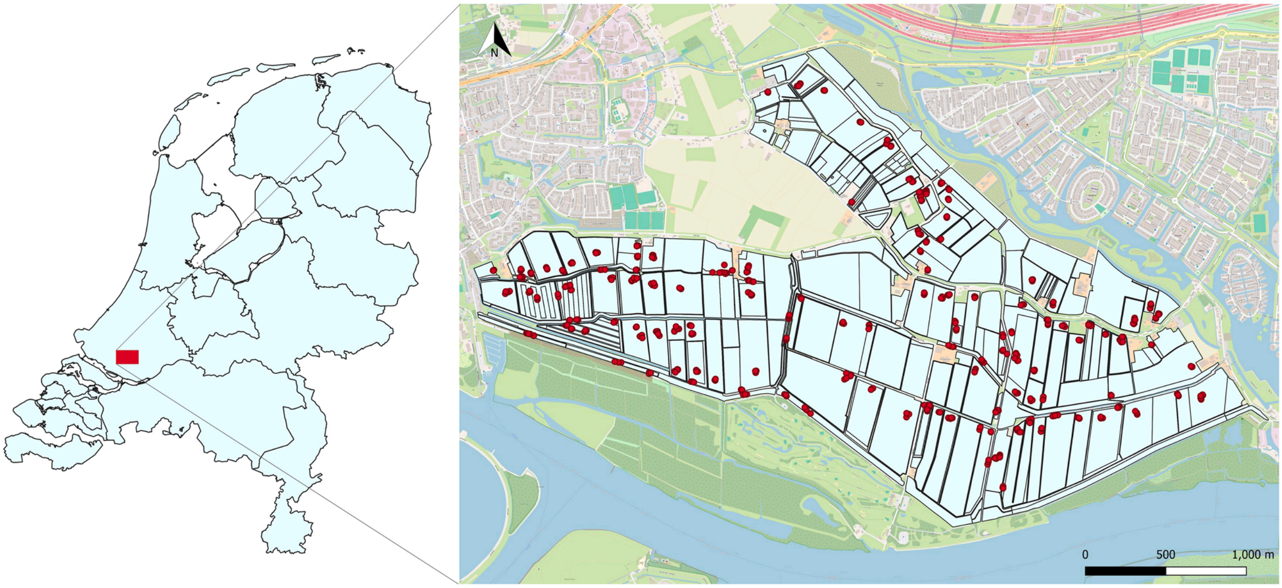

Fig. 1. Map of the study area, Buijtenland van Rhoon (Netherlands). Red dots represent all sampling locations of 2022 and 2023.

average was 38.1 ton ha^{-1} and wheat yield was 7 ton ha^{-1} (FAOSTAT, 2024). This situation provided us with a unique opportunity to evaluate factors related with arthropod abundance in a productive system that was rich in high-diversity semi-natural habitats.

In total, 120 sites were surveyed in 2022 and 62 in 2023. These sites represented 32 different land-use types, and were selected to include a variety of crops (e.g. flax, oilseed rape, common bean, asparagus, etc.) and semi-natural habitats such as dikes, extensively managed grasslands, grass-clover mixtures, perennial wildflower strips, nature-friendly ditch banks (shallowly sloping banks from which the nutrient-rich topsoil had been removed) and moist meadowlands created on former arable land. Whenever possible, we sampled multiple sites per land-use type (Table S1, Figure S1). Most crops were annual, e.g. wheat and potato, and only a few were perennial crops, e.g. silvergrass. The surveyed grasslands did not receive fertilizers nor had livestock. Fewer sites were sampled in the second year compared to the first year due to time constraints. In the first year, the sites were selected to have a large variety of different semi-natural habitats and crop types. In the second year, 54 out of 62 sites were repetitions of sites sampled in the first year. In case of crop fields, these generally had a different crop type in the second year. Thus, in total 128 unique sites were sampled (henceforth defined as site identity).

2.2. *Sampling methods*

2.2.1. *Arthropod sampling*

In both 2022 and 2023, arthropods were sampled at the selected sites three times a year between the end of April and the beginning of July with pyramid emergence traps. Specifically, the first round of sampling occurred between the end of April and the beginning of May, the second round occurred between mid-May and the beginning of June, and the third round occurred between the end of June and the beginning of July. The number of sampling rounds was selected to cover a substantial part of the growing season of most crops existing in the study area and to coincide with the breeding season of the Northern lapwing (*Vanellus vanellus*), an important target species of nature-inclusive farming in this area, that forages on invertebrates on the soil (Johansson and Blomqvist, 1996). At some sites, one or two of the annual samplings failed, for example because cattle or farm machinery destroyed the traps or slugs in the container made counting of arthropods impossible. The final dataset included 534 samplings from 182 site-year combinations.

The emergence traps were manufactured at Wageningen University & Research. These traps have a shape of a pyramid occupying 1 m^2 at the bottom and are 1.4 m height. Each trap has a metal frame covered by black tarpaulin material that does not allow light to penetrate, and at the top a transparent plastic container is located to collect arthropods (Figure S1-D). For each sampling round, emergence traps were placed in the field for one continuous week. During this period, the dark inner side of the trap causes both aboveground and ground-dwelling arthropods to fly or crawl from the soil and vegetation under the trap towards the light at the top, where a transparent container has been mounted containing a 33 % Propyleenglycol solution. After collection, arthropods were stored in a 70 % ethanol solution until identification (Sarthou et al., 2014; Marrec et al., 2015). In the lab, all specimens were counted and identified to at least the order level. Hemiptera, Hymenoptera and Coleoptera were further identified to the family level because of their high functional relevance for agricultural ecosystems.

2.2.2. *Management data*

After each field season, farmers were interviewed to obtain management data for each site (see Supplementary Materials). Specifically, we obtained data on fungicide, herbicide and fertilizer usage, and any kind of cultivation and mowing activities. This information was used to derive the following variables: number of days after last mowing and cultivation event, number of fungicide and herbicide applications within 21 days prior to insect sampling, total N fertilizer and organic N (in kg per hectare) applied to the field in each respective year prior to insect sampling. Days after last cultivation event corresponds with the last tillage moment. In case of crops that were not recently cultivated, like asparagus and silvergrass, the number of days after cultivation was set to 500 days. Total N fertilizer was calculated by summing up N in kg per hectare from all types of fertilizers used in the respective year prior to sampling, while organic N only included N from slurry and manure. Number of fungicide and herbicide applications within 21 days prior to insect sampling were selected to represent "herbicide-pressure" and “fungicide-pressure” during the maximum period when its components are active according to the labels of the products that were used. During 2022 and 2023, insecticide applications occurred only in 4 out of 110 sampled crop fields, and each of these 4 fields had a different crop type (potato, sugar beet, Brussel sprout and onion). Taking into account the low number of fields where insecticides were used, insecticide application had no effects on the majority of our studied fields, and were therefore not included in the analysis.

2.2.3. Landscape variables

Landscape characteristics were studied through three variables, namely landscape complexity, field size, and distance to field edge. Landscape complexity was quantified as the proportion of arable land in a 200 m radius around the traps where arthropods were sampled. We chose a relatively small radius, because with emergence traps we collect arthropods that are coming from the soil and the vegetation, and these are generally not very mobile and mostly affected by what occurs in the direct vicinity of the traps (McCravy, 2018). In semi-natural habitats the proportion of arable land was on average 0.46 (range: 0–0.84), while in crop fields the average was 0.63 (range: 0.20–0.93). Field size was quantified as the size (in ha) of the field in which a trap was located. Lastly, within crop fields (but not in semi-natural fields, such as dikes), we quantified the distance (in m) of the traps to the edge of the field. For this purpose, we placed emergence traps at different distances to the edge in the different fields, yet at similar distance across the three sampling rounds.

2.2.4. Vegetation surveys

To collect data on vegetation characteristics, in May or the beginning of June of each year, three 1 m^2 plots within a radius of 3 m around each emergence trap were set up. Within these plots, all vascular plant species were identified, their cover (in %) was estimated and total plant height was measured, using a bamboo ruler placed at the centre of each plot. We then averaged plant species richness, total plant cover, and plant height across the three plots for each site.

2.2.5. Soil sampling

From each study site, three samples of the upper 20 cm of the soil (pooled in one bag) were obtained using a 1.4 cm diameter soil auger in April or May of 2022 and 2023. These were taken to the lab and analyzed for soil organic matter through the loss-on ignition method (Hoogsteen et al., 2015) and total soil nitrogen level by digestion in tubes H_2SO_4 – salicylic acid – H_2O_2 and selenium (Walinga et al., 1995; Li et al., 2018).

2.3. Data analysis

2.3.1. Differences between crop fields and semi-natural habitats

To assess whether agricultural fields generally differ in arthropod diversity and abundance from semi-natural habitats, we ran 12 linear mixed models. In these, either arthropod total abundance (log-transformed), Shannon-diversity (at the order-level, including all arthropods, or at the family-level, within Coleoptera, Hemiptera or Hymenoptera), or the abundance of a specific (log-transformed + 1) taxonomic group (Diptera, Araneae, Coleoptera, Hemiptera, Hymenoptera, Collembola, Thysanoptera) was modelled in response to land-use category (crop fields vs. semi-natural habitats), sampling year to correct for annual differences, and day of the year (Julian date) to assess changes across the sampling season. Data from all 120 sites from 2022 and 62 sites from 2023 were used and we included unique site identity as a random factor in our model to account for the fact that each site was sampled three or sometimes six times, when there was overlap between 2022 and 2023. Models were fitted using the *nlme* R package (Pinheiro et al., 2017), with the *lme* function. Model fitting was done using a REML procedure and significance testing was done with Wald t-tests integrated in the *lme* function.

Next, to investigate whether different types of crops supported different arthropod abundances and diversity and how this compared to semi-natural habitats, we restricted the analyses to the six most commonly grown crops (potato n=12 site-year combinations, alfalfa n=8, flax n=11, spelt n=10, winter wheat n=17, and spring wheat n=11), as well as to semi-natural habitats (n=73 site-year combinations). We then ran the same models as described above but land-use type now included seven categories (semi-natural habitat plus six crops). Post hoc pairwise t-tests with the *emmeans* package were done to detect significant differences among land-use types for visualization purposes (Russell, 2018).

2.3.2. Relationships between arthropods and management, landscape composition, vegetation and soil properties

2.3.2.1. Within crop fields.

To examine relationships between arthropod diversity and abundances and the management of crop fields, we adopted a model averaging approach. We constructed linear mixed effects models using the same 12 response variables as above, i.e. total arthropod abundance, abundance for seven orders separately, order diversity, and family diversity for three orders separately (all diversity indices calculated with Shannon-index). Response variables describing arthropod abundance were again log-transformed to achieve normal error distribution. To avoid multicollinearity, fixed variables that strongly correlated with other fixed variables (Pearson's correlation coefficient > 0.5) and variance inflation factor higher than 2 were excluded, specifically organic N applied as fertilizer in the year prior to sampling, plant height (in cm) and total nitrogen in the soil (in ppm). The full models contained 12 remaining fixed variables. Fixed variables related to management were the number of fungicide applications within the 21 days before sampling, the number of herbicide applications within the 21 days before sampling, total N applied as fertilizer in the year prior to sampling, and days after cultivation. Additional factors that could potentially explain arthropod communities and that were also included were proportion of arable land, field size (in ha), distance between the trap and the field edge (in m), plant species richness, plant cover (in %), soil organic matter (in %), year, and the day of year (Julian date). All fixed variables were Z-transformed to be able to compare effect sizes. Unique site identity was included as a random factor. For each response variable, a full model was fitted with the *lme* function from the *lme4* package (Bates et al., 2009). Then, models with all possible combinations of fixed variables were fitted using the *dredge* function from the *MuMIn* package (Barton, 2012), and from each model the AIC value was calculated (Burnham and Anderson, 2004). Models with Δ AICc$\leq$4 from the best performing model were considered competitive. These models were included in a model averaging approach (Symonds and Moussalli, 2011), in which averaged parameter estimates were calculated based on the Akaike weights of the competitive models. Averaged parameter estimates and statistical significance were calculated with the *model.avg* function from the *MuMIn* package (confidence level set at 95 %).

This analysis was first done for all samples from crop fields (324 samplings on 83 unique sites, 27 of which were repeated, thus a total of 110 site-year combinations), where the type of crop was not included as a fixed factor, since we were specifically interested in relations with management activities. To further assess whether the relationships between arthropods and management were (partly) explained by confounding effects of the cultivated crops (that are often confounded with management) we re-ran these analyses with a selection of crops which had at least 8 sampled fields (205 samplings on 56 unique sites, 14 of which were repeated, thus a total of 70 site-year combinations) but now including crop type as a fixed factor, in addition to the other variables described above. When results from analyses with crop type do not differ from results without crop type we report results from the first set of analyses. Differences between the two sets of analyses are described in the main text. All results derived from models with crop type as a fixed factor are available in Supplementary Materials.

2.3.2.2. Within semi-natural habitats.

To assess how management affects arthropod abundance/diversity within semi-natural habitats, we restricted our analyses to data from the six semi-natural habitat types that occurred in the study area (210 samplings from 47 unique sites, 25 of which were repeated, thus a total of 72 site-year combinations; see each habitat in Figure S1). Similarly to the previous analysis, to avoid multicollinearity fixed variables with a Pearson's correlation coefficient >0.5 and variance inflation factor >2 were excluded, specifically plant height (in cm) and total nitrogen in the soil (in ppm). Meanwhile, number of days after mowing was included in the models as a fixed variable. In addition, proportion of arable land, field size (in ha), plant species richness, plant cover (in %), soil organic matter (in %), year, and the day of year (Julian date) were included as covariates. The fixed variables related to fungicide and herbicide applications, amount of N fertilizer and days after cultivation were not included since they were not applicable in semi-natural habitats. We followed the same two-step model averaging approach as for the crop field data but here including semi-natural habitat type as an additional fixed factor, to see whether some effects previously attributed to management were actually driven by land use type. In general, these results did not differ greatly from the first approach, and can be found in Supplementary Materials.

3. Results

3.1. Differences between crop fields and semi-natural habitats

In our study system, total arthropod abundance in crop fields was 38 % lower than in the simultaneously sampled semi-natural habitats (Table S2). Similarly, compared to semi-natural habitats, crop fields had a lower abundance of Diptera, Coleoptera, Hemiptera, Hymenoptera, Collembola, and a lower family diversity of Coleoptera, Hemiptera and Hymenoptera (for all $p<0.001$, except Coleoptera abundance $p=0.013$; Table S2). In contrast, the abundance of Thysanoptera was higher in crops than in semi-natural habitats ($p<0.001$). Araneae abundance and total order diversity did not differ significantly between semi-natural habitats and crops. Additionally, the abundance and diversity of all arthropod orders increased with time of the year (Table S2).

Zooming on the most commonly cultivated crop types revealed that, apart from Thysanoptera abundance, none of the other arthropod taxa occurred in significantly higher numbers in any of the individual crops compared to semi-natural habitats. Potato was the crop with the lowest abundance and diversity of most arthropod groups, and abundances were significantly lower in potato fields than in semi-natural habitats for all arthropod groups except for Araneae abundance (Fig. 2, Table S3). Similarly, compared to semi-natural habitats, flax fields also had significantly lower abundance and diversity of most arthropod groups, except for Coleoptera, Araneae and Thysanoptera abundances where the abundances did not differ significantly. Alfalfa had significantly lower Diptera and Hymenoptera abundances and marginally lower total arthropod abundance ($p=0.043$) than semi-natural habitats, while diversity and abundance of other groups of arthropods did not differ from semi-natural habitats (Fig. 2, Table S3). Spelt showed significantly lower Coleoptera and Hymenoptera family diversities, Coleoptera abundance, marginally lower Hymenoptera abundance ($p=0.040$), and higher Thysanoptera abundance compared to semi-natural habitats (Fig. 2, Table S3). Spring wheat only differed from semi-natural habitats in having lower Coleoptera and Hymenoptera family diversities, lower Collembola abundance, and higher Thysanoptera abundance (Fig. 2, Table S3). Finally, winter wheat had lower Coleoptera and Hymenoptera family diversities, lower Diptera, Coleoptera and Collembola abundances, higher Thysanoptera abundance and marginally higher order diversity ($p=0.038$), than semi-natural habitats (Fig. 2, Table S3).

3.2. Relationships between arthropods and management, landscape composition, vegetation and soil properties

3.2.1. Within crop fields

Most variables related to management did not show any significant relation with arthropod communities (Fig. 3, Figure S2, Tables S4-27) within crop fields. The number of days after the last cultivation was an exception and showed a significant positive relation with total arthropod abundance, Hymenoptera and Collembola abundances ($p\leq0.001$) and Coleoptera family diversity ($p=0.032$), yet only in the set of models where crop type was included as a fixed factor and only the most common crops were considered (Figure S3, Tables S21-22 and S25).

Day of the year was the strongest factor driving variation in abundance and diversity of arthropods (Fig. 3, Tables S4-15). From the end of April until the beginning of July there was a significant increase of arthropods of all studied orders, as well as an increase in the diversity of different orders and families of Coleoptera, Hemiptera and Hymenoptera ($p<0.001$).

In the models where the effects of crop type were not considered, plant cover showed a positive relationship with the total arthropod abundance, Diptera, Hemiptera, Hymenoptera, Thysanoptera abundance, order diversity, Coleoptera and Hymenoptera family diversity (all $p<0.001$, Fig. 3, Tables S4, S7-9, S11–13 and S15). However, when accounting for crop type, there was no significant relation anymore between plant cover and total arthropod abundance, Diptera, Hymenoptera, Thysanoptera abundance, order diversity, Coleoptera family diversity (Figure S3, Tables S16, S19, S21 and S23-25). Hemiptera abundance and Hymenoptera family diversity were still positively related with plant cover when also accounting for crop type ($p=0.044$ and $p<0.001$ respectively, Tables S20 and S27).

Plant species richness and field size were significantly negatively related to Thysanoptera abundance ($p\leq0.001$, Fig. 3, Table S11), yet these relationships disappeared once crop type was included in the model (Figure S3, Table S23). In contrast, the percentage of organic matter in the soil was significantly negatively correlated with Araneae abundance; however, this was only the case in the model with crop type as a fixed factor ($p=0.001$, Figure S3, Table S17).

3.2.2. Within semi-natural habitats

Within the different types of semi-natural habitats, the number of days after mowing was positively related to total arthropod abundance, Araneae, Hemiptera, Hymenoptera and Thysanoptera abundance, and order diversity (all $p\leq0.001$, Fig. 4, Table S28-29, S32–33, S35–36). Moreover, plant cover was also positively related to total arthropod abundance, Diptera, Hemiptera (all $p<0.001$), Coleoptera ($p=0.018$) and Hymenoptera abundance ($p=0.028$, Fig. 4, Tables S28, S30-33). However, when accounting for semi-natural habitat type, there was also a significant relation between plant cover and Araneae abundance (Figure S4, Table S41).

Total abundance of arthropods and the abundance of each order of arthropods increased with day of the year, except for Diptera and Collembola abundance (all $p<0.001$, Fig. 4, Table S28-35). This was also the case with the order diversity ($p<0.001$), yet there was no significant relationship between day of the year and Coleoptera, Hemiptera and Hymenoptera families diversity (Fig. 4, Table S36-39).

4. Discussion

Our study provides unique insights into how arthropod abundances and higher-taxa diversity differed between a variety of crop fields and semi-natural habitats, and which (management-related) factors drive arthropod diversity and abundances in both land use types. We show that, in most cases, arthropod abundance and diversity was lower in crop fields than in semi-natural habitats. However, there were large differences between the different types of crops. For example, the abundance and diversity of a number of arthropod taxa in cereals was often similar to that in semi-natural habitats. Surprisingly, within crop fields we found no significant relationships between the abundance and diversity of arthropod taxa and management practices that are often linked to insect decline in other studies, such as fungicide or herbicide application, or N fertilization. We only found a significant relationship between days after cultivation and some of the arthropod abundance and diversity variables. Within semi-natural habitats, we found more consistent relationships between management activities and arthropod

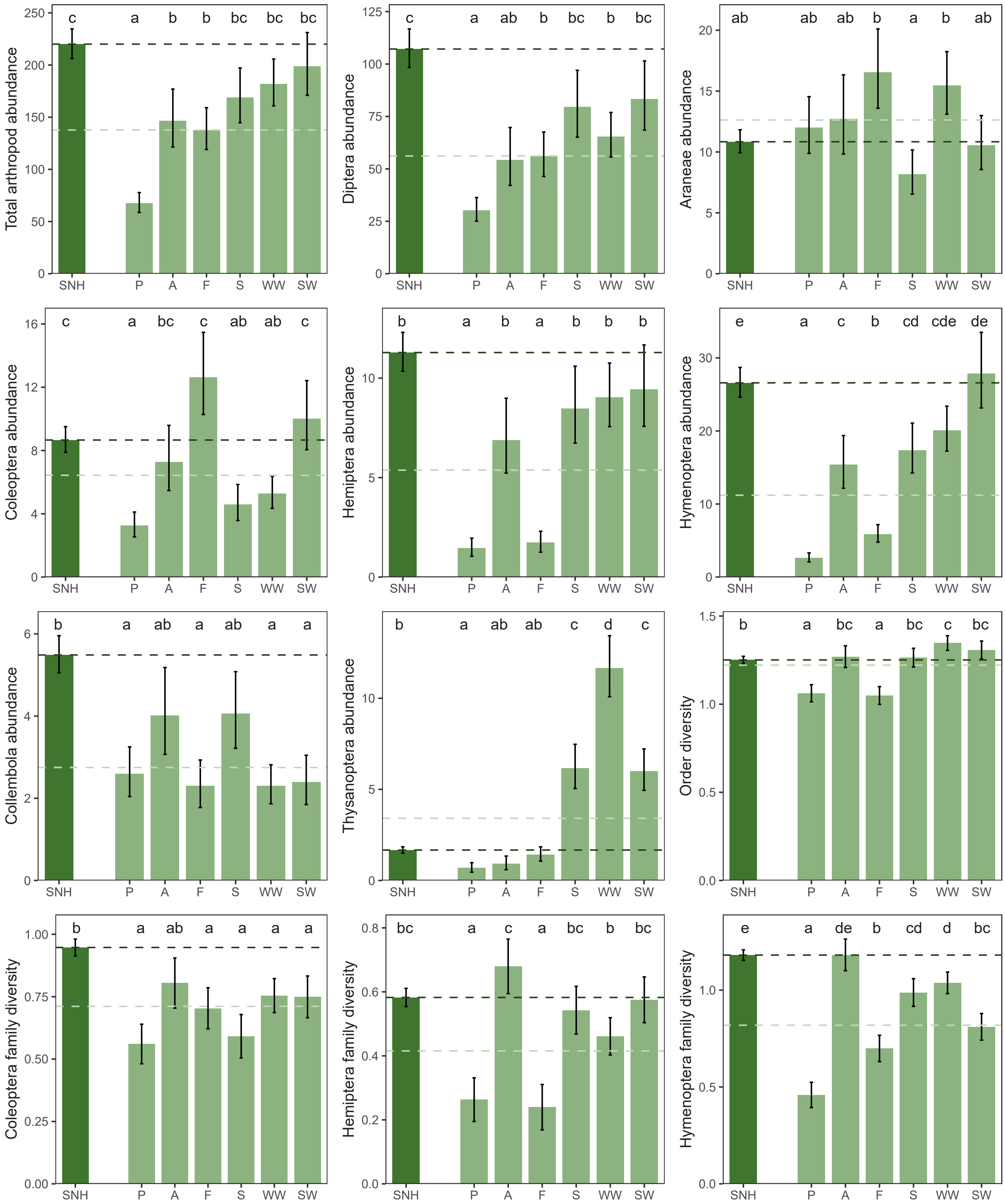

Fig. 2. Average (± SE) abundance or Shannon diversity of arthropods in different land-use types (SNH – semi-natural habitats, P – potato, A – alfalfa, F – flax, S – spelt, WW – winter wheat, SW – spring wheat). Dotted lines represent average abundance / diversity indicators in semi-natural habitats (dark green) and crops fields (light green). Letters above the bars indicate which land-use types significantly differed from each other in the respective abundance/diversity measure.

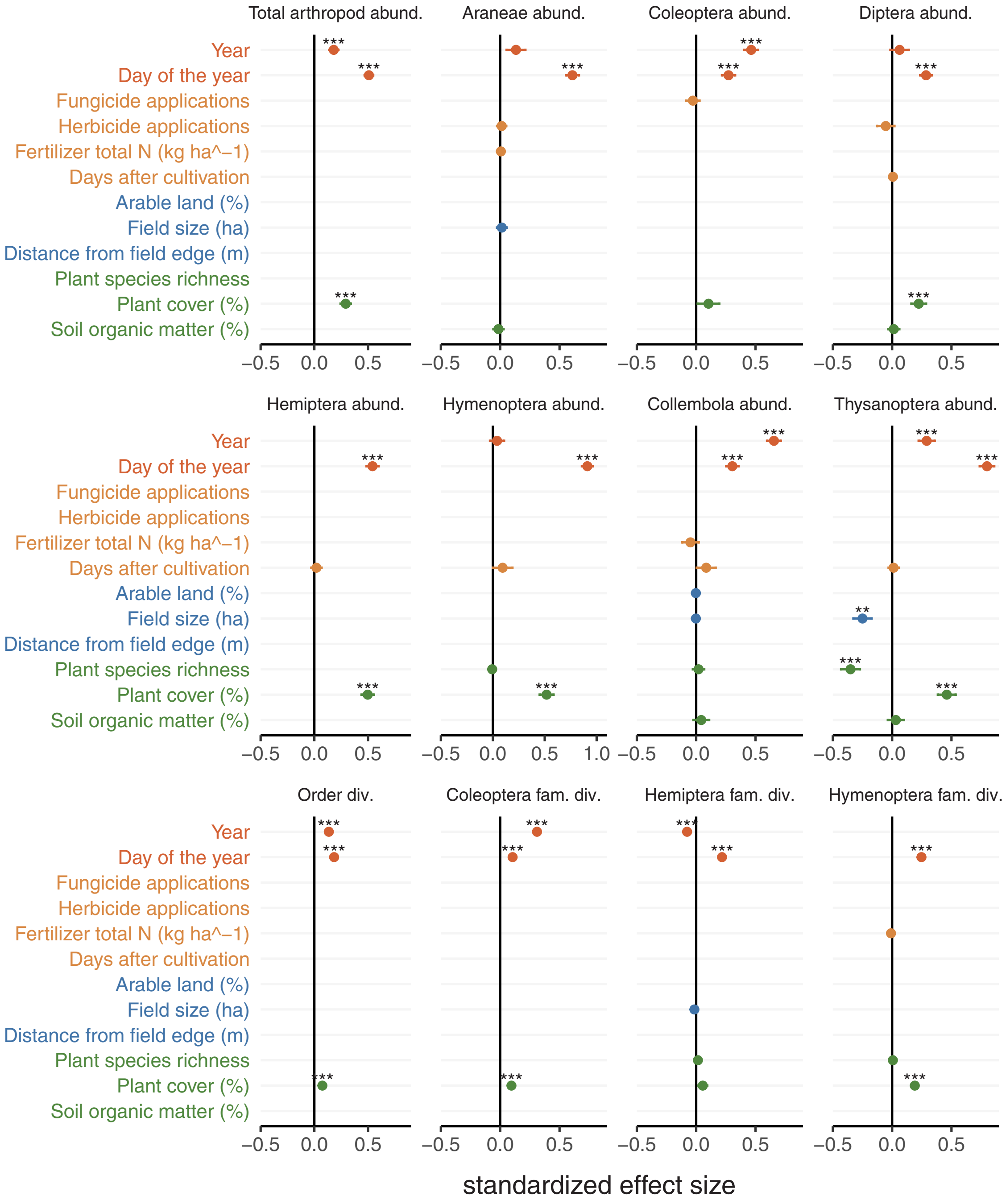

Fig. 3. Estimated effects of time (red), management activities (yellow), landscape factors (blue), vegetation and soil properties (green) on the abundance and diversity of arthropods in crop fields, based on models where crop type was not included as a predictor. Points represent fixed effects that were in the best candidate models after model averaging and lines represent error bars. All predictors were standardized to interpret parameter estimates on a comparable scale. All response variables regarding abundance were log-transformed. P-values of the best selected models for each model parameter are given as: $^*P < 0.05$;$^{**}P < 0.01$;$^{***}P < 0.001$ (see details in Supplementary Materials). For models where crop type was additionally included as a predictor, refer to Fig. S3.

diversity and abundances, with the abundances of several arthropod orders, as well as total arthropod abundance and diversity, increasing with the number of days after mowing. Moreover, our study showed consistent relationships between plant cover and the abundance and diversity of several groups of arthropods, in both the crop fields and semi-natural habitats. These results imply that the choice of crop to be planted might have direct consequences on arthropods, based on the timing of cultivation and thus the amount of plant cover available for arthropods during spring and summer.

4.1. Differences between crops and semi-natural habitats

In general, semi-natural habitats contributed to higher abundances and diversity of arthropods of various taxa than crop fields. This is in line with previous studies on ground-dwelling arthropods (Hoffmann et al., 2021), pollinators (Öckinger and Smith, 2007), and natural enemies (Blaauw and Isaacs, 2012). A possible explanation is the permanence, the more varied vegetation structure and higher plant species richness in semi-natural habitats (Zurbrügg and Frank, 2006; Moreira et al., 2016), which may thereby provide a wider range of resources and overwintering sites for arthropods (Geiger et al., 2009; Cole et al., 2017;

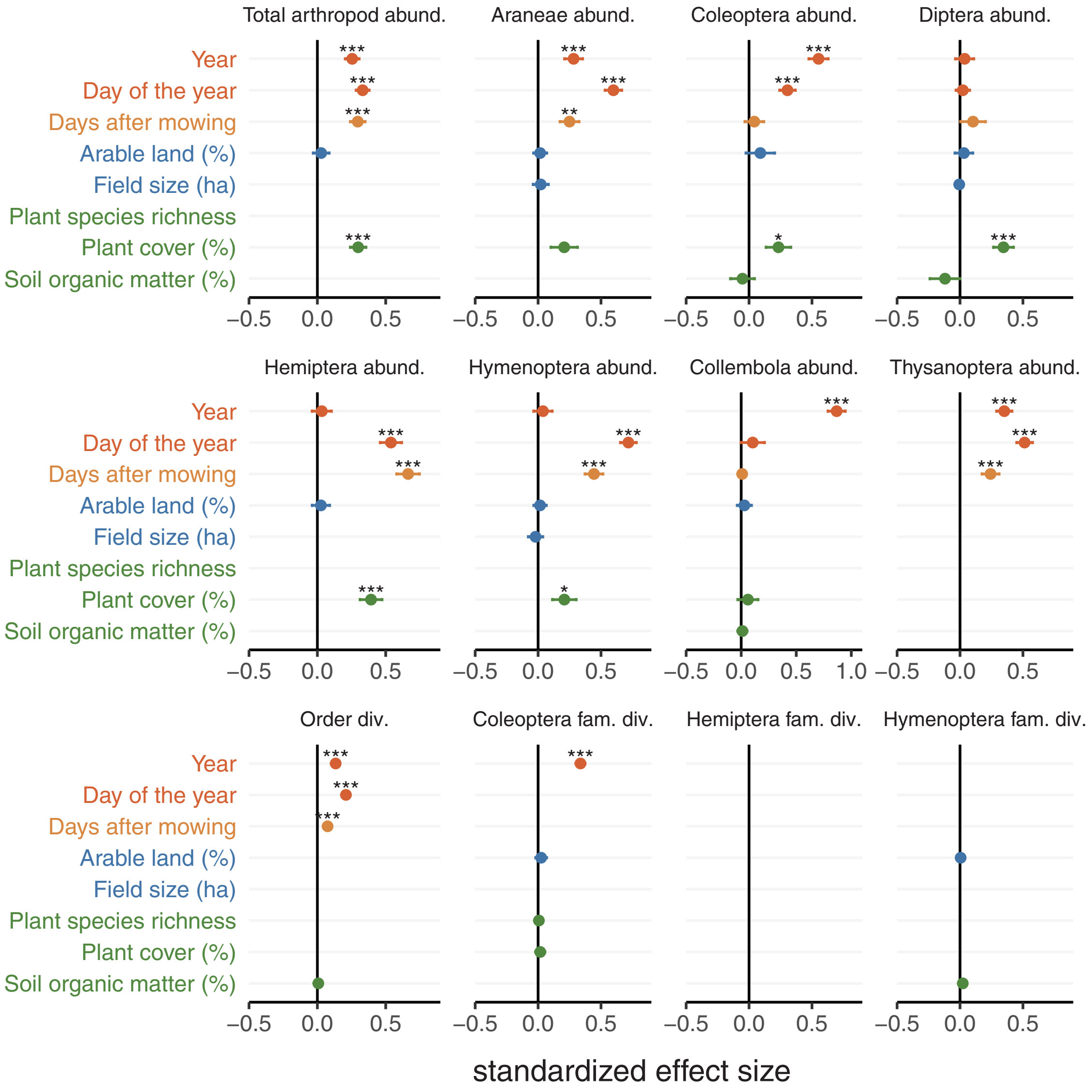

Fig. 4. Estimated effects of time (red), management activity (yellow), landscape factors (blue), vegetation and soil properties (green) on the abundance and diversity of arthropods in semi-natural habitats, based on models where semi-natural habitat type was not included as a predictor. Points represent fixed effects that were in the best candidate models after model averaging and lines represent error bars. All predictors were standardized to interpret parameter estimates on a comparable scale. All response variables regarding abundance were log-transformed. P-values of the best selected models for each model parameter are given as: $^{*}P < 0.05$;$^{**}P < 0.01$;$^{***}P < 0.001$ (see details in Supplementary Materials). For models where semi-natural habitat type was additionally included as a predictor, refer to Fig. S4.

Hoffmann et al., 2021). However, this relationship with vegetation does not apply to all arthropods, due to the distinct biology and phenology of some groups. For instance, pollen beetles tend to overwinter in oilseed rape fields rather than in semi-natural habitats (Sutter et al., 2018). Nonetheless, when looking at abundances of specific families that generally are considered pests, like leaf beetles and aphids, their numbers are higher in some crops compered to semi-natural habitats (Table S52 – *Chrysomelidae*, S53 - *Aphididae*). In our study, the abundance of Araneae and order diversity did not differ between semi-natural habitats and crop fields. In Öberg et al. (2007), the observed number of linyphiid spiders differed among habitat types, while the number of lycosid spiders did not. Hence, it might be worthwhile to distinguish between these groups in further studies. In addition, while our study focused on relatively coarse biodiversity indicators (Shannon diversity of arthropod orders, or of arthropod families within Hymenoptera, Coleoptera or Hemiptera), it is possible that larger differences between crop fields and semi-natural habitats exist when focusing on species-level biodiversity indicators.

When considering individual crops and total arthropod abundance, our results suggest that cereals generally support high arthropod numbers (similar to semi-natural habitats), potatoes support very low numbers and flax and alfalfa support intermediate levels. However, results differed markedly between the different arthropod groups. The low levels of arthropod abundances and diversities on potato fields might be caused by the late cultivation of potato, and hence late appearance of plant biomass that can be used by arthropods as resources. This is supported by the significant relationship between arthropods and plant cover observed in our findings (Fig. 3). Meanwhile, cereal crops (i.e. spelt, spring and winter wheat) generally yielded similar arthropod abundances and Hemiptera family diversity as semi-natural habitats. This is notable with rove beetles and chalcid wasps, where high abundance occurred in semi-natural habitats and some cereals crops (Table S52 - *Staphylinidae*, S54 - *Chalcidoidea*). Such results can be explained by the ability of cereals to provide plant resources and high vegetation cover relatively early in the growth season (Ritchie et al., 1998). Therefore, cereal crops have a high relative importance to maintain Hemiptera diversity and high abundance of many taxa, which is relevant for farmland birds that can forage on these arthropods

(Silva-Monteiro et al., 2023). Additionally, we observed significantly higher Thysanoptera abundance in cereal crops, particularly in winter wheat, compared to semi-natural habitats. This may be attributed to Thysanoptera's role as pests of cereal crops (Vîrteiu et al., 2018). Moreover, flax fields had the highest number of Coleoptera individuals, which was a result of a high abundance of two pest species, *Aphthona euphorbiae* and *Longitarsus parvulus* (Ferguson et al., 1997) (Table S52 – *Chrysomelidae*). Therefore, a high abundance of arthropods in crops does not always result in overall positive effects, as it may sometimes indicate a large number of pests, which can be harmful to the crops. Finally, alfalfa had comparable Coleoptera and Hymenoptera family diversity levels as semi-natural habitats, while none of the other crops did. This crop has been described in the past as being favorable for a wide range of natural enemies, due to its temporal stability and providing relatively high plant diversity compared to other crops (Summers, 1998).

4.2. Relationships between arthropods and management, landscape composition, vegetation and soil properties

In crops, of all management-related variables, only days after cultivation explained variation in the diversity and/or abundance of some arthropod taxa: it was positively related to total arthropod abundance, Hymenoptera and Collembola abundances, and Coleoptera family diversity. However, this was only the case when crop type was included as a fixed factor in the models and only the most common crops were considered. The absence of significant results is especially striking in case of total N fertilizer, since Kleijn et al. (2010) observed a positive relationship between fertilizer input and the abundance of Araneae and Hymenoptera on grasslands. There was no relationship between arthropods and fungicide or herbicide applications, even though the range in application frequency was relatively wide (Figure S2), so that effects should have been detected if these were sufficiently strong. Therefore, other variables were more important in determining arthropod numbers. According to our results, a cultivation event likely reduces the abundance of arthropods that later recover and recolonize the terrain (Thorbek and Bilde, 2004; van Capelle et al., 2012; Shearin et al., 2014; Tamburini et al., 2016; Appenfeller et al., 2022). Soil disturbances can be damaging for a range of arthropods, due to direct mortality of arthropods, removal of plant resources, habitat, nesting, and hiding sites, making them vulnerable for bird predation. For instance, cultivation might have a negative impact on Collembola because they live on the soil surface and in the soil (Dányi and Traser, 2008), so that they are directly affected by ploughing. In this study, days after cultivation did not show a link with other groups of arthropods such as Araneae and Diptera, which could be a consequence of the short term effect of soil disturbance and quick recovery of these arthropods after the disturbance.

The observed relatively consistent positive relations between plant cover and abundance of arthropods in crops is in line with the results of other studies (Silva et al., 2010; Norton et al., 2014; Smith et al., 2015; Sáenz-Romo et al., 2019; Blaise et al., 2022). In our study, plant cover was confounded with crop type, which is likely due to timing differences in planting or sowing between crops. For example, winter wheat is sown in winter, thus in spring the fields are already covered with some vegetation, while potatoes are only planted in late spring, so that potato fields are bare until relatively late in the season. This suggests that differences in arthropod abundances and diversities between crops are largely mediated by the timing of planting and plant cover. It is worth noting that in this study arthropods were studied in April-July, which is relatively early in the season. However, if there were additional sampling rounds in August-September, perhaps some relationships would flip, if early-planted crops are also early-harvested. The negative relationship between plant species richness and Thysanoptera abundance was only observed in the set of models without crop type as a predictor. This implies that differences in crop type were driving the relationships between plant species richness and Thysanoptera abundance. Specifically, Thysanoptera were highest in cereals, where they are often present as pests (Gaafar et al., 2011).

In semi-natural habitats, one of the main drivers of variation in arthropod abundance and diversity was days after mowing, which was in line with our expectations. Specifically, when more time has passed after a mowing event, there was a higher abundance of all arthropods, Araneae, Hemiptera, Hymenoptera and Thysanoptera, and a higher order diversity. Mowing can cause direct mortality of arthropods, especially of those in egg or larval stages (Humbert et al., 2010). Furthermore, mowing can remove substrate that arthropods rely on for nesting and foraging, affect arthropods by changing plant species composition, by supressing woody vegetation, and by creating a uniform plant height that is less attractive for pollinators (Morris, 2000; Black et al., 2011). Therefore, the effects of mowing might be strongest on groups that rely on a tall vegetation, like Hemiptera and Hymenoptera (Proske et al., 2022; Steidle et al., 2022). For total arthropod abundance as well as that of some of the individual taxa we found a positive relation with plant cover that was additional to that of days after mowing. This may be explained by semi-natural habitat types with less bare soil or that regrow faster after mowing supporting higher arthropod abundances. It highlights the importance of plant biomass for maintaining and promoting overall arthropod numbers.

There are several limitations of this study due to the design of the emergence traps and the timings of the samplings. Firstly, some orders were present in very low abundance, and could therefore not be analyzed. For instance, Lepidoptera, Orthoptera and Neuroptera were caught in only 22 %, 5 % and 17 % of the samples, often with only one or few individuals. Different sampling methods are needed to study these orders, for example transect counts for butterflies. Secondly, the sampling period did not cover the whole growing season of all crops present in the area, due to the high variety of crops and their different phenologies. For example, winter wheat is sown already in November or December, whereas other crops, e.g. potato, are harvested only in September or October. It was not feasible within the current study to place the traps year-round, and therefore we focused on the growing season of most crops and at the same time covering the breeding season of an important farmland bird species present in the area that relies on invertebrates, the Northern lapwing (Johansson and Blomqvist, 1996). Thirdly, this study aimed at understanding the contribution of semi-natural habitats and crop fields in an agricultural landscape for arthropod abundance, hence the focus on arthropod orders. A detailed analysis on the level of functional groups, families or even species could provide additional insights, but was outside the scope of the current study. Fourthly, most crops studied were annuals, with a few perennials like asparagus and silvergrass. Perennial crops are harvested yearly without ploughing, leading to less disturbance, hence allowing arthropods to use its habitat more continuously. This study did not explore arthropod responses to these crops due to limited number of perennial crop fields, but this could be a valuable focus for future research.

5. Conclusions

Our data originate from an area where insecticide use is deliberately used as little as possible. This may have resulted in an underestimation of the differences between semi-natural habitats and crop land. However, in all other respects, management of arable land in the study area was at the extreme high end of what can be encountered in Europe. Furthermore, in our study area, management of the semi-natural habitats was often specifically targeted towards producing biodiversity benefits (e.g. establishing wild flower strips, creating nature-friendly ditch banks), which may have enlarged the contrasts in arthropod abundance between semi-natural habitats and crop land. Considering this, even though semi-natural habitats on average supported more arthropods than crop fields, the differences with some of the crops were surprisingly small. The abundance of overall arthropods seems to be primarily driven by plant cover and on crop fields plant cover is strongly related to the cultivated crop. During spring and early summer, early sown crops that rapidly develop biomass, such as cereals, support much more arthropods than late sown crops such as potato or flax. This means that shifts in the type of crops that are being cultivated can have major consequences for arthropods in agricultural landscapes independent of associated agrochemical usage. This might have strongly contributed to insect decline over the past century, in addition to the loss of semi-natural habitats (Potts et al., 2010). For example, in 1900 the winter sown Rye was cultivated in the Netherlands on more than 200000 ha (CBS, 2002), while in 2016 this had declined to 2000 ha (CBS, 2017). Winter sown Rye has entirely been replaced by silage maize which is sown in late spring.

Our results suggest that this must have resulted in a significant decline in availability of arthropod food for farmland birds. At the same time, reduced prey availability has been described as one of the drivers of farmland birds decline, since it may compromise chick survival during the breeding season (Stanton et al., 2018). Moreover, our findings indicate that arthropods are predominantly driven by food availability (living and dead plant biomass), while disturbances caused by management (herbicides, fungicides, fertilizers, cultivation) are less important. Most likely, many arthropod species are highly resilient due to their short generation time, large population sizes and the existence of favorable habitat in the surroundings of crop fields where they can find refuge. Therefore, these arthropods might be able to rapidly recolonize the crop field after the management disturbance. This does not imply that specific groups do not suffer from agricultural intensification. For instance, bees and butterflies, which have a crucial role in agriculture as pollinators, have declined drastically during the last decades due to intense conventional agriculture (Goulson et al., 2015; Habel et al., 2019). It should be emphasized that in Buijtenland van Rhoon the application of insecticides was very limited, and our study does not cover this aspect of agricultural intensification. Other studies have already demonstrated clear negative effects of insecticide application on non-target arthropod groups (Siviter and Muth, 2020; Nicholson et al., 2024). In conclusion, semi-natural habitats are the backbone for supporting arthropods in agricultural landscapes. On productive land, the type of crops cultivated, rather than the exact management, may be the most influential factor determining arthropod abundance and diversity.

CRediT authorship contribution statement

Fons van der Plas: Writing – review & editing, Supervision, Methodology, Conceptualization. **David Kleijn:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Iryna Litovska:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The authors want to thank the farmers for allowing us to perform this study on their land and for providing management data; Julie Condé and Gaëlle Guérin for their help identifying arthropods; Femke van Beersum and Yu Araya for their field assistance; Henk-Jan van der Kolk for helping with vegetation surveys; and Jan van Walsem for analyzing the soil samples in the laboratory. This study was financed by the Cooperative Buijtenland van Rhoon and Plant Ecology and Nature Conservation Group of Wageningen University.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109298.

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