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Hedgerows have contrasting effects on pollinators and natural enemies and limited spillover effects on apple production

Gabriella A. Bishop [*], Thijs P.M. Fijen, Brooke N. Desposato, Jeroen Scheper, David Kleijn

Plant Ecology and Nature Conservation Group, Wageningen University, Droevendaalsesteeg 3a, 6708PB Wageningen, the Netherlands

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ABSTRACT

Agricultural intensification has resulted in a decline in insect biodiversity and threatens the provision of valuable ecosystem services. Agri-environment schemes (AESs) have been implemented in an effort to conserve biodiversity on farmland and increase agricultural sustainability, but their effectiveness can vary widely. To better determine which factors influence AES effectiveness, the relative roles of local habitat features, habitat quality, and landscape context need to be further explored. The aim of this study was to determine the most important factors influencing field margin AES effectiveness in commercial apple orchards, in terms of arthropod biodiversity conservation and ecosystem service provision. We surveyed wild bees and aphid natural enemies in field margins and apple trees in 20 orchards, ten bordered by hedgerow field margins (an AES) and ten with herbaceous field margins (no hedgerows present, not an AES). We considered field margin floral resources and the cover of semi-natural habitat in the surrounding landscape as indicators of local habitat quality and landscape context, respectively. We furthermore quantified pollination and pest control as measures of ecosystem service delivery and the relationship between arthropod communities and apple yield (initial and final fruit set) and quality. We found that hedgerow presence strongly predicted both pollinator and natural enemy communities and that these relationships were more pronounced than those with local habitat quality and landscape context. Hedgerows were negatively related to wild bee richness and abundance within the orchard, and positively related to natural enemy richness and abundance at the field margin but not within the orchard. We found no relationships between local and landscape factors and ecosystem service delivery, and no relationship between wild bee communities and apple yield, suggesting that apple is not pollen limited in our study system. There was, however, a negative relationship between natural enemy richness and initial fruit set. We conclude that annually cut hedgerows can benefit the conservation of natural enemies, but have limited arthropod-mediated private benefits for apple production, and likely need to be supplemented with additional local habitat resources for the conservation of wild bees. Our findings indicate that local habitat factors can strongly influence biodiversity regardless of landscape context, but that AESs likely need to be designed with separate biodiversity and ecosystem service targets, and specific taxonomic groups, in mind.

1. Introduction

The intensification of agriculture is one of the major contributors to biodiversity decline (Foley et al., 2005; Habel et al., 2019; Kleijn et al., 2009). While mechanization and the use of fertilizers and agrochemicals has greatly increased crop production, these trends are also coupled with widespread habitat loss, fragmentation, and pollution within agricultural landscapes (Robinson and Sutherland, 2002; Tscharntke et al., 2005). These impacts have resulted in a marked decrease in insect biodiversity (Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019), which in turn threatens the provision of economically valuable ecosystem services, such as pollination and pest control (Dainese et al., 2019; IPBES, 2016; Klein et al., 2007). Ecological intensification has been proposed as a solution to support biodiversity while maintaining high crop yields by partially replacing external agricultural inputs with the enhancement of ecosystem services (Bommarco et al., 2013; Kleijn et al., 2019). Several strategies aimed at biodiversity conservation and sustainable agricultural production have been widely implemented and are often subsidized by governments in the form of agri-environment schemes (AESs) in an effort to mitigate the

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* Corresponding author.
E-mail address: Gabriella.bishop@wur.nl (G.A. Bishop).

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negative effects of intensive agriculture (Batáry et al., 2015). However, farmer uptake remains low, especially of schemes with greater potential to support biodiversity (Cole et al., 2020), so an understanding of how AESs can be designed to better incentivize adoption by farmers is still needed.

Many widespread AESs targeting biodiversity conservation in agricultural landscapes aim to maintain or create field margin habitats, such as flower strips or hedgerows (Albrecht et al., 2020). Field margins provide permanent habitats for biodiversity in otherwise highly disturbed landscapes, and can make up most of the permanent habitats in intensive landscapes with few natural areas. Historically, permanent field margin habitats provided benefits to farmers, such as field delineation and fencing (Forman and Baudry, 1984; Robinson and Sutherland, 2002). With the intensification of agriculture, field sizes have increased and alternatives to natural field margins, such as wire fencing, have become widely available, so the need for these permanent field margins has decreased and their extent has subsequently been reduced (Robinson and Sutherland, 2002). The subsidization of habitats as AESs that would otherwise be removed or abandoned can replace the lost incentive and allows their biodiversity conservation benefits to be maintained (Kleijn et al., 2011). If field margin AESs additionally provided benefits to farmers, for example through improved ecosystem service delivery or crop yield, this could further incentivize and motivate farmers to conserve or implement them (Fijen et al., 2022; Morandin et al., 2016). Field margin AESs have been shown to benefit pollinator and natural enemy biodiversity and ecosystem service delivery in various crop systems (Blaauw and Isaacs, 2014, 2015; Morandin et al., 2014; Williams et al., 2015), which can carry over to crop production with demonstrable economic impact (Morandin et al., 2016). However, the effectiveness of AESs can vary, and their benefits do not consistently spill over into the crop field (Albrecht et al., 2020; Lowe et al., 2021; Zamorano et al., 2020). Recent meta-analyses highlight that factors influencing the effectiveness of AESs need to be further examined (Albrecht et al., 2020), especially those determining effects on ecosystem service delivery (Lowe et al., 2021), if adequate design and implementation of AESs are to be achieved.

At the local scale, the quality of a habitat, which may be indicated by the resources (e.g., food or shelter) it provides, can affect its ability to support biodiversity, so the relative quality of AESs may explain the variation in their effectiveness for biodiversity and ecosystem service enhancement (Albrecht et al., 2020; Scheper et al., 2013). For example, greater wild bee species richness and abundance are associated with wildflower strips that have high plant species richness and that provide more pollen and nectar resources (Schubert et al., 2022). Similarly, hedgerows with high plant species diversity and fewer gaps in them have higher bumblebee and spider abundance (Garratt et al., 2017), and hedges supplemented with flowers in the understory perform better than standard hedges in supporting bumblebee richness and abundance when compared to herbaceous field margins (von Königslöw et al., 2021). Even when flower richness explains arthropod abundance and ecosystem service provision, wildflower strips sown as an AES that fail to enhance floral diversity beyond the level present in the pre-existing field margin may result in an ineffective AES (Mei et al., 2021). Understanding the relative role of habitat quality in AES effectiveness for biodiversity conservation could thus contribute to the targeted design of AESs.

The effectiveness of an AES can also be influenced by landscape context (Batáry et al., 2011; Scheper et al., 2013). The amount, type, or configuration of natural and semi-natural habitats surrounding crop fields plays a role in determining the makeup of arthropod communities found within those fields (Chaplin-Kramer et al., 2011; Kennedy et al., 2013; Martin et al., 2019). Arthropods thus often respond positively to the improvement of both local and landscape habitat conditions (Gonthier et al., 2014). As a result of these findings, it has been recommended to implement conservation measures on multiple scales (Kennedy et al., 2013). When adopting AESs, however, farmers cannot control the context of the landscape in which their farms are located, despite the fact this context may ultimately affect the success of an AES. For example, an AES in a complex landscape may not have strong effects on pollinator communities due to the existing high coverage of natural habitats, but neither will one in an extremely simplified, or cleared, landscape due to the lack of source populations (Scheper et al., 2013). Altering landscape context is not a practical or actionable recommendation for an individual farmer, but increasing the local habitat quality of AESs would be. To design AESs that address relevant conservation goals while also incentivizing uptake by farmers, an understanding of the relative importance of local and landscape factors and how they interact to determine AES effectiveness is needed.

To determine the most important factors influencing field margin habitat effectiveness, we examined the individual and interactive effects of local and landscape factors on pollinators and natural enemies within apple orchards in south Limburg, the Netherlands. Commercial apple cultivation benefits from multiple arthropod-provided ecosystem services, namely pollination and biological pest control (Cross et al., 2015; Pardo and Borges, 2020). Orchards furthermore are often bordered by hedgerows, a type of field margin habitat that can act as valuable wind breaks (Norton, 1988) but that also is a culturally and historically important agricultural landscape feature (Forman and Baudry, 1984). Hedgerows in our study area are considered an AES as their maintenance is often subsidized by the government, and while they are not managed specifically for arthropod conservation, hedgerows in general provide resources for arthropods as well as other animals (Batáry et al., 2010; Dondina et al., 2016; Ponisio et al., 2016). We examined the effects of hedgerow presence and habitat quality, using field margin floral resources as a habitat quality measure, on pollinator and natural enemy richness and abundance and on pollination and pest control ecosystem service delivery within apple orchards. We additionally tested if landscape context moderated the effects of these local habitat factors. Subsequently, we examined the relationship between arthropod biodiversity and ecosystem service measures and apple yield and quality. Specifically, we asked 1) How do hedgerow presence, field margin floral resources, and landscape context affect arthropod biodiversity in apple orchard field margins; 2) How do these factors affect arthropod communities and ecosystem service delivery within apple orchards; 3) Do these effects carry over to apple yield and quality?

2. Methods

2.1. Study sites

Twenty conventionally managed apple orchards were selected in the region of south Limburg, the Netherlands (50.763–50.877 N, 5.729–5.971 E). Study orchards ranged from 0.4 to 8.5 ha in size (mean ± SD = 2.7 ± 0.45 ha), but were often situated within a larger grouping of orchards. Orchards included seven apple varieties (Boskoop, Elstar, Evelina, Joly Red, Jonagold, Junami, and Wellant) and were on loam or silty loam textured soils. Ten orchards had a hedgerow on one or more sides of the orchard (aspect of hedgerows varied), and ten orchards (controls) had no hedgerow on any side but only had herbaceous field margins (Fig. 1). All sites were at minimum 1 km in distance from any other study site (mean ± SD = 2.07 ± 0.91 km), which is greater than the typical foraging distance of most wild bee species, the most mobile group in our study (Zurbuchen et al., 2010). The cover of semi-natural habitat was calculated within a 500 m radius and did not significantly differ between sites with and without a hedgerow field margin (Table A.1; Netherlands national land use, Hazeu et al., 2020). Hedgerows at study sites are subsidized for their cultural, aesthetic, and wildlife (e.g., birds and small mammals) conservation value, but are not specifically managed for arthropod biodiversity. They contained one or a mix of the following species: *Crataegus monogyna* (Jacq.) (common hawthorn), *Carpinus betulus* (L.) (European hornbeam), and *Alnus glutinosa* (L.) (common alder). Hedgerows were approximately 1–2 m in height and 1–1.5 m in width and are cut every year.

Fig. 1. Typical a) hedgerow and b) herbaceous (control) field margins of the study sites.

2.2. *Arthropod community and habitat quality surveys*

We chose wild bee pollinators and aphid natural enemies as our focal arthropod groups since both groups provide ecosystem services to apple production. Bees make up the large majority of apple pollinators, which also include hoverflies and to a much lesser extent other groups (e.g., Lepidoptera, Hemiptera, and Coleoptera) (Pardo and Borges, 2020). We limited our pollinator surveys to bees because hoverflies typically have low visitation rates to apple and have significantly lower apple pollination success compared to bees (Bernauer et al., 2022; Garratt et al., 2016). We did, however, include hoverflies as pest enemies in our study. Several groups of pests such as moths, mites, and leaf miners threaten apple production (Agnello, 2004), but aphids (in particular the rosy apple aphid, *Dysaphis plantaginea* (Passerini)) are among the major pests that cause economic losses (Blommers et al., 2004) due to leaf curling and fruit deformation (Agnello, 2004). European earwigs (*Forficula auricularia* (L.)) are a primary contributor to aphid biological control in apple orchards (Dib et al., 2010; Mueller et al., 1988), but several other groups predate or parasitize aphids in this study system (e.g., Coccinellidae, Syrphidae, and Braconidae; Dib et al., 2010).

The arthropod community and habitat quality surveys are described in the following two sub-sections. For an illustrative overview of all sampling locations within study orchards, see Figure A.1.

2.2.1. *Surveys within field margins*

2.2.1.1. Wild bees. We measured wild bee communities during apple bloom (April-May) in 2021. To record the richness and abundance of wild bees in apple orchard field margins, we established 150 m^2 transects along a field margin at each site. Field margins were selected that were at minimum 100 m in length with intact vegetation and that were accessible. At sites with hedgerows, the transect was established directly next to the hedgerow, and included its undergrowth. Hedgerows in our study area are intensively managed so that they seldom flower, so these transects were comparable to those at control sites in that they were established within herbaceous groundcover. Transect surveys (Westphal et al., 2008) using butterfly nets were conducted for an observation period of 15 min, during which all bees utilizing the habitat within the transect were recorded, excluding catching and handling time. Specimens were either identified to species in the field where possible or collected into vials containing paper wetted with ethyl acetate for later pinning and identification using relevant taxonomic keys (Falk and Lewington, 2016; Anon, 2020, 2016). Surveys were carried out between the hours of 10:00 and 18:00, and due to the cold and rainy spring, they were conducted both under optimal (> 15 °C, wind < 3 Beaufort (< 12 km/h), clear to low cloud cover) and sub-optimal (9–15 °C, wind ≤ 3 Beaufort (up to 19 km/h), low to moderate cloud cover) conditions, though always conducted on dry days. Sites were all surveyed twice, once each in the morning and afternoon. *Apis mellifera* (L.) individuals were recorded but were not considered wild pollinators as there are no feral populations in our study system and because their presence is strongly influenced by hive placement by farmers within their orchards. In the Netherlands, *Bombus terrestris* (L.) and *B. lucorum* (L.) workers and queens cannot be readily separated without molecular techniques (Alferink et al., 2020) and were thus grouped into one complex.

2.2.1.2. Natural enemies. We measured natural enemy communities after apple bloom (June-July) in 2021, since pest pressure is greatest during the fruit development period (Agnello, 2004). To record the richness and abundance of natural enemies in apple orchard field margins, sweep samples (Morandin et al., 2014) were collected at three locations along the field margin transect: in the center, and midway between the center and each edge. Ten 180° sweeps were made into the vegetation at each sample location using a 35 cm diameter net. When a hedgerow was present, sweeps were made simultaneously into the hedge vegetation and the herbaceous undergrowth. Surveys were conducted between 10:00 and 18:00 on dry days with low to moderate cloud cover, temperature > 13 °C, and wind < 3 Beaufort (< 12 km/h). Sites were all surveyed twice, once each in the morning and afternoon. Samples were transferred to labelled and sealed bags and placed in a cooler before being frozen and stored in 70% ethanol for later identification. Identification to species level (except for lacewings and parasitoid wasps, which were identified to family or superfamily) was performed with relevant taxonomic keys (Bot and Van de Meutter, 2020; Krediet et al., 2022; Roy and Brown, 2021). Spiders and harvestmen were identified by a local expert (Aart Noordam).

2.2.1.3. Floral resources. Floral resources were recorded in the same field margin transects during each bee and natural enemy survey (except for five sites, where one floral survey represented both bee rounds) according to the methods of Scheper et al. (2015). All flowering species within the transect were identified using ObsIdentify and relevant taxonomic keys (Rose, 2006; Streeter and Hart-Davies, 2016) and individual flower units were counted. The flower cover of each species was calculated as the total number of flower units * the mean surface area of one flower unit, divided by the transect area. The cover of all species was summed and multiplied by 100 to calculate total % flower cover of the transect. Thus, two measures of floral resources were recorded: flower richness and flower cover.

2.2.2. *Surveys within apple trees*

2.2.2.1. Wild bees. To record the richness and abundance of wild bees visiting apple flowers, three transects were conducted along tree rows, one at each of three increasing distances from the focal field margin: 10, 30, and 50 m (see Figure A.1). Transects were 75 m in length and 7.5 min in observation duration, and only one side of a tree row was surveyed in each transect. When tree rows were oriented perpendicularly to the focal field margin, we split transects at each distance class into ten consecutive segments of 7.5 m that were each surveyed for 45 s. All bees observed to make contact with an apple flower stigma were recorded and if necessary caught for later identification. One site used microcolonies of *B. terrestris* workers as managed pollinators, so at this site *B. terrestris/lucorum* workers (but not queens) on apple flowers were not considered as wild bees.

2.2.2.2. Bee visitation rate. Surveys of bee visitation rate, a widely used indicator of pollination services to crops (Kleijn et al., 2015), were conducted on six apple trees per site, with two trees (minimum 20 m apart) from within the pre-established transects at each distance class. During visitation surveys, we simultaneously observed one low (approximately 1–1.5 m in height) and one high (approximately 1.5–2 m in height) branch on each tree. All bee visits with stigma contact to the flowers on the focal branches were recorded during a period of 20 min (Fijen and Kleijn, 2017). Branches were marked with colored tape so that the same branches at each site were observed during both sampling rounds. The number of open flowers on each branch was recorded prior to the start of each survey. Flower counts for the focal branches were used to calculate percentage bloom by dividing the number of open flowers by the total number of individual (not composite) buds counted at the first survey. This value was then averaged across the 12 branches to yield an estimate of percentage bloom of the apple orchard during each sampling round, as the stage of bloom might affect the abundance and visitation of bees.

The visitation rate per flower was calculated separately for wild bees and managed (*A. mellifera* and in the case of one site, *B. terrestris/lucorum* workers, see above) bees by dividing the number of visits by the number of open flowers for each branch. Visitation rate was calculated separately for these two groups because it was assumed that only wild bees would be affected by the environmental variables examined in this study, whereas managed bees are primarily affected by placement of hives within the orchards by the farmers. Managed bee visitation was still calculated, however, as it is an additional indicator of pollination services relevant for apple production.

2.2.2.3. Natural enemies and pests. To record natural enemies and pest infestation within apple trees, we combined visual surveys with tap sampling (Happe et al., 2019). Twelve trees were surveyed at each site, with four trees from within the pre-established transects at each distance class. Two branches (one low, one high) were surveyed per tree. Branches were inspected for aphid colonies. The number of colonies was recorded and the number of individuals in each aphid colony was counted; exceptionally large colonies (e.g., when entire leaves were curled due to infestation) were collected for later counting. Aphids on apple trees included the woolly apple aphid (*Eriosoma lanigerum* (Hausm.)), the rosy apple aphid (*D. plantaginea*), and the green apple aphid (*Aphis pomi* (De Geer)). In the case of the woolly apple aphid, whose wool makes counting individuals difficult, the size (cm^2) was visually estimated and the number of individuals was calculated according to Gontijo et al. (2013). Branches were tapped thrice over a 35 cm diameter net and captured natural enemies were collected into vials. Natural enemies were placed into a cooler before being frozen and stored in 70% ethanol for later identification. Earwigs made up a large proportion of observations (82.4%), so natural enemy abundances within apple trees were split into earwig and non-earwig counts.

2.2.2.4. Aphid predation rate. Aphid predation rate was estimated with aphid sentinel prey cards (Boetzl et al., 2020; Geiger et al., 2010). Ten adult pea aphids (*Acyrthosiphon pisum* (Harr.)) were affixed to one side of a 5 × 5 cm piece of black fine-grained sandpaper using clear nail polish. After drying, the cards were used within 36 h. Nine cards were placed at each site, with three cards on three different trees from within the pre-established transects at each of the three distance classes. At each distance class, two cards were placed on the two trees previously marked for the bee visitation surveys, and a third card was placed on a tree between these two trees. Cards were attached to a branch with twist ties and were collected after 24 h, when the number of remaining aphids on each card was recorded. Predation rate was calculated as the number of aphids removed from the card divided by the total number of aphids placed on the card.

2.3. Apple yield and quality

To investigate the relationship between arthropod communities and apple yield, we measured apple yield and quality from the same 12 branches for which we measured bee visitation rate in each orchard. Shortly after initial fruit development, the total number of apples on each focal branch was counted (initial fruit set). The count was performed a second time at harvest (final fruit set). Fruit set was calculated as the count of fruit divided by the total number of individual (not composite) buds recorded for that branch at the beginning of the flowering period. Five apples were harvested from each focal branch, if there were at least five apples present (mean ± SD = 3.9 ± 1.6 apples). For these apples, the weight, maximum diameter, seed set, and symmetry were recorded. Symmetry was visually assessed and if moderate or severe asymmetry was present (see de Groot et al., 2015), the apple was marked as not symmetrical. Symmetry was then calculated as the number of symmetrical apples divided by the total number of apples. These indicators were chosen because they are related to pollination success and are important to commercial yield and quality (Garratt et al., 2014; Pardo and Borges, 2020). One control site was harvested by the farmer prior to final yield data collection, so this site was excluded from all yield analyses.

2.4. Statistical analysis

2.4.1. Arthropod communities. We used linear models and a multimodel inference approach (Grueber et al., 2011; Harrison et al., 2018) in R version 4.1.2 (R Core Team, 2021) to analyze the effects of local and landscape factors on several response variables. Response variables included wild bee and natural enemy richness and abundance in field margins and apple trees, and wild bee visitation and aphid predation in apple trees. To determine the relative influence of local and landscape factors, we considered hedgerow presence, flower richness, and flower cover as local habitat factors, and the percentage of semi-natural habitat in the surrounding 500 m as a landscape habitat factor. These variables comprised model fixed effects, and all two-way interactions between local and landscape variables were included. Hedgerow presence did not affect field margin flower richness and cover on average (Table A.5), so the effects of these factors on arthropod communities could be considered independently. For models of data collected on apple trees, preliminary analyses showed that distance into the orchard did not significantly predict any response variable ($p > 0.10$ for all models), so we removed this factor and pooled data by summing within sites for each round (except for visitation rate, which was averaged across branches). Additional covariates of interest, including temperature, percentage bloom of apple trees, aphid infestation (total number of individuals across all species), and time of predation card deployment, were also included as candidate fixed effects when relevant to response variables. Due to the right-skewness of the flower cover and aphid infestation data, these variables were log transformed. Predictor variables were standardized according to Gelman (2008) using the arm package (Gelman and Su, 2021) in order to obtain directly comparable model coefficients and to interpret model-averaged main effects in the presence of interactions. All variables were averaged across sampling rounds to remove the element of pseudoreplication from the data.

Full model averaging was performed using the MuMIn package (Barton, 2020) on a candidate model set where the maximum number of predictors was set to four to limit model overparameterization, with the difference in Akaike information criterion corrected for small sample size (AICc) between the best model and the other candidate models limited to four (Burnham et al., 2011). We validated model assumptions on a model representing the fullest possible model in the model set (Hoeting et al., 1999) using the DHARMa package (Hartig, 2021) and checked for predictor collinearity using the performance package (Lüdecke et al., 2021). Spatial autocorrelation was checked using the DHARMa package, and no models exhibited significant spatial autocorrelation. Response variables were square root or log+ 1 transformed when necessary to improve residual scatter. Model-averaged beta coefficients were considered 'strong' predictors of response variables if their 95% confidence intervals did not overlap zero. For wild bee visitation rate, a single outlier had high influence within the model on the effect of flower cover and was removed, but model averaging results including the outlier are presented in Table A.17.

2.4.2. Apple yield and quality. As a secondary analysis step, to determine if differences in arthropod communities in turn impacted apple production, we investigated the effect of species richness (apple tree wild bee and natural enemy richness) and ecosystem service delivery (wild bee visitation rate, managed bee visitation rate, and aphid predation rate) on the measured apple yield and quality indicators (see

Section 2.3) with linear models. We chose to not include arthropod abundances in addition to the selected predictor variables as abundance and richness were highly correlated (r = 0.80 and 0.53 for bees and natural enemies, respectively). Within models, natural enemy richness showed collinearity with both aphid predation rate and wild bee visitation rate (model variance inflation factors > 3) and so models containing its combination with either of these respective predictor variables were excluded from the candidate model set. Because yield parameters depend on apple variety, we estimated the influence of apple variety as a fixed effect. To do so, only varieties represented by at least three sites were included in the analyses (N = 14 sites). Predictor variables were averaged across sampling rounds and then standardized by subtracting the mean and dividing by the standard deviation (i.e., z-scores) prior to analyses. Response variables were averaged within site. The model of final fruit set showed remaining residual heteroskedasticity, so the response variable was reciprocal transformed. Model averaging was performed using the same procedure as described above, with variety being specified as a constant fixed effect within all models.

3. Results

3.1. Arthropod communities and habitat quality

In total 475 wild bee and 926 natural enemy individuals were recorded, comprising 40 and 51 species, respectively (Tables A.3-A.4). Natural enemies included spiders (Araneae), harvestmen (Opiliones), ladybird beetles (Coccinellidae), earwigs (Dermaptera), lacewings (Chrysopidae), parasitic wasps (Braconidae and Chalcidoidea), and hoverflies (Syrphidae). Other aphid predators were not encountered. The most abundant wild bee species was *B. terrestris/lucorum* (workers and queens combined), while the most abundant natural enemy species was *F. auricularia* (European earwig). A greater number of species of both wild bees and natural enemies were observed in field margins than within apple trees (33 bee species and 34 natural enemy species; and 21 bee species and 30 natural enemy species, respectively). The large difference in the number of bee species between the field margins and apple trees was primarily due to the presence in the field margins of non-crop pollinating species such as *Nomada* cuckoo bees (Table A.3). More *Nomada* species were observed in control field margins (9 species) than in field margins with hedgerows (4 species). Natural enemies collected in apple trees were primarily earwigs, ladybird beetles, spiders, and harvestmen, while in field margins hoverflies and parasitic wasps were also recorded (Table A.4). More spider species were found in hedgerow field margins (16 species) compared to control field margins (8 species), which mainly drove the overall difference in natural enemy richness between field margin types. Average abundances for wild bees and natural enemies in field margins and apple trees are presented in Table A.2.

Floral richness and cover did not significantly differ between hedgerow and control field margins during both bee and natural enemy surveys (Table A.5). On average, during bee surveys there were 8.4 ± 0.9 and 8.6 ± 0.9 (mean ± SE) flowering plant species in hedgerow and control field margins, respectively, and during natural enemy surveys there were 9.1 ± 0.9 and 8.4 ± 0.9 (mean ± SE) species, respectively. Flower cover was relatively higher for both hedgerow and control field margins during the bee surveys (0.419 ± 0.103% and 0.656 ± 0.161% mean ± SE, respectively) compared to during the natural enemy surveys (0.116 ± 0.047% and 0.135 ± 0.056% mean ± SE, respectively). For a list of all floral species recorded see Table A.6.

3.1.1. Arthropod communities within field margins. Wild bee richness and abundance in apple orchard field margins were not strongly related to any local or landscape habitat factor (Table 1). Natural enemy richness and abundance, on the other hand, were strongly positively predicted by hedgerow presence and flower cover (Fig. 2), with hedgerow presence having a relatively larger effect compared to flower cover (Table 1). There was no strong evidence of moderating effects between landscape and local habitat factors (no strong two-way interactions).

3.1.2. Arthropod communities within apple trees. Wild bee richness and abundance within apple orchards were strongly negatively predicted by hedgerow presence (Fig. 3), but not by landscape context or other local habitat factors. Natural enemy communities in apple trees, as well as bee visitation rate to apple flowers and aphid predation rate within apple trees, were not strongly predicted by any habitat factor. There was furthermore no strong evidence of moderating effects between landscape and local habitat factors (no strong two-way interactions).

3.2. Apple yield and quality

Initial fruit set was strongly negatively predicted by natural enemy richness (Table 2, Fig. 4), but no other yield or quality measure was predicted by arthropod species richness or ecosystem service measures.

4. Discussion

Hedgerows are a commonly implemented field margin AES in northwestern Europe and have been shown to positively affect bees and natural enemies within agricultural environments (Castle et al., 2019; Dainese et al., 2017; Hannon and Sisk, 2009; Kremen et al., 2019), with greater effects being realized by hedgerows higher in quality (e.g., more species- or flower-rich) (Garratt et al., 2017; von Königslöw et al., 2021).

Table 1

Standardized full model-averaged coefficients (beta values) of all arthropod community models.*

Predictor	Response: Field margin				Response: Apple trees						
	Bee rich	Bee abun	NE rich	NE abun	Bee rich	Bee abun	Bee visits	NE rich	EW abun	NE abun	Aphid pred
Flower richness	0.0284	0.1077	-0.0103	-0.0523	0.0108	0.0089	0.0060	0.0459	-0.3423	0.0259	0.0166
Flower cover	0.2649	0.3376	**0.5012**	**2.9537**	0.0169	-0.0026	0.0052	0.0375	-2.1678	0.0568	-0.0621
% SNH	1.1472	0.5120	-0.0009	-0.0748	0.0307	-0.0025	0.0005	0.0162	0.0047	-0.0257	-0.0038
Hedgerow	-0.6641	-0.2096	**0.6176**	**3.9867**	**-0.9303**	**-0.4793**	0.0004	0.0022	-4.8180	-0.0239	0.0015
Aphids	–	–	–	–	–	–	–	0.1738	-0.1899	0.3380	-0.0195
% Bloom	–	–	–	–	-0.0666	-0.0144	-0.0004	–	–	–	–
Temperature	-0.1190	-0.1421	-0.0405	-0.0923	0.0141	0.0281	0.0022	-0.1188	-0.4218	0.0150	–
Daytime	–	–	–	–	–	–	–	–	–	–	-0.0003
% SNH * Hedgerow	-0.2452	-0.0103	–	–	–	–	–	–	–	–	–
% SNH * Flower richness	–	–	–	–	–	–	0.0036	–	–	–	–
% SNH * Flower cover	–	0.0341	–	–	–	–	–	–	–	–	–

* Presence of a coefficient indicates that the predictor variable was retained in the model averaging process. Bold coefficient values indicate that the 95% confidence interval does not include zero. Wild bee abundance beta coefficients are on the log scale, and those for margin natural enemy richness and apple tree abundance are on the square-root scale. Bee rich = wild bee richness; bee abun = wild bee abundance; bee visits = wild bee visitation rate per flower; NE rich = natural enemy richness; EW abun = earwig abundance; NE abun = natural enemy abundance (excluding earwigs on apple trees); aphid pred = aphid sentinel prey card predation rate; % SNH = percentage semi-natural habitat; hedgerow = hedgerow presence; aphids = total aphid infestation; % bloom = percentage bloom of apple orchard; daytime = time of day of predation card deployment. For coefficients and their confidence intervals from all models in the model averaging sets see tables A.7-A.18.

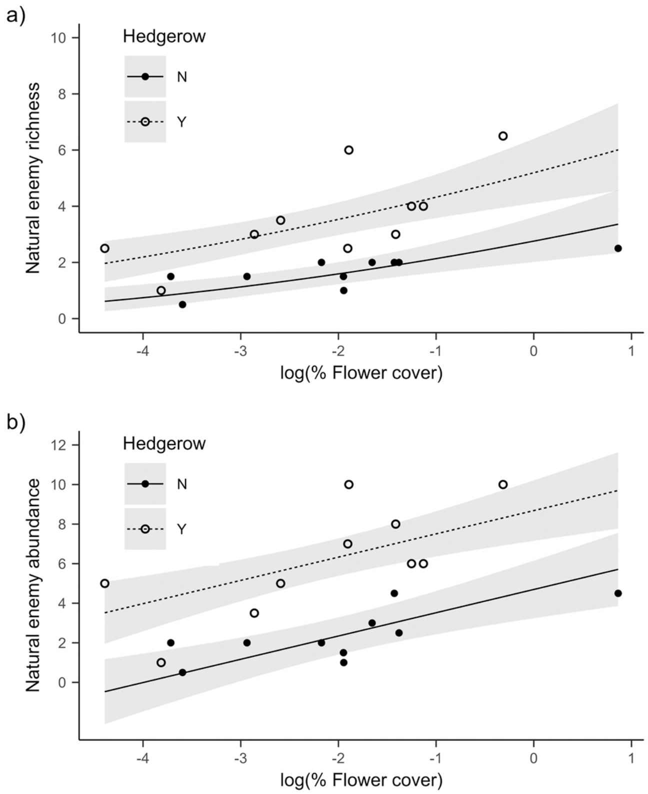

Fig. 2. Model-averaged predictions and 95% confidence intervals of the marginal effects of hedgerow presence and flower cover on field margin natural enemy a) richness and b) abundance. Points represent raw data. Hedgerow N = control field margin; hedgerow Y = hedgerow field margin.

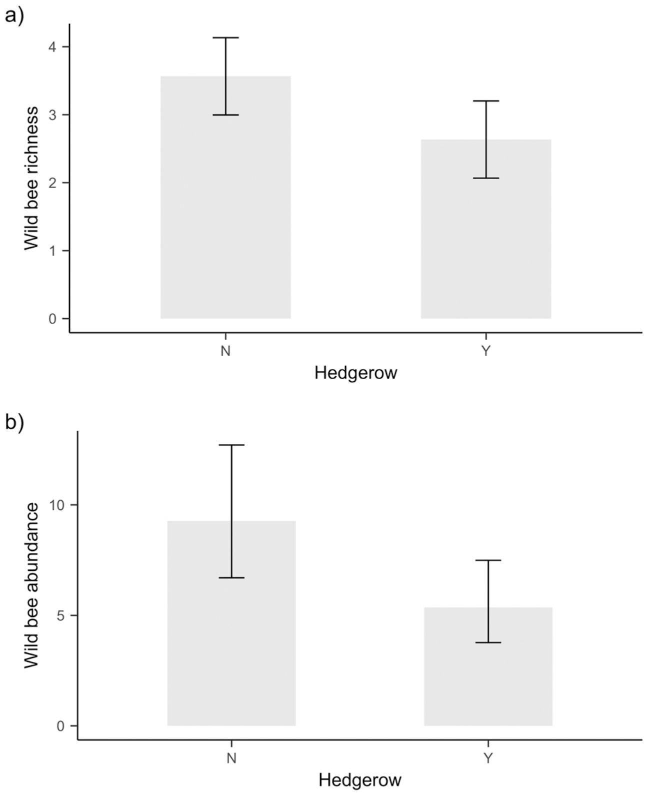

Fig. 3. Model-averaged predictions and 95% confidence intervals of the marginal effect of hedgerow presence on apple tree wild bee a) richness and b) abundance (per 3 pooled transects). Hedgerow N = control field margin; hedgerow Y = hedgerow field margin.

Here we demonstrate that relatively small, annually cut hedgerows can have contrasting effects on different arthropod groups. Additionally, the effects of local habitat factors differed between arthropod taxa as well as between field margin and apple tree arthropod communities. Orchards bordered by hedgerows had lower wild bee richness and abundance within apple trees, but had higher natural enemy richness and abundance in the field margin. We found no effects of local and landscape factors on ecosystem service delivery, and limited spillover effects on crop yield. Overall, local habitat factors, as opposed to landscape context, most strongly and consistently predicted arthropod communities in apple orchards, but these effects likely only have implications for the effectiveness of field margin AESs as conservation measures and not as ecological intensification measures, since we did not observe clear impacts on ecosystem services and apple production.

4.1. *Arthropod communities within field margins*

Typically hedgerows provide enhanced floral resources that can support wild bees (Castle et al., 2019; Kremen et al., 2019). However, this is not the case in our study system because farmers manage their hedgerows to limit flowering due to the risk of fire blight (*Erwinia amylovora* (Burrill)) (Schouten, 1992), a widespread pome fruit disease (EPPO, 2014). Hedgerow margins did not have greater floral resources than control margins, which may explain why hedgerows did not support more bees. In addition, compared to field margins with hedgerows, control field margins had relatively higher richness and abundance of ground-nesting solitary and kleptoparasitic bee species, which might suggest that these sites harbored more suitable nesting locations, for example due to more soil exposure (Sardiñas et al., 2016). Natural enemies, on the other hand, likely benefited from the vegetation structural diversity provided by the woody hedge species (Bartual et al., 2019). Flower cover in field margins also strongly predicted field margin natural enemy richness and abundance, likely due to the increased provision of nectar to nectivorous natural enemies (Landis et al., 2000; Morandin et al., 2014) but potentially also due to structural diversity provided by flowering species in herbaceous ground cover (Mateos-Fierro et al., 2021). These combined effects support previous studies that demonstrate the benefits of both woody and herbaceous habitats for natural enemies (Bartual et al., 2019; Bianchi et al., 2006), and indicate the importance of local habitat characteristics, since landscape context did not predict field margin natural enemy communities. These findings also might indicate that natural enemy communities in field margins are more limited by floral resource availability compared to bee communities, as bees were not strongly predicted by floral resources. However, as abundant alternative floral resources (apple trees) were available for bees during the bee sampling period, this finding should be interpreted with care.

It is commonly observed that landscapes with greater proportions of natural habitat support larger wild bee communities (Boetzl et al., 2021; Kennedy et al., 2013). While landscape context was generally positively correlated with field margin wild bee richness and abundance, this effect was not strong, possibly indicating that other unmeasured factors additionally determined bee communities. Furthermore, the effects of local habitat factors on arthropod communities were not dependent on landscape context, which supports the findings of a recent meta-analysis (Albrecht et al., 2020) and suggests that farmers can influence arthropod communities within field margins regardless of the type of landscape their farm is within. However, our study was limited by only considering the percentage of surrounding semi-natural habitat, while other measures such as landscape habitat richness or configuration may also influence pollinator and natural enemy dynamics (Haan et al., 2020; Senapathi et al., 2017), and thus may not have been captured in our results.

Table 2
Standardized full model-averaged coefficients (beta values) of all apple yield and quality models.*

Predictor	Response					
	Initial fruit set	Final fruit set	Seed set	Diameter	Weight	Symmetry
Wild bee richness	1.8843	–	–	–	–	–
NE richness	**-10.8752**	–	–	-0.7985	-0.4855	–
Wild bee visits	–	–	–	–	–	-3.8947
Managed bee visits	-2.6767	–	–	–	–	3.1372
Aphid predation	–	–	-0.0566	1.7954	6.0507	–

* Presence of a coefficient indicates that the predictor variable was retained in the model averaging process. Bold coefficient values indicate that the 95% confidence interval does not include zero. NE richness = natural enemy richness. For coefficients and their confidence intervals from all models in the model averaging sets and for the individual apple varieties see tables A.19-A.24.

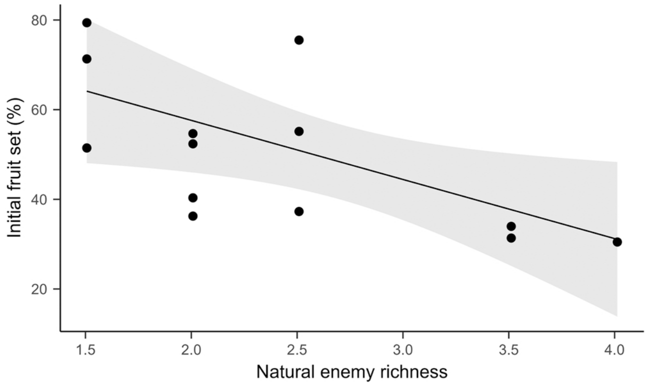

Fig. 4. Model-averaged predictions and 95% confidence interval of the marginal effect of natural enemy richness on initial fruit set. Points represent data averaged over site. Predictions are over the most frequent apple variety (Elstar).

4.2. *Arthropod communities within apple trees*

Arthropod communities within apple trees were overall less predicted by local and landscape factors compared to those in the field margin. However, wild bee communities were strongly negatively predicted by hedgerow presence. In addition to potentially providing fewer nesting resources, hedgerows may have influenced bee movement patterns. Linear landscape elements act as guides to bee movement (Van Geert et al., 2010), and thus bees are more likely to fly parallel to and alongside hedges than perpendicular to them (Cranmer et al., 2012). Due to this movement behavior, dispersal is significantly lower into fields when bees have to move away from a hedgerow as opposed to along it, and nearly zero when bees have to cross a hedgerow (Klaus et al., 2015). This effect combined with the lack of additional floral resources provided by hedgerows in our study system might explain why our results do not align with the positive effects observed in previous studies (Castle et al., 2019; Kremen et al., 2019). Furthermore, wild bees found on apple trees were not affected by landscape context, which contrasts with previous studies that show that crop fields in landscapes with high coverage of natural habitats have greater bee richness and abundance (Kennedy et al., 2013; Marini et al., 2012; Martins et al., 2015). Orchards represent the only major mass-flowering crops in our study area, and as bee sampling took place during apple and pear bloom, this likely influenced the measured relationship between landscape context and wild bee communities on apple trees (Fijen et al., 2019; Galpern et al., 2021). A high proportion of mass-flowering crops in a landscape can also dilute bee densities within mass-flowering crop fields, obscuring the effect of surrounding semi-natural habitat (Holzschuh et al., 2016).

Natural enemies in apple trees were not strongly predicted by hedgerow presence or by other local and landscape factors. This may be due to the relatively low movement of natural enemies between hedgerow and orchard habitat (Lefebvre et al., 2017). The orchards in our study are intensively managed and receive multiple insecticide applications per year, which likely strongly mediates the effects of local and landscape habitat context on natural enemy communities (Happe et al., 2019; Ricci et al., 2019; Tscharntke et al., 2016; Veres et al., 2013) and could explain why natural enemies within apple trees were not predicted by these factors. Additionally, orchards are relatively stable and undisturbed environments compared to arable fields, meaning that landscape context could play a lesser role in influencing natural enemy communities within this study system (Stutz and Entling, 2011) compared with the positive effect of landscape complexity that is typically observed across crop types (Chaplin-Kramer et al., 2011).

4.3. *Ecosystem service delivery and apple yield*

Although local habitat characteristics predicted arthropod communities in field margins and within orchards, they did not predict ecosystem service delivery to apple trees. One possible outcome of field margin AESs is an 'exporter', or spillover, effect of arthropod communities and their associated services into the crop field (Morandin and Kremen, 2013). Our findings indicate a lack of spillover effects from the field margin onto measures important to crop production, which supports previous studies (Albrecht et al., 2020; Zamorano et al., 2020). In turn, apple tree arthropod species richness and ecosystem service delivery largely did not affect apple yield and quality, suggesting that variation in arthropod communities due to environmental factors does not carry over to crop yield. Crop management practices have a relatively large contribution to yield (Gervais et al., 2021; Sutter et al., 2017) and thus may mask the effects of arthropod communities (Dainese et al., 2019). Furthermore, while several studies have recorded positive effects of bee communities on apple yield (Blitzer et al., 2016; Pardo and Borges, 2020; Pérez-Méndez et al., 2020), it has been previously shown in the Netherlands that supplemental hand pollination does not increase apple yield or quality compared to standard insect pollination, suggesting that apples are not pollen-limited in this study system (de Groot et al., 2015; Garratt et al., 2021). Our findings may indicate support for this conclusion, since the recorded variation in bee richness and visitation rates did not correspond to any relationship with yield measures. However, visitation rate alone does not take into account other factors of pollination success, such as per-visit pollen deposition, which in apple differs across pollinator species and thus may influence the relationship between ecosystem service delivery and yield measures (Park et al., 2016).

Although wild bee abundance within apple trees was lower in orchards with hedgerows, this difference was not observed in wild bee visitation rate to apple flowers, suggesting that hedgerow presence did not in turn influence apple pollination services. On average, the difference in wild bee abundance between hedgerow and control sites was primarily due to a difference in solitary bee abundance, and to a much lesser extent in bumblebee abundance (Table A.25). A higher relative abundance of bumblebees within orchards with hedgerows could have compensated in overall visitation rate, since bumblebees spend less time per individual flower visit compared to solitary bees (Park et al., 2016). Alternatively, pollinators might have altered their foraging behavior due to decreased resource competition (Balfour et al., 2015) and visited more flowers with the reduction in competitors (Inouye, 1978).

The negative relationship observed between natural enemy richness and initial fruit set may indirectly indicate a dependence of natural enemies on pest densities (Martin et al., 2016), although natural enemy communities on apple trees were not strongly predicted by aphid abundance in our models. Natural enemies in apple orchards have been shown to be very sensitive to pesticide use (McKerchar et al., 2020; Porcel et al., 2018), so an indirect effect of pesticide use, where higher toxicity loads reduced natural enemy and pest communities simultaneously and resulted in positive effects on yield, could explain this finding. However, while all orchards in this study were conventionally managed, we did not explicitly measure pesticide use.

5. *Conclusions*

We demonstrate that overall, local habitat factors, as opposed to landscape context, most strongly predict arthropod community richness and abundance in apple orchards. Differences in arthropod communities were mainly associated with hedgerow presence; however, this association was positive for natural enemies in field margins, and negative for wild bees in apple trees. To mitigate these potentially negative impacts, our findings suggest that field margins with hedgerows should be enhanced in other ways, for example by increasing ground-nesting resources. Enhancing floral resources within the ground cover along hedgerows, for example by reducing mowing frequency, likely would additionally support both bees and natural enemies. Our findings furthermore indicate that arthropods within habitats such as field margins are more affected by habitat context than those within the crop field, possibly due to the intensive management practices within crop fields. This implies that even if local factors more strongly affect arthropod communities than landscape factors, which is advantageous to farmers from a practical perspective, ultimately field margin AESs may have limited private benefits for farmers. Hedgerows in our study system have other benefits, such as historic, cultural, and aesthetic services and the conservation of other taxa such as birds and mammals, and thus they should remain subsidized. However, our study does indicate that the provision of arthropod-mediated ecosystem services to apple might not be included among these benefits. Our study points to the need to design AESs with separate conservation and ecosystem service delivery goals in mind (Ekroos et al., 2014; Kleijn et al., 2011; Macfadyen et al., 2012; Senapathi et al., 2015), and potentially also different species groups in mind. While field margin AESs may effectively promote biodiversity conservation, other AES strategies, such as enhancing habitats in orchard alleyways, may be better suited for ecosystem service delivery (Mateos-Fierro et al., 2021; Saunders and Luck, 2018), and should be continually studied to incorporate them into subsidization schemes.

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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 underlying this publication are available at https://doi.org/10.5061/dryad.sqv9s4n6s.

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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.2023.108364.

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