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The effects of agrochemicals on Lepidoptera, with a focus on moths, and their pollination service in field margin habitats

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ABSTRACT

In agricultural landscapes, field margins are potential habitats for moths and butterflies (Lepidoptera). However, because of their proximity to agricultural sites, field margins can be affected by inputs of pesticides and fertilizers. In the present study, we assessed the use of field margins by caterpillars as habitat. Furthermore, the effects of realistic field margin input rates of various agrochemicals on moths, especially on their caterpillar stages, were studied in field, semi-field, and laboratory experiments. Our monitoring results indicate that, although caterpillars were found in field margins, their mean abundance was 35–60% lower compared to meadows. In a field experiment, the insecticide treatment (pyrethroid, lambda-cyhalothrin) significantly reduced the number of caterpillars and only 15% of the sampled caterpillars occurred in the insecticide-treated plots. Furthermore, the insecticide affected the community composition of the caterpillars, whereas the fertilizer treatment slightly increased the caterpillar abundance. In laboratory experiments, *Mamestra brassicae* caterpillars were shown to be very sensitive when exposed to insecticide-treated leaves (rate that kills 50% of the test caterpillars (LR50) after 48 h: 0.78% of the recommended field rate; this rate corresponds to the arable spray drift input in field margins at a distance of 3–4 m from the crop), and the caterpillars also appeared to avoid feeding on the treated leaves. In addition, in a semi-field study, 40% fewer eggs of *Hadena bicruris* moths were found on *Silene latifolia* plants sprayed with the insecticide compared to control plants and the flowers of insecticide-treated plants were less likely to be pollinated by moths. Overall, these studies illustrate that moths use field margins as habitats and that they can be affected by realistic input rates of agrochemicals. As caterpillars are important prey organisms and adult moths can act as pollinators, inputs of agrochemicals in field margins should be reduced to maintain biodiversity in agricultural landscapes.

1. Introduction

Agriculture is the most common form of land use in Europe (Stoate et al., 2009). As a result, a large portion of European biodiversity can now be found in agricultural landscapes (Robinson and Sutherland, 2002). Modern agricultural landscapes are often subject to intensified use, which is characterized by, for example, increased field sizes, decreased crop diversity, a reduced availability of semi-natural habitats, and high inputs of agrochemicals (pesticides and fertilizers) in fields (Stoate et al., 2001; Robinson and Sutherland, 2002). This intensified management of agricultural sites has negative effects on biodiversity, such as plants, birds, and invertebrates (Wilson et al., 1999; Stoate et al., 2001). The loss and degradation of semi-natural habitats in agricultural landscapes and the intensification of agricultural management are thought to be major reasons for declines in the abundances of moths (Fox, 2012). For instance, agricultural intensification has been shown to decrease species richness of moths and abundance of nationally declining moth species in the UK (Merckx et al., 2012).

Moths and butterflies belong to the Lepidoptera, a species-rich insect order. Although a large portion of research on Lepidoptera has focused on butterflies (New, 2004), the majority of Lepidoptera (approximately 90%; Shields, 1989) are classified as moths. Field margins are common semi-natural habitats (Marshall and Moonen, 2002) that are often vegetated with grasses and herbs. Because the large majority of caterpillars are herbivores, and a majority of adult moths (and butterflies) visit flowering plants, field margins are a potential habitat for Lepidoptera, especially in agriculture-intensive regions in which these elements represent a majority of semi-natural habitats (Hahn et al., 2014b). Adult moths have been found to benefit from extended-width field margins in terms of the overall species richness (Merckx et al., 2012) and the

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abundance of certain species (Merckx et al., 2009; Merckx et al., 2010), possibly because of an increased host and nectar plant availability (e.g., the results of Pywell et al., 2004 for butterflies). Furthermore, field margins can increase the connectivity of 'stepping stone' habitats for moths (e.g., solitary trees) which may mitigate the negative consequences of habitat fragmentation (Slade et al., 2013). However, field margins can receive substantial inputs from agrochemicals that are applied on adjacent agricultural sites via spray drift or direct overspray (Rautmann et al., 2001; de Jong et al., 2008; Otto et al., 2013; Schmitz et al., 2013) and that might be detrimental to Lepidoptera (Sinha et al., 1990; Davis et al., 1991; Cilgi and Jepson, 1995; de Jong et al., 2008).

Herbicides and fertilizers may influence Lepidoptera via changes in host plant abundance, diversity (Longley and Sotherton, 1997; Fox, 2012), or quality (Hahn et al., 2014a). Insecticides can directly target juvenile and adult Lepidoptera and cause lethal effects (Sinha et al., 1990; Davis et al., 1991; Cilgi and Jepson, 1995; Abivardi et al., 1998). Furthermore, insecticides can also cause sublethal effects or act as a repellent to moths. These effects include, for example, avoidance of oviposition on sprayed surfaces by the adults (Kumar and Chapman, 1984; Gist and Pless, 1985; Abivardi et al., 1998; Seljasen and Meadow, 2006) or antifeedant effects against caterpillars (Kumar and Chapman, 1984).

The negative effects of agrochemicals on Lepidoptera might affect other organisms as well. For example, adults contribute to the transport of pollen as they visit flowers (Clinebell et al., 2004; Alarcon et al., 2008; Devoto et al., 2011) and hence can provide pollination services. In addition, both caterpillars and adults are important prey for various organisms such as birds (Wilson et al., 1999) and bats (Vaughan, 1997).

We hypothesized that agrochemicals, especially insecticides, affect Lepidoptera in various ways. One of the most commonly used insecticide in winter wheat in Germany (Freier et al., 2008) is Karate Zeon (Syngenta; active ingredient: lambda-cyhalothrin), a pyrethroid with contact, stomach action and repellent properties. We assumed that this insecticide could reduce the number of caterpillars in field margins due to toxic and antifeedant effects. Furthermore, synthetic pyrethroids have been found to act as ovipositional repellent for a moth species (Gist and Press, 1985), and we presumed that such an effect would reduce the pollination service of a specialized moth pollinator (*Hadena bicruris*) whose females pollinate *Silene latifolia* flowers during their oviposition.

To assess if field margins are used as habitats by caterpillars and to determine whether moths and their pollination services are affected by agrochemical inputs in field margins, we conducted four studies: First, we surveyed the occurrence of caterpillars in actual field margins. Second, we analyzed the effects of realistic input rates of an insecticide, an herbicide, and fertilizer in field margins on caterpillars in a field experiment. Third, we applied realistic field margin insecticide rates on host plants and assessed the survival and feeding behavior of *Mamestra brassicae* caterpillars in laboratory experiments. Fourth, we evaluated the avoidance of insecticide-treated flowers by moths regarding pollination and oviposition in a semi-field experiment.

2. Methods

The methods section is divided into four chapters that describe the design and statistics of each of the four experiments. The aim of the first study (Section 2.1) was to assess whether caterpillars use field margins as habitats. It was assumed that agrochemical inputs would have a negative effect on caterpillar abundance, and we therefore also sampled meadows for comparison that received no agrochemical inputs. The subsequent experiments focused on the effects of agrochemicals on caterpillars (Section 2.2, field experiment; Section 2.3, laboratory experiments) and adult moths (Section 2.4, semi-field study).

2.1. Caterpillars in field margins

2.1.1. Study design and sampling methods

Caterpillars were surveyed in cereal field margins and meadows in the area surrounding Landau, Germany, using sweep nets (300 sweeps per site and transect length of approximately 180 m) on sunny to partly cloudy days when the vegetation was dry. Overall, 14 field margins and twelve meadows were sampled for caterpillars during an initial sampling phase in May (18–26 May 2011). In addition, caterpillar abundances were assessed in nine cereal field margins and eleven meadows during a second sampling period in June (9–17 June 2011). The surveyed meadows had a size of approximately 1–1.5 ha. The field margins were between 1–2 m wide, which is a common margin width in the study area (Hahn et al., 2014b), and were vegetated with grasses and herbs. In Germany, field margins less than 3 m in width can receive high inputs of pesticides from overspray and spray drift because farmers are not forced to maintain a certain distance from such narrow elements during pesticide applications (Schmitz et al., 2013; Hahn et al., 2014b).

If possible, the same field margins and meadows were surveyed for caterpillars in both sampling phases (i.e., = six field margins and seven meadows). However, if a study site was mown between the first and the second sampling period and, hence, the vegetation height was inadequate (<30–40 cm) for appropriate sampling with sweep nets, another unmown site was chosen.

The sampled caterpillars were identified at the family level (Carter and Hargreaves, 1987; Porter, 1997; Rennwald and Rodeland, 2004; Bellmann, 2009). If a clear identification of a caterpillar was not possible, it was reared to an adult state.

In addition to caterpillars, the vegetation of the sampling sites was also assessed. The details of the identified plant species are presented in the supplementary data (part 1).

2.1.2. Statistics

Data for caterpillars in field margins and in meadows were compared for each phase using the Primer (Version 6) statistical program and the PERMANOVA+ add-on (Anderson et al., 2008). We conducted permutational analyses of variance for the analysis of caterpillar abundance (PerAnova, univariate data, resemblance matrices: Euclidean distance) and the caterpillar communities at family level (PerManova, multivariate data, resemblance matrices: Bray Curtis distance). Each analysis was based on 999 permutations.

2.2. Effects of agrochemicals on caterpillars in a field experiment

2.2.1. Study design

Caterpillars were sampled during the course of a field experiment with the aim of identifying the individual and combined effects of repeated agrochemical applications (duration of the experiment: 2010–2012) on the flora (Schmitz et al., 2013,b; Schmitz et al., 2014a,b) and fauna of field margins. In the experiment, 64 plots (each 8 m × 8 m) were created within an extensively managed hay meadow located near Landau, Germany. The plots were assigned to one of seven treatments (either a single application of fertilizer (F), herbicide (H), or insecticide (I), or a combination of these treatments (F + I, H + I, F + H, F + H + I)), or the control (C). Each treatment and the control were replicated eight times within a randomized block design (see Schmitz et al., 2013 for more details on the experimental design).

The applications of the agrochemicals and their application sequences mimicked the field management of winter wheat fields in the study area with their recommended agrochemical products. Both chosen pesticides were among the five most commonly used pesticides in winter wheat fields in Germany at the beginning of the study (Freier et al., 2008). The fertilizer and pesticide application rates used for the plots corresponded to the mean input rates for the first meter of a field margin directly adjacent to a field (25% of the in-field rate for fertilizer and 30% of the in-field rate for pesticides, see Schmitz et al., 2013). The application of the agrochemicals was conducted as described below in each year of the experiment (2010–2012).

Fertilizer was applied twice per year in April. At first, a granular NPK (nitrate, phosphorus, potassium) fertilizer (14% N, Floral Düngemittel, application rate: 25 kg N/ha) was applied, and approximately two weeks later a calcium carbonate and ammonium nitrate fertilizer (27% N; Raiffeisen Markt, application rate: 25 kg N/ha) was used.

As a herbicide, we applied Atlantis WG (sulfonylurea; recommended field rate 400 g/ha, actual application rate 120 g/ha, active ingredients (a.i.) 30 g/kg mesosulfuron-methyl, 6 g/kg iodosulfuron-methyl-natrium, 90 g/kg mefenpyr-diethyl (Safener), mode of action: inhibitors of plant cell division (e.g., acetolactate synthase), Bayer CropScience) once a year in April.

The applied insecticide, Karate Zeon (pyrethroid: recommended field rate 75 mL/ha, actual application rate, 22.5 mL/ha, a.i. lambda-cyhalothrin 7.5 g/ha; mode of action: nonsystemic insecticide with contact and stomach action, repellent properties, Syngenta), was sprayed once per year at the end of May or at the beginning of June.

The pesticides were applied using a purpose-built and air-assisted experimental field sprayer on wheels (Schachtner Gerätetechnik) equipped with an 8-m spray boom and 15 flat-fan TeeJet nozzles (XR 11,002-VS; Schachtner Gerätetechnik).

2.2.2. Sampling of caterpillars

Caterpillars were sampled in the second year of the field experiment at the end of May (30 May 2011; six days after the insecticide application) and at the end of June (27 June 2011; 34 days after the insecticide application) using sweep nets. On the sampling dates, the sky was sunny, and the vegetation was dry. We swept 80 times per plot in May and 100 times per plot in June (overall 5120 and 6400 sweeps, respectively).

An overview of the plant species in each treatment (assessed in June 2011) is given in the supplemental data (part 2). Furthermore, the vegetation data are presented and discussed in detail in Schmitz et al. (2014a,b).

2.2.3. Statistics

The three-factorial design of the study allowed for the consideration of the effects of the three treatment factors (fertilizer, herbicide, and insecticide) on the caterpillars. Each factor had two levels (0: not applied; 1: applied). The effects of the factors were assessed using the Primer (Version 6) program with the PERMANOVA+ add-on (Anderson et al., 2008). We analyzed the effects of fertilizer, herbicide, and insecticide on caterpillar abundance (PerAnova, univariate data, resemblance matrices: Euclidean distance, 999 permutations) and on the caterpillar community at the family level (PerManova, multivariate data, resemblance matrices: Bray Curtis distance, 999 permutations) for each sampling phase.

2.3. Toxic and repellent effects of insecticide-treated host plants on Mamestra brassicae *caterpillars*

2.3.1. Study design

The aim of these experiments was to assess the toxic and repellent effects of plant material (leaves) treated with an insecticide against caterpillars of the cabbage moth *Mamestra brassicae* L.

The English plantain, *Plantago lanceolata* L., was used as the host plant for the caterpillars. Seeds were obtained from a commercial seed supplier (Appels Wilde Samen GmbH, Darmstadt, Germany). The plants were cultivated individually in 7 × 7 cm pots with universal potting compost (Compo Sana Qualitäts-Blumenerde, Compo, Münster, Germany) in a climate chamber (20 °C, 16/8 h light/dark cycle) for approximately ten weeks prior to the start of the experimental treatment.

Eggs of *M. brassicae* were provided by the Laboratory of Entomology, Wageningen University and Research Centre, The Netherlands. After hatching, the caterpillars were housed in plastic containers (17 × 12 × 5.5 cm; lined with a layer of paper towels to absorb moisture) at room temperature (approximately 20 °C). The caterpillars were fed untreated leaves of *P. lanceolata* until they were 14 days old.

The insecticide (Karate Zeon, see Section 2.2) was applied by dipping the aboveground parts (leaves) of the potted plants into a beaker filled with the desired insecticide concentration for approximately ten seconds. The plants were treated with the insecticide at 4%, 2%, 1%, 0.5%, or 0.25% of the recommended field rate (=75 ml Karate Zeon/ha, water volume 400 L/ha) for the toxicity test. To test for repellent effects on caterpillars (repellence test), we treated plants with 1% of the recommended field application rate. Control plants were dipped in water for both experiments. The plants were left to dry and subsequently stored in the climate chamber.

2.3.1.1. Toxicity test. The toxicity test was started two hours after the insecticide or water treatment of the plants (when the plant surfaces had dried). For each replicate, two fresh leaves of either a treated or a control plant and three *M. brassicae* caterpillars (14-days old) were carefully introduced into a transparent plastic container (diameter 10 cm). For each insecticide rate and the control, the test was replicated five times. The test vessels were stored in a climate chamber (20 °C, 16/8 h light/dark cycle), and fresh leaves (from the treated or control test plants, respectively) were provided each day. Mortality was assessed at 24 h, 48 h, 72 h, 96 h, 120 h, and 144 h after the test was started.

2.3.1.2. Repellence test. The test of the repellence effects on the feeding of *M. brassicae* caterpillars was started two hours after the insecticide or water application to the plants. Twenty 15-day-old *M. brassicae* caterpillars were individually transferred into 20 transparent plastic containers (diameter 10 cm), each of which contained one *P. lanceolata* leaf treated with insecticide (1% of the recommended field rate) and one leaf treated with water (control). The caterpillars were able to choose the leaf on which to feed. The leaves were assessed for traces of herbivory at 24 h, 48 h, 72 h, 96 h, 120 h, and 144 h after the start of the test.

2.3.2. Statistics

The LR50-values (LR50: lethal rate 50, i.e., the rate that kills 50% of the individuals) at 24 h, 48 h, 72 h, 96 h, 120 h, and 144 h of exposure were calculated using the package ‘drc’ (Ritz and Streibig, 2005) in R (Version 3.1.0, R Core Team, 2014).

2.4. Effects of an insecticide on moth pollination and egg-laying behavior

2.4.1. Study design

We studied the indirect effects of an insecticide (Karate Zeon, see Section 2.2) on adult moths and the pollination services provided by these moths.

As a test plant species, we used the White Campion (*Silene latifolia* subsp. *alba* (Mill.) Greuter & Burdet). This species is

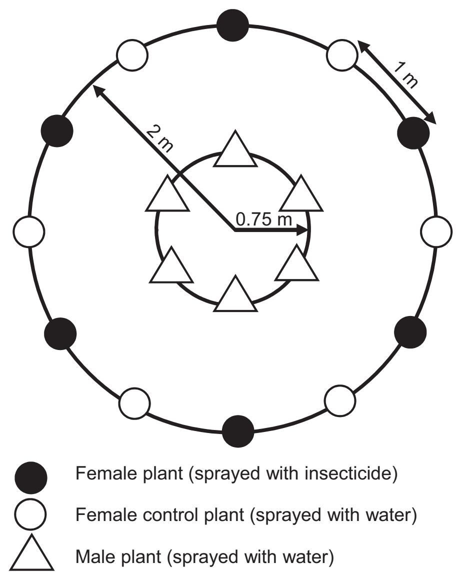

Fig. 1. Design of the pollination experiment with *Silene latifolia* plants. There were 36 and 34 unpollinated female flowers on the insecticide-treated and control plants, respectively. Approximately 60 min after insecticide application, the flowers were exposed to natural pollination for one night.

commonly found in disturbed or cultivated habitats (Jürgens, 1996), including field margins. *Silene latifolia* is specialized for nocturnal moth pollination, and a main pollinator is the moth *Hadena bicruris* Hufn. (Noctuidae), whose caterpillars feed on the developing seeds (pollinating seed predator) (Kephart et al., 2006). *Silene latifolia* is a dioecious plant species; hence, self-pollination cannot occur because the male and female flowers are developed on different plant individuals. The test plants were grown from seeds (provided by Appels Wilde Samen GmbH, Darmstadt, Germany) and cultivated individually in 10-cm pots containing universal potting compost (Compo Sana Qualitäts-Blumenerde, Compo, Münster, Germany), in a climate chamber (20 °C, 16/8 h light/dark cycle). When the roots of the plants penetrated the pots, each plant was potted in a 2-L plant container (diameter: 16 cm) and stored outdoors until flowering started. Male and female plants were then identified.

In the pollination experiment, we used twelve female and six male *S. latifolia* plants. The female test plants were divided into two groups and sprayed either with 30% of the field application rate of the insecticide Karate Zeon (six plants, 36 unpollinated flowers) or with water (six plants, 34 unpollinated flowers) using a hand-operated sprayer (Blumensprüher OASE, EMSA, Emsdetten, Germany). After the spraying, the plants were stored indoors for approximately 60 min until sunset. The six male plants (each with at least 20 flowers) were used as pollen donors and remained unsprayed. The test plants were exposed to natural pollination during one night (4–5 September 2012) in a semi-field design (Fig. 1). The next morning, each female flower was carefully wrapped in gauze to avoid any contact with further pollinators or seed predators. Nine days later, the seed numbers of the flowers were compared between treated and untreated plants. Furthermore, we examined the ovaries of the flowers to search for eggs or caterpillars of the specialized moth pollinator (*H. bicruris*) to assess if the flowers had been used for oviposition.

2.4.2. Statistics

The data were analyzed using Primer (Version 6) software with the PERMANOVA + add-on (Anderson et al., 2008). The treatment (insecticide or control) was included as a fixed factor and the plant individual (nested in the treatment) as a random factor. The analyses focused on the number of pollinated flowers (PerAnova, univariate data, resemblance matrices: Euclidean distance, 999 permutations) and on the numbers of seeds and *Hadena* offspring (eggs or caterpillars) per flower (PerManova, multivariate data, resemblance matrices: Bray Curtis distance, 999 permutations).

3. Results

3.1. Caterpillars in field margins

Overall, in the cereal field margins, 68 (4.9 ± 0.9, mean ± SE per site) and 105 (11.7 ± 1.6) caterpillars were recorded during the study phases in May and June, respectively, while in the meadows 139 (11.6 ± 2.6) and 199 (18.1 ± 3.6) caterpillars, respectively, were

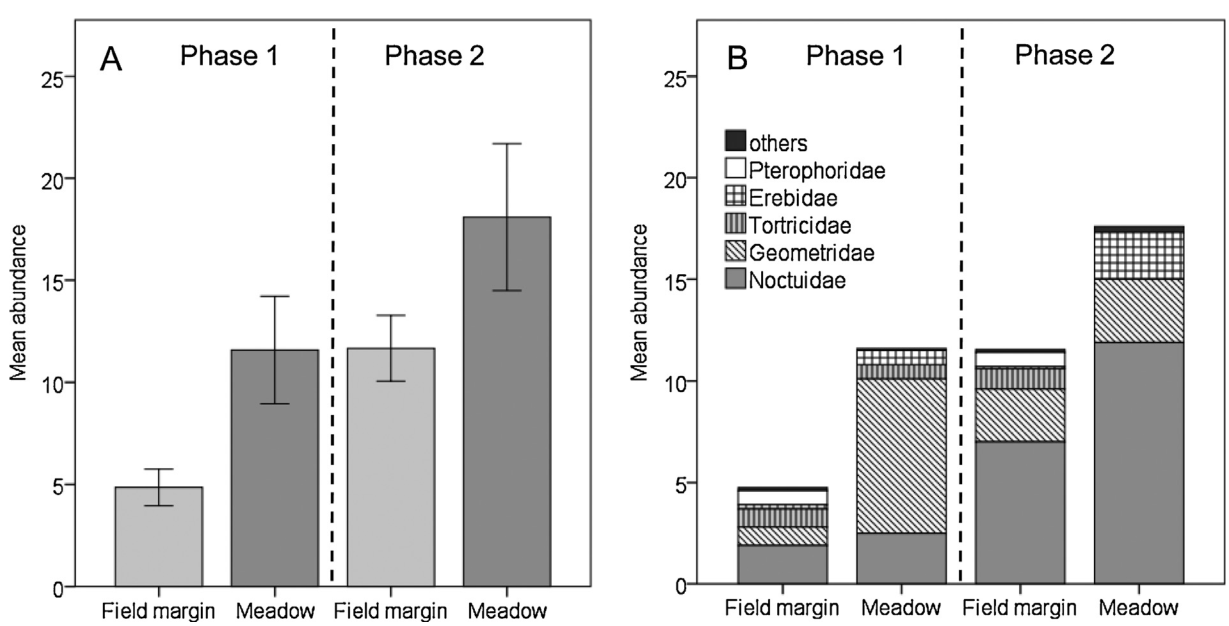

Fig. 2. Overall mean caterpillar abundance ± SE (A) and mean caterpillar abundance per family (B) in the sampled field margins (N_{phase1}: 14, N_{phase2}: 9) and meadows (N_{phase1}: 12, N_{phase2}: 11). Families with very low caterpillar numbers were pooled (others: Crambidae, Hesperiidae, Lycaenidae, Nymphalidae, and Pieridae).

sampled. The caterpillars of the field margins and meadows could be classified into nine and seven families, respectively; Noctuidae and Geometridae were the most abundant groups in both habitats (Fig. 2). Overall, the caterpillar number was smaller in the field margins compared with the meadows, significantly in phase 1 (PerAnova; $p = 0.018$) but not in phase 2 (PerAnova; $p = 0.141$). The community composition of the lepidopteran families differed significantly between the two habitats for both phases (PerManova, phase 1: $p = 0.002$; phase 2: $p = 0.011$) (Fig. 2).

In general, fewer species of flowering plants were present in field margins compared to meadows (phase 1: field margins: 8.6 ± 0.9; meadows: 11.5 ± 1.0; phase 2: field margins: 10.2 ± 0.9; meadows: 13.1 ± 1.2).

3.2. Effects of agrochemicals on caterpillars in a field experiment

On the first and the second sampling dates, 76 and 62 caterpillars were counted, respectively. Overall, the plots that had received an insecticide treatment were characterized by low numbers of caterpillars (Fig. 3).

The results of the PerAnovas confirmed that the insecticide treatment reduced caterpillar abundance significantly, both at six and at 34 days after application (PerAnova; sampling 1: $p_{insecticide} = 0.001$, sampling 2: $p_{insecticide} = 0.001$). Herbicide treatments did not result in any significant effect on caterpillar abundance at either sampling date (PerAnova; sampling 1: $p_{herbicide} = 0.322$, sampling 2: $p_{herbicide} = 0.437$). The fertilizer addition slightly increased the caterpillar abundance for the second sampling date but showed no effect during the first sampling (PerAnova; sampling 1: $p_{fertilizer} = 0.171$, sampling 2: $p_{fertilizer} = 0.039$).

Regarding the composition of the caterpillar families, the insecticide treatment caused significant effects (PerManova; sampling 1: $p_{insecticide} = 0.001$, sampling 2: $p_{insecticide} = 0.001$) due to the strongly reduced caterpillar numbers in the families Geometridae and Noctuidae (Fig. 3). Furthermore, the fertilizer (F) treatment showed an effect on the caterpillar community in the first sampling (PerManova; sampling 1: $p_{fertilizer} = 0.022$, sampling 2: $p_{fertilizer} = 0.257$) which could be attributed to higher numbers of Geometridae (treatments without F ($N = 32$): 0.66 ± 0.26; treatments with F ($N = 32$): 1.00 ± 0.20 caterpillars per plot; mean ± SE)

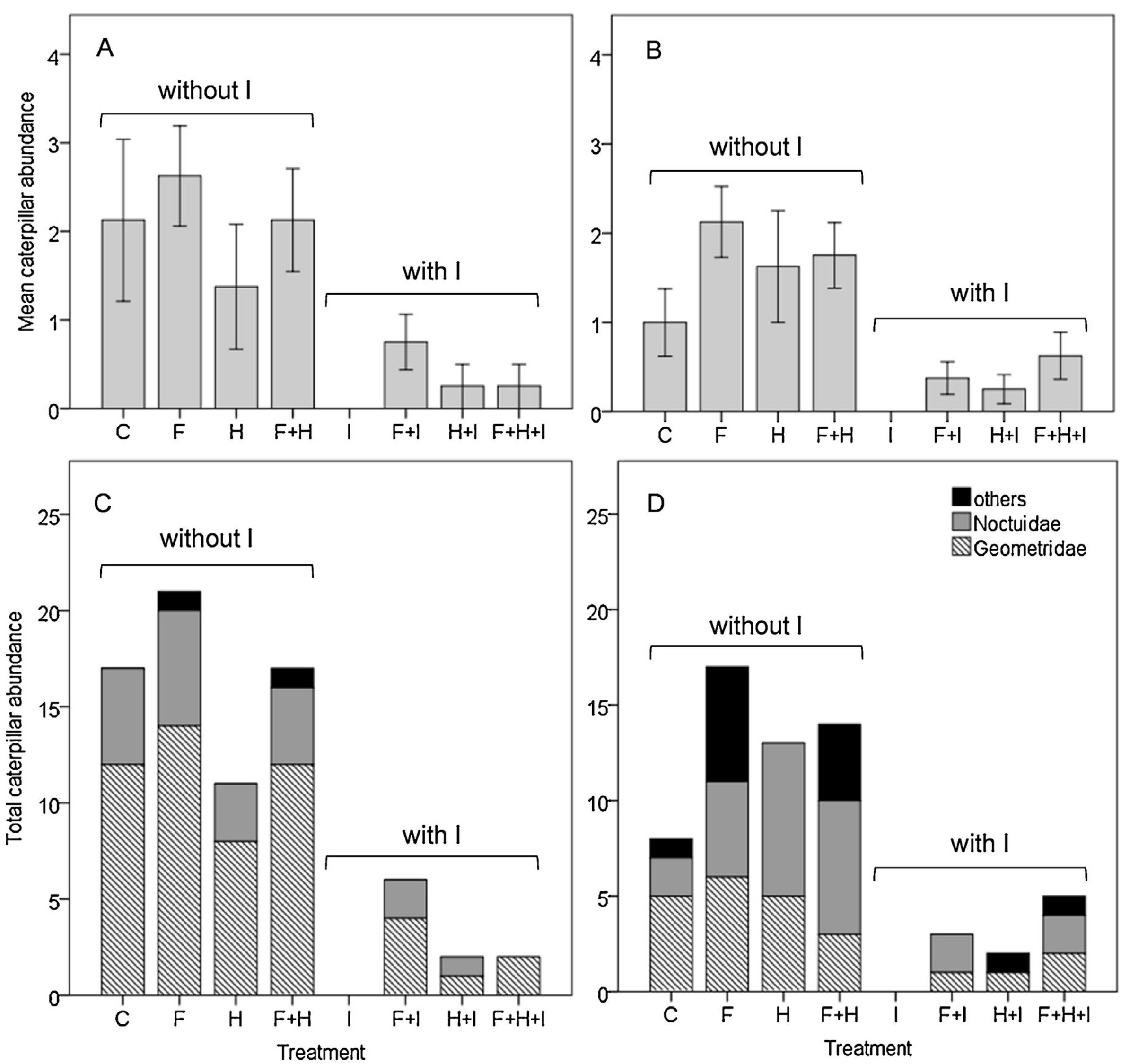

Fig. 3. Mean caterpillar number ± SE per plot and treatment (A, B) in the field experiment (treatments: C: control, F: fertilizer, H: herbicide, I: insecticide, F + H, F + I, H + I, and F + H + I; $N = 8$ replicates per treatment) and total number of caterpillars per family per treatment (C, D). (A, C) represent sampling date 1 (=6 days after insecticide treatment) and (B, D) represent sampling date 2 (=34 days after insecticide treatment). Families with low caterpillar numbers were pooled (others; (C): Tortricidae; (D): Erebidae, Lycaenidae, Nymphalidae, Pterophoridae, and Tortricidae).

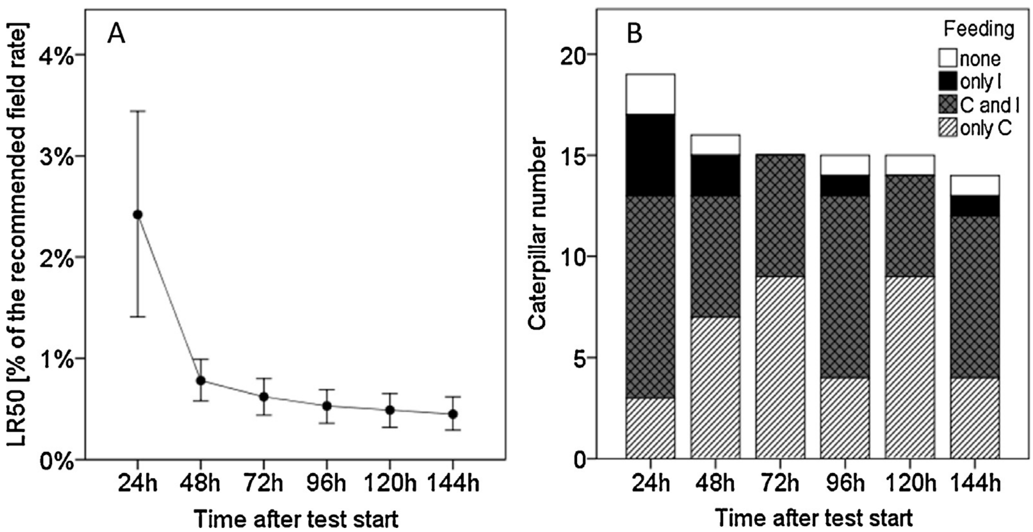

Fig. 4. (A) LR50 values (black dots) and confidence intervals (bars) of 14-day-old *Mamestra brassicae* caterpillars fed with insecticide-treated leaves (Karate Zeon, pyrethroid) for 24 h to 144 h. $N=5$ replicates per treatment, with 3 caterpillars per replicate. (B) Food choices of 15-day-old caterpillars at 24 h to 144 h after their introduction into test vessels. $N=20$, with one caterpillar per replicate. 'only C': caterpillars fed only untreated control leaves; 'only I': caterpillars fed only leaves treated with 1% of the recommended field rate of an insecticide (Karate Zeon); 'C and I': caterpillars fed untreated and insecticide treated leaves; 'none': no feeding. Dead caterpillars are not included.

and Noctuidae (without F ($N=32$): 0.28 ± 0.10; with F ($N=32$): 0.38 ± 0.13 caterpillars per plot). The herbicide treatment had no significant effect on the composition of the caterpillar community (PerManova; sampling 1: $p_{\text{herbicide}}=0.453$, sampling 2: $p_{\text{herbicide}}=0.647$).

3.3. Toxic and repellent effects of insecticide-treated host plants on Mamestra brassicae caterpillars

From the toxicity test, the results demonstrate that the insecticide affected *M. brassicae* caterpillars at low application rates. For example, the LR50 value after 48 h was 0.78% of the field rate (Confidence Interval (CI): 0.58–0.99%). The LR50 values decreased with increasing time to 0.45% (CI: 0.29–0.62%) after 144 h (Fig. 4a). All caterpillars in the control group survived (mortality $_{\text{control}}$: 0%).

Table 1
Results of the pollination and oviposition experiment with *Silene latifolia* plants.

	Control[a]	Insecticide[b]
Flowers		
Overall number of flowers	34	36
Pollinated flowers	34	26
Pollinated flowers per plant ((%); mean ± SE)	100 ± 0	72 ± 6
Seeds		
Seeds per flower (mean ± SE)	206 ± 25	194 ± 28
Seeds per pollinated flower (mean ± SE)	206 ± 25	269 ± 27
Seeds per plant (mean ± SE)	1243 ± 267[c]	1164 ± 212
Hadena eggs and caterpillars		
Overall number of *Hadena* offspring	18	11
Hadena offspring per flower (mean ± SE)	0.5 ± 0.1	0.3 ± 0.1
Hadena offspring per plant (mean ± SE)	3.1 ± 0.7[c]	1.8 ± 0.5

[a] Control: 5 plants with 6 flowers each and 1 plant with 4 flowers (=34 flowers)
[b] Insecticide: 6 plants with 6 flowers each (=36 flowers)
[c] The calculations of the numbers of seeds and *Hadena* offspring per plant are based on 6 flowers per plant. In the case of the one control plant that held 4 flowers, the numbers (911 seeds and 1 *Hadena* egg per 4 flowers) were increased by 50% (1367 seeds and 1.5 *Hadena* eggs, respectively) to be comparable to the other plants with 6 flowers.

In the feeding behavior experiment (repellence test), the caterpillars only occasionally fed solely on insecticide-treated leaves. The caterpillars primarily fed either on the control leaves or their diet consisted of a mixture of both treated and untreated leaves (Fig. 4b).

3.4. Effects of an insecticide on moth pollination and egg-laying behavior

The treatment with the insecticide resulted in a significant reduction in the number of pollinated flowers per *S. latifolia* plant (PerAnova, $p=0.004$). Approximately 30% of the insecticide-treated flowers were not pollinated and, hence, developed no seeds, whereas all of the control flowers produced seeds (Table 1). In addition, a multivariate analysis that included the number of seeds per flower and the number of *Hadena* offspring indicated a significant difference between the insecticide treatment and the control (PerManova, $p=0.005$). *Hadena bicruris* females only oviposited single eggs on the flowers, and overall, the number of *Hadena*-offspring (eggs or caterpillars) was reduced by nearly 40% on insecticide-treated plants compared with control plants (control: 18; insecticide: 11; Table 1). We recorded approximately 30% more seeds in the pollinated flowers of insecticide-treated plants (control: 206 seeds; insecticide: 269; Table 1).

4. Discussion

4.1. Caterpillars in field margins

Caterpillars depend on the availability of host plants for their development, whereas many adult Lepidoptera feed on nectar. Field margins are common elements in agricultural landscapes and provide habitats for various plant species (Joenje and Kleijn, 1994; Hamre and Austad, 1999; Tarmi et al., 2002). Hence, field margins represent potential habitats for adult and juvenile Lepidoptera (e.g., Feber et al., 1999), and wider field margins have the potential to increase the abundance and species richness of adult moths (Merckx et al., 2009, 2012). Though the occurrences of adult butterflies and moths in field margin habitats have been recorded in various studies (e.g., Boutin et al., 2011; Feber et al., 1996; Dover, 1999; Field et al., 2005, 2007; Kuussaari et al., 2007; Merckx et al., 2009, 2010, 2012), less information is available for their caterpillars (e.g., Feber et al., 1999).

In our first experiment, we sampled caterpillars in cereal field margins to determine whether these elements are used as habitats for the development of caterpillars. Overall, we found caterpillars from nine families (Fig. 2). However, as field margins can be strongly affected by the management of the adjoining agricultural site, which we hypothesized could influence the occurrence of caterpillars, we also sampled caterpillars in meadows, which represent a less disturbed semi-natural habitat element. Compared with the meadows, the field margins harbored a smaller number of caterpillars (Fig. 2). There are three factors that could contribute to this observation. First, the abundance of caterpillars could be affected by differences in habitat size. Meadows provide a greater patch size compared with field margins, and certain studies have found a positive correlation between patch size and population density for insects (Connor et al., 2000; Krauss et al., 2003). Nonetheless, connections between density and area are probably species specific; they depend on migration characteristics (e.g., Bowman et al., 2002; Hambäck & Englund 2005), and there seem to be differences between specialists and generalists (Krauss et al., 2003). Second, a linear shape of a habitat can be associated with a reduced number of individuals (Ewers and Didham, 2007) because linear elements (e.g., field margins) have a higher ratio of edge to interior and, hence, pressure from edge-related stressors (e.g., predation or parasitism, see Paton, 1994) might be more important than in non-linear habitats (e.g., meadows). Third, field margins are exposed to inputs of agrochemicals that might affect caterpillar abundances either directly or indirectly (Feber et al., 1996; Longley and Sotherton, 1997). Possible indirect effects include changes in the abundance, diversity, or quality of host plants; for instance, we found fewer flowering plant species in field margins compared to meadows.

4.2. Effects of agrochemicals

To assess the effects of agrochemicals (fertilizer, herbicide, and insecticide) on caterpillars, their abundance and community composition were studied in field experiment plots, which received single or combined applications of these three agrochemicals (see Section 2.2).

4.2.1. Fertilizer

The application of fertilizer tended to increase the abundance of caterpillars in the plots (Fig. 3). Studies on the effects of an increase in nitrogen levels on the abundance and development of herbivores, including Lepidoptera, found positive (Wheeler and Halpern, 1999; Haddad et al., 2000; Butler et al., 2012) and negative effects (Fischer and Fiedler, 2000; Kula et al., 2014). Such differences between species may depend on their adaption to increased nitrogen levels in host plants (Kula et al., 2014) or to changes in microclimate caused by advanced plant growth (WallisDeVries and Van Swaay, 2006). Possible explanations for the higher caterpillar numbers in the fertilized plots could be (1) that the additional supply of nitrogen increased the host plant quality for certain species (Haddad et al., 2000) or (2) that the fertilizer inputs altered the composition of plant communities (Schmitz et al., 2014a), thereby promoting the occurrence of certain plant species (Boatman, 1994; Inouye and Tilman, 1995; Schmitz et al., 2014a) that might be beneficial to the herbivores that rely on them. However, the responses of plant species to fertilizer inputs also vary, and a number of smaller species tend to be overgrown by grasses (Kleijn and Snoeijing, 1997; Schmitz et al., 2014a). When evaluating the effects of fertilizer inputs over several years, fertilizer was found to reduce plant species richness (Kleijn and Snoeijing, 1997; Schmitz et al., 2014a) and, hence, fertilizer inputs may decrease the abundance and diversity of caterpillars and other herbivores as well. We assessed the effects of fertilizer on caterpillar abundance and community composition in the second year of the field experiment in which the plant community composition had not been altered in response to the fertilizer treatments (Schmitz et al., 2014a). However, a year later (in 2012), the plant community of a plot receiving a fertilizer treatment could be clearly distinguished from that of a control plot (see the results for the community composition analysis in Schmitz et al., 2014a), which could possibly also lead to changes in the occurrences and abundances of caterpillars.

4.2.2. Herbicide

In addition to fertilizers, plants can also be affected by herbicides (Kleijn and Snoeijing, 1997; Schmitz et al., 2014a). These effects include not only lethal effects but also sublethal effects, such as reductions in flowering and seed production (Schmitz et al., 2014b). As a result, herbicides can change the density of individual plant species as well as the composition of the plant community and, furthermore, the resources that the plants provide for herbivores and pollinators (Schmitz et al., 2013; 2014a, b). Although lethal effects directly diminish the availability of host plants, decreased flowering might reduce the nectar resources for adult Lepidoptera. A decreased seed number could affect not only lepidopteran species, which feed on seeds during their development (e.g., *H. bicruris*), but also diminish the abundance of plant species in the future (Schmitz et al., 2014b) and thereby negatively affect the Lepidoptera that rely on these species as caterpillar hosts. Moreover, sublethal herbicide application rates might reduce the quality of host plants and cause higher mortality rates or prolonged development times for herbivores (Kjær and Elmegaard, 1996; Hahn et al., 2014a). Nonetheless, there were no significant effects of the herbicide applications on caterpillar abundance detected in the plots of the field experiment. One reason might be that herbicide effects on the host plant quality (Hahn et al., 2014a) and plant resources appear to be rather species-specific, and their identification would most likely require another sampling method that would allow the assessment of individual host plant species with their associated caterpillars. However, although individual plant species displayed herbicide effects even during the first year of the field experiment, changes in the plant community composition were first apparent in the third year (Schmitz et al., 2014a). Accordingly, effects on caterpillars might possibly also be detected at this time.

4.2.3. Insecticide

The most marked effects on caterpillar abundance and community structure in the field experiment were caused by the insecticide. In plots receiving an insecticide treatment, the abundance of caterpillars was extremely low compared with plots receiving no insecticide application (Fig. 3). Significant reductions in caterpillar numbers were even recorded during the second sampling period, nearly five weeks after the insecticide application. There are two possible explanations. First, the insecticide used, a pyrethroid, might be directly toxic to the caterpillars at lower concentrations than the recommended field rate. To obtain further insight into this topic, we assessed the effects of leaves treated with the same insecticide used in the field experiment (Karate Zeon) on the survival of 14-day-old *M. brassicae* caterpillars. The caterpillars exhibited a high mortality rate even at low insecticide rates. The LR50 value (48 h) for *M. brassicae* caterpillars was approximately 0.78% of the recommended field rate (=0.059 g a.i. ha^{-1}). This amount of pesticide input would occur at a distance of 3–4 m from the applied agricultural field in an arable spray drift scenario (Rautmann et al., 1999). Other studies have also confirmed that caterpillars can be highly sensitive to insecticides. For example, Cilgi and Jepson, 1995 detected toxic effects of deltamethrin deposits on cabbage leaves for *Pieris brassicae* caterpillars at rates of 0.19% of the field application rate (=0.012 g a.i. ha^{-1}). Pyrethroids can also have ovicidal activities against lepidopteran eggs (Tysowsky and Gallo, 1977; Gist and Pless, 1985). In the field experiment, the insecticide was applied at 30% of the recommended field rate. In view of the low LR50 values for *M. brassicae* caterpillars in the laboratory assessment, the lepidopteran offspring (eggs and caterpillars) in the insecticide-sprayed plots might have died from contact with the sprayed plant surfaces, but more information on the toxic effects on other caterpillar species would be necessary to prove this theory.

Second, certain pesticides, including pyrethroids, are known to repel caterpillars and adult moths (Kumar and Chapman, 1984; Gist and Pless, 1985; Blair, 1991; Abivardi et al., 1998). To test for such effects on caterpillars, we observed the feeding behavior of *M. brassicae* caterpillars when they were forced to choose between leaves treated with 1% of the recommended field rate of a pyrethroid insecticide and untreated control leaves. The caterpillars in the feeding experiment did not completely avoid the insecticide-treated leaves, but they appeared to prefer insecticide-free leaves (Fig. 4B), which indicates minor antifeedant effects. In cases in which the caterpillars had fed on both leaves, it appeared that more plant material had been consumed from the untreated leaves, but this was not quantified during the experiment. However, the addition of untreated leaves in the test systems increased the survival of the *M. brassicae* caterpillars. In the toxicity test, the mortality in the 1% treatment was approximately 75% after 48 h, whereas only 25% of the caterpillars died after the same amount of time in the feeding experiment.

In addition to the effects on caterpillars, we also included experiments that assessed the effects of this insecticide on adult moths. For female Lepidoptera, the choice of an oviposition site is a particularly crucial event because caterpillars are rather immobile and thus depend on a suitable host plant (Renwick and Chew, 1994). Therefore, females typically assess both the physical and chemical characteristics of a plant prior to oviposition (Renwick and Chew, 1994). Certain lepidopteran species have been observed to avoid oviposition on insecticide-treated surfaces (Kumar and Chapman, 1984; Gist and Pless, 1985; Seljasen and Meadow, 2006). Thus, in the field experiment, the reduced caterpillar numbers in the insecticide-treated plots might also result from reduced oviposition by the adult females. To test this hypothesis, we assessed the egg deposition of moths (*H. bicruris*) in a semi-field experiment using *S. latifolia* plants (see Section 2.4). There were approximately 40% fewer *H. bicruris* eggs on the insecticide-treated flowers, indicating that *Hadena* moths avoided oviposition on insecticide-treated flowers. Hence, the low caterpillar numbers in the insecticide-treated plots of the field experiment might result not only from the toxic effects of the insecticide but also from the repellent effects on the adults.

4.3. Insecticide effects on the pollination of Silene latifolia

In addition to the lethal or sublethal effects on moths and their offspring, insecticides can also affect pollination and the seed number of *S. latifolia* flowers. Overall, flowers of *S. latifolia* sprayed with insecticide were less likely to be pollinated compared with flowers of control plants. Pollination is an important service in ecosystems, and approximately 87% of angiosperm plant species rely on animal pollination (Ollerton et al., 2011). Little information is available concerning the role of moths as pollinators in ecosystems (Clinebell et al., 2004; Alarcon et al., 2008; Devoto et al., 2011), although moths have been observed to carry pollen of various plant species. However, if deterrent effects of insecticides reduce the probability that flowers will be pollinated, this could negatively affect the biodiversity of agro-ecosystems, but more data are necessary to confirm this hypothesis.

We recorded approximately 30% more seeds in the pollinated flowers of the insecticide-treated plants than in the control (Table 1). This increase might be caused by a longer foraging time of the visiting moths on the sprayed flowers (see Labouche and Bernasconi, 2010), as a reduced number of flower visitors might result in an increased availability of nectar at each flower. The higher seed number in the pollinated insecticide flowers compensated for the reduced overall number of pollinated flowers (Table 1, see seeds per flower and seeds per pollinated flower) and, hence, we would not expect negative consequences for *S. latifolia* populations in the field if female plants were sprayed with the applied insecticide (Table 1, seeds per plant). Indeed, in the case of *S. latifolia*, the reduced oviposition of *H. bicruris* and the associated reduction in seed predation by the caterpillars might even have beneficial effects on the reproduction of the plant species. However, moths exhibit strong temporal fluctuations in their abundance and community composition (Devoto et al., 2011), and long-term observations and the consideration of other plant species are thus necessary to gain further insight into this topic.

5. Conclusion

Field margins are an important habitat for moths in agricultural landscapes and are used as a developmental habitat for caterpillars, but field margins are also exposed to inputs of agrochemicals. Overall, our experiments illustrate that moths are affected by low and realistic rates of agrochemicals in various ways. Insecticides can have particularly strong negative effects on Lepidoptera, acting lethally on the offspring or as repellents to deter oviposition by adult females. Herbicides and fertilizers might affect the availability and quality of host plants.

Caterpillars are an important food source for birds, shrews, and various invertebrates. Hence, negative effects on their abundances most likely influence other species. Furthermore, a reduction in the pollination service provided by adult moths might also have an impact on plant species. For this reason, field margins should be protected from any input of agrochemicals.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2015.04.002.

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