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Butterfly richness and abundance in flower strips and field margins: the role of local habitat quality and landscape context

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ABSTRACT

Flower strips, which are created on arable land by sowing species-rich seed mixtures, are considered to have a high potential to counteract species decline of butterflies in the agricultural landscape. However, it remains largely unexplored how various factors (design, habitat quality, landscape context) interact to determine the occurrence of butterflies in flower strips. Therefore, butterflies were surveyed in 15 flower strips differing in age (first and second growing season). Flower strips were compared with 15 field margins, which were adjacent to arable land and were dominated by grasses. The field studies were conducted during two summers (2013, 2014) in Lower Saxony (Germany). Additionally, based on a literature study, 17 environmental variables likely to be decisive for the occurrence of butterflies were identified and recorded during these field studies or analyzed in GIS. Supported by a PCA, 8 environmental variables for flower strips and 7 for field margins, were selected and included in linear mixed-effects models in order to calculate their effect on butterflies.

We documented 19 butterfly species and 1,394 individuals in the flower strips and 13 species and 401 individuals in the field margins. The number of flowering plant species was the key factor for the occurrence of butterflies - both in flower strips and field margins. The diversity of the surrounding landscape (Shannon-Index H) had an additional significant influence on butterflies in flower strips, with more species and individuals being observed on areas with a lower Shannon-Index.

Number of flowering plant species is the key driver of butterfly diversity and abundance, which improves the habitat quality of flower strips in agricultural landscapes. In order to promote butterflies optimally, flower strips must have a good supply of flowers even over several years. This requires careful design and management, as flower supply often decreases with increasing age of the flower strips. The study indicates that flower strips have a particularly high effect in structurally simple landscapes.

1. Introduction

Recent declines of pollinators are startlingly evident (Potts et al., 2010). Since butterflies react rapidly to changes in habitat quality, they are especially affected (Hambler et al., 2011; Thomas et al., 2004) and the decline has already been observed in previously widespread butterfly species (Fox et al., 2015). Land use intensification is a main driver of the decline of butterfly diversity (Brittain et al., 2010; Fox et al., 2015; Warren et al., 2001).

In principle, flower strips, defined here as strips on arable land which are managed specifically by sowing a species-rich seed mixture (e.g. Supplementary data: Table A.1) with the aim of creating flower-rich and structurally rich habitats, can counteract biodiversity loss in temperate farmland (Haaland et al., 2011; Ouvrard et al., 2018; Sutter et al., 2018; Uyttenbroeck et al., 2015). Studies show that flower strips can especially promote butterflies in the agricultural landscape: Flower strips were more species-rich and/or more individual-rich than other habitats of the agricultural landscape (Aviron et al., 2011: flower strips vs. conventional fields, Haaland and Bersier, 2011: flower strips vs. extensively used meadows, Haaland and Gyllin, 2010: flower strips vs. greenways). For that, however, it is important that certain basic conditions and design options are taken into account, such as the composition of seed mixture, suitable soil conditions, the management of the flower strips and the life span of the flower strips (Aviron et al., 2011; Haaland and Bersier, 2011;

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Haaland and Gyllin, 2010).

There is still a considerable need for research on optimizing the design of flower strips (Holland et al., 2015; Uyttenbroeck et al., 2017) and it is still unclear which factors determinate species richness and abundance of butterflies in flower strips. Previous studies have revealed that various factors at the local level influence the occurrence of butterflies in flower strips (e.g. Woodcock et al., 2014: flora and management; Dollar et al., 2013: management; Pywell et al., 2011a: flora, management and age). For other habitats, however, several studies have already shown that both local scale habitat characteristics, as well as land use and connectivity with surrounding landscapes, are relevant factors for the occurrence of butterflies (Luppi et al., 2018; Sybertz et al., 2017; Delattre et al., 2010; Ouin and Burel, 2002). However, the transfer of results from other semi-natural habitats to flower strips is inadequate, as flower strips represent new landscape elements (Wagner et al., 2014). In Germany and Switzerland, the seed mixtures of flower strips generally do not contain any grass species (Haaland et al., 2011). Hence, they can hardly be equated with species-rich meadows or field margins, defined here as occasionally mown, grass-dominated strips adjacent to arable land. Flower strip species composition also differs from perennial tall herb communities and ruderal. Therefore, the explicit analysis of flower strips is necessary, especially when examining how a variety of different factors of different scales (design of flower strips, habitat quality and landscape context) interact to determine the occurrence of butterflies.

In light of these issues, the aim of our study was to find and to compare key factors that determine butterfly occurrence in flower strips and field margins. Utilizing linear mixed-effect models we wanted to answer the following research questions: (1) Which factors (site-specific characteristics, including growing season or vegetation, as well as heterogeneity and connectivity of the surrounding landscape) determine the occurrence of butterflies (species richness and abundance) in flower strips? (2) Which of these factors determine the occurrence of butterflies in field margins? (3) How do flower strips affect adjacent areas? (4) How can this knowledge be used to promote the occurrence of butterflies in the agricultural landscape?

2. Materials and methods

2.1. Study sites

The study was carried out in the vicinity of Zeven (district of Rotenburg, Lower Saxony, Germany (53°17′38.47 N, 9°16′33.51 E), Fig. 1). About 70% of the districts area is used for agriculture (LSN, 2018).

Ten flower strips, with five having repeat measurements, resulting in a total sample size of 15 flower strips, and 15 field margins were examined (Table 1). The flower strips studied were created on maize fields by sowing a species-rich seed mixture of 13 perennial flowering plant species (Supplementary data: Table A.1). During their life span of 1.5 years, no tillage, fertilization, or plant protection measures were permitted on the flower strips. Field margins were located next to maize fields, were grass-dominated and were mown occasionally. Concerning the flower strips, we focused on different ages (growing seasons, Table 1). The flower strips of the first growing season (2013) were also examined in 2014 when they were in the second growing season. Given the high degree of interannual variability in butterfly occurrences, five new flower strips in their first growing season were additionally investigated in 2014. All flower strips were 6 m wide (Table 1), were created by the same 'Rotenburger seed mixture 2013' (Supplementary data: Table A.1) and were located between maize fields and unsealed farm tracks. The field margins were examined in 2014 and were between 1 and 4 m wide

Table 1
Overview of the investigated flower strips and field margins.

a) Flower strips			
Year	**Width**	**Growing season**	**Number of study sites**
2013	6 m	1. Growing season	n = 5
2014	6 m	1. Growing season	n = 5
2014	6 m	2. Growing season [1]	n = 5
b) Field margins			
Year	**Width**	**Adjacent area**	**Number of study sites**
2014	2–4 m	Maize fields	n = 5
2014	1–2 m	Flower strips 1. growing season	n = 5
2014	1.5–3 m	Flower strips 2. growing season	n = 5

[1] repetition measurements of the 5 flower strips from 2013.

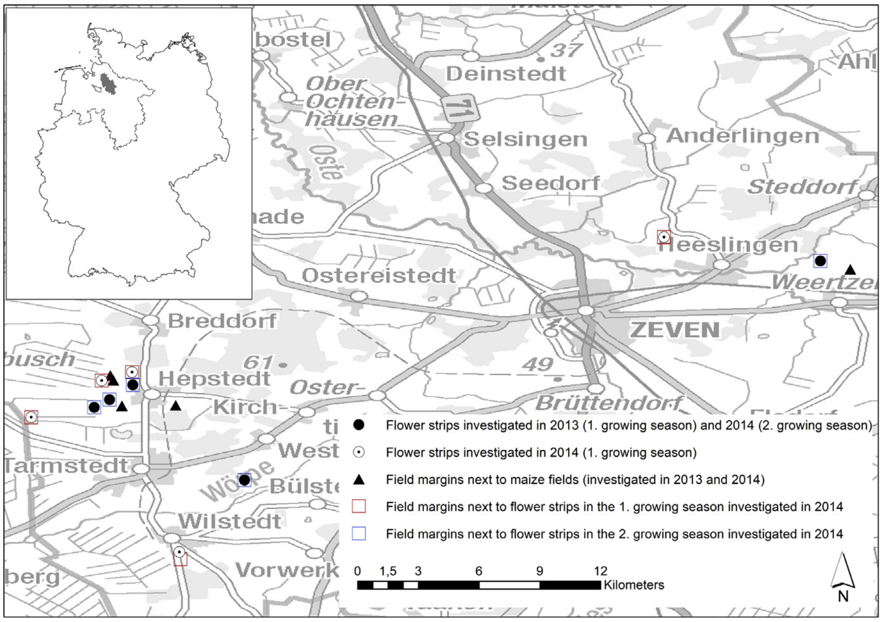

Fig. 1. The study area district Rotenburg (Wümme) (grey section in the small picture) is located in Lower Saxony (outlined in black), Germany. The study sites are located in the vicinity of Zeven (data basis: GeoBasis-DE / BKG, 2017; MU Nds., 2018).

(Table 1). The field margins were also located next to maize fields. Moreover, we additionally investigated field margins next to flower strips of the first and second growing season in order to analyze the influence of neighboring flower strips.

2.2. Response variables: number of butterfly species and individuals

The butterflies were surveyed between June and August 2013 and 2014 by standardized visual observations of imagines using line-transects following Settele (1999). A transect of 125 m was sampled for each study site. The width of the transect was based on the width of flower strips of 6 m. Due to the narrower field margins, the transect width was based on the width of the respective field margin (1–4 m, Table 1). Consecutive dates of surveys were blocked in rounds (2–7 days in each round). In 2013, we conducted 4 rounds with a total of 8 inspections per study site. In 2014, there were 5 rounds with a total of 11 inspections per study site.

If individual species could not be determined, they were included in the protocols as species complexes (*Artogeia rapae/napi*, *Thymelicus lineola/sylvestris*) or families (Blues). For taxonomic determination we used Settele and Steiner (2009) and Tolman and Lewington (2009). The nomenclature follows the latter.

The number of recorded butterfly species (as a proxy for species richness, defined by the total sum of recorded species) and the number of individuals (as a proxy for abundance, defined by the total sum of recorded individuals) were used as response variables.

2.3. Explanatory variables: characteristics of the habitat type and the surrounding landscape

2.3.1. Determination, description and recording of variables affecting butterflies

A systematic literature review within the Web of Science database was carried out using the search terms 'butterfl*' and 'flower strip*' or 'field margin' in the categories 'title', 'summary' and 'keywords' for the publication years from 2014 to 2018 (*stands for any group of characters). Further publications were supplemented using the snowball system, whereby additional references were included from the bibliographies of the Web of Science articles. Based on the literature review, we identified the main parameters that are demonstrably influential for the occurrence of butterflies in flower strips, field margins or comparable structures in the agricultural landscape (Table 2). As the spatial scale plays an important role in the analysis and evaluation of biodiversity (Ekroos et al., 2013; Ekroos and Kuussaari, 2012; Gabriel et al., 2010), we structured the variables into two scales.

Based on the results of the literature review (Table 2), we selected seven main parameters of different spatial scales which could be described by different variables (Table 3). In total, we recorded 16 variables in flower strips and 11 variables in field margins.

To record the vegetation structure (Table 3), five sample plots (1 × 1m) were randomly distributed on each study site (random quadrats, Traxler, 1997) and surveyed in both years, four times between June and August. At each collection date, the location of sample plots was re-measured (temporary plots, Traxler, 1997). The floristic features (Table 3: Abundant flowering of the study sites) were recorded at the same time as the vegetation structure and also with the same number of repetitions. The variables of landscape heterogeneity and of connectivity were calculated by GIS-analyses within a 1 km buffer around each study site (Table 3). The landscape heterogeneity (Shannon Diversity Index, Shannon Evenness Index and Edge Density; Lang and Blaschke, 2007) are based on CORINE Land Cover Data which were generalized to a minimum size of 10 hectares (GeoBasis-DE / BKG, 2012). The connectivity (effective mesh size; Jaeger, 2000) was estimated from digital topographic maps and orthophotos (MU Nds., 2018). On this basis, all linear elements representing potential habitats or corridors for butterflies

Table 2

Variables determining butterfly occurrences in flower strips, field margins or comparable structures in the agricultural landscape. References indicating investigated flower strips are underlined.

Main parameters (group)	Sources
Year of investigation	Aviron et al. (2011); Aviron et al. (2007a); Feber et al. (1996)
Scale: Study site	
Habitat type	Aviron et al. (2011); Aviron et al. (2007a); Berg et al. (2011); Feber et al. (1996); Haaland and Bersier (2011); Kuussaari et al. (2007); Weibull et al. (2003); Wix and Reich (2018)
Habitat quality	Dover and Settele (2009); Ekroos and Kuussaari (2012); Kuussaari et al. (2007)
Patch geometry (e.g. width, length, shape, size)	Clausen et al. (2001); Cole et al., (2015); Delattre et al. (2010); Dover (1996); Dover and Settele (2009); Field et al. (2007), 2006, 2005; Korpela et al. (2013); Kuussaari et al. (2007); Pywell et al. (2004); Saarinen et al. (2005); Skórka et al. (2013); Sparks and Parish (1995); Sybertz et al. (2017); Wix and Reich (2018)
Insolation	Clausen et al. (2001), Dover (1996), Pywell et al. (2004)
Growing season/Age	Haaland and Bersier (2011); Korpela et al. (2013); Pywell et al. (2011a); Wix and Reich (2018)
Vegetation structure (e.g. amount of trees and shrubs, vegetation high)	Berg et al. (2013); Clausen et al. (2001); Dover et al. (2000); Haaland and Gyllin (2010); Pywell et al. (2004); Sparks and Parish (1995); Sybertz et al. (2017); Wix and Reich (2018)
Flora (e.g. floral composition, grass-herb-ratio, abundant flowering, nectar plants and larval food plants)	Berg et al. (2013); Clausen et al. (2001); Cole et al., (2015); Dover et al. (2000); Dover (1996); Ekroos et al. (2008); Feber et al. (1996); Field et al. (2006); Gabriel et al. (2010); Haaland and Bersier (2011); Haaland and Gyllin (2010); Kuussaari et al. (2007); Lebeau et al., (2016); Meek et al. (2002); Noordijk et al. (2009); Pywell et al. (2011a); Pywell et al. (2004); Saarinen et al. (2005); Saarinen (2002); Skórka et al. (2013); Sparks and Parish (1995); Sybertz et al. (2017); Woodcock et al., (2014); Wagner et al. (2014); Wix and Reich (2018)
Management (e.g. grazing, (partial) mowing (time), removal of cuttings, use of pesticides)	Aviron et al. (2007b); Dollar et al. (2013); Feber et al. (1996); Giuliano et al., (2018); Kruse et al., (2016); Noordijk et al. (2009); Pywell et al. (2011a); Saarinen (2002); Snoo (1999); Snoo et al. (1998); Valtonen et al. (2006); Woodcock et al., (2014)
Scale: Surrounding landscape	
Land use of the adjacent field (e.g. habitat type, type of crop)	Dover (1996); Pywell et al. (2004); Saarinen et al. (2005); Sybertz et al. (2017)
Management of the adjacent field (e.g. organic farming)	Clausen et al. (2001); Jonason et al. (2011); Rundlöf et al. (2008); Rundlöf and Smith (2006); Sybertz et al. (2017); Taylor and Morecroft (2009)
Shelter by adjacent structures (e.g. hedges, bushes, buffer strips)	Clausen et al. (2001); Dover et al. (1997); Dover (1996); Pywell et al. (2004); Sybertz et al. (2017)
Landscape heterogeneity, landscape type, landscape composition (percentage of organically managed farmland in a district)	Aviron et al. (2007a), 2011; Berg et al. (2011); Dainese et al., (2015); Dover and Settele (2009); Ekroos and Kuussaari (2012); Gabriel et al. (2010); Haaland and Bersier (2011); Jonason et al. (2011); Korpela et al. (2013); Ouin and Burel (2002); Rundlöf et al. (2008); Rundlöf and Smith (2006); Šálek et al., (2018); Skórka et al. (2013); Sybertz et al. (2017); Toivonen et al. (2017), 2016, 2015; Weibull et al. (2003); Weibull et al. (2000)
Connectivity (e.g. isolation, fragmentation, barriers)	Aviron et al. (2007b); Brückmann et al. (2010); Delattre et al. (2013), 2010; Dover and Settele (2009); Ouin and Burel (2002)

Table 3

Overview of all explanatory variables recorded for each flower strip or field margin. Non-bold x in columns FS (Flower strips) and FM (Field margins) indicate variables that were recorded in the respective habitat type. Bold variables and X in columns FS (Flower strips) and FM (Field margins) are the selected variables (for selection see chapter 2.4).

Main parameter	Variable	Abbreviation	Description	FS	FM
Characteristics of the survey	**Year**	**year**	Year in which the surveys were carried out.	**X**	
Scale: Study sites					
General characteristics of the study site	**Width**	**width**	Absolute width of the study site [m].	x	**X**
	Age/Growing season	**gro_sea**	The life span of flower strips. Variable coded in R: 1 = flower strips which are in their first growing season, 2 = flower strips which are in their second growing season	**X**	
	Adjacent area	**adj_area**	Habitat type adjacent to the study site. Variable coded in R: 0 = maize field, 1 = flower strip which are in their first growing season, 2 = flower strip which are in their second growing season		**X**
Vegetation structure of the study sites	**Open-ground proportion**	**op_ground**	Average open-ground proportion [%] of all five sample plots (1 × 1m) of a study site. This variable was recorded at each round.	**X**	**X**
	Dominant height of vegetation	**dom_veghigh**	For each vegetation layer, the average of the vegetation cover and the vegetation height was formed from the five sample squares. The average vegetation height of the layer with the highest coverage represents the dominant vegetation height in cm. This variable was recorded at each round.	x	**X**
	Maximum height of vegetation	**max_veghigh**	Maximum value of the vegetation height [cm] of all five sample plots (1 × 1 m) of a study site. This variable was recorded at each round.	**X**	x
Abundant flowering of the study sites	**Number of flowering species**	**no_flower**	Sum of all recorded flowering, herbaceous plant species (the plant species of the seed mixture included) with a medium abundance on the study site (from a cover level of 10%). This variable was recorded at each round.	**X**	**X**
	Cover level/Stand cover of flowering species	cover_flower	Cover level [%] of all recorded flowering, herbaceous plant species (the plant species of the seed mixture included). This variable was recorded at each round.	x	x
Growth of the plants from the seed mixture	Total number of plant species	no_seedmix_total	Sum of recorded plant species of the seed mixture (from a cover level of 1%). This variable was recorded at each round.	x	
	Number of flowering plant species of the seed mixture	**no_seedmix_flow**	Sum of recorded flowering plant species of the seed mixture. This variable was recorded at each round.	**X**	
	Cover level/Stand cover of plant species of the seed mixture	cover_seedmix_total	Sum of cover level [%] of all recorded plant species of the seed mixture (from a cover level of 1%). This variable was recorded at each round.	x	
	Cover level/Stand cover of flowering plant species of the seed mixture	cover_seedmix_flow	Sum of cover level [%] of all recorded flowering plant species of the seed mixture. This variable was recorded at each round.	x	
Scale: Surrounding landscape					
Landscape heterogeneity	**Diversity of habitat types**	**shan_H**	Shannon Diversity Index (H) calculated from habitat types within a 1 km buffer around a study site. $H = \sum_{i=1}^{m} Pi^{*}\ln Pi$ P = proportion of the habitat type i, m = number of habitat types (Lang and Blaschke, 2007). The proportion of each occurring habitat type within a 1 km buffer around a study site was determined on the basis of Corine Land Cover 10 (GeoBasis-DE / BKG, 2012)	**X**	**X**
	Evenness of habitat types	shan_E	Shannon Evenness Index (Even) calculated from habitat types within a 1 km buffer around a study site. $Even = \frac{H}{\ln m}$ H = Shannon Diversity Index (see description of shan_H), m = number of habitat types (Lang and Blaschke, 2007). The proportion of each occurring habitat type within a 1 km buffer around a study site was determined on the basis of Corine Land Cover 10 (GeoBasis-DE / BKG, 2012)	x	x
	Structural diversity	ed	Edge Density: Total edge within a 1 km buffer around a study site in meters per hectare (Lang and Blaschke, 2007). The edge density was determined on the basis of Corine Land Cover 10 (GeoBasis-DE / BKG, 2012) and calculated with the Extension for ArcGIS "V-LATE 2.0 beta"	x	x
Connectivity	**Effective mesh size**	**mesh**	Effective mesh size calculated from potential habitats and corridors for butterflies within a 1 km buffer around a study site in ha. $mesh = \frac{1}{At}\sum_{i=1}^{n} A_i^2$ n = number of patches, A_i = sizes of the n patches; A_t = total area of the 1 km buffer (Jaeger, 2000). The effective mesh size was determined on the basis of digital topographic maps, orthophotos and Corine Land Cover 10 (GeoBasis-DE / BKG, 2012; MU Nds., 2018)	**X**	**X**

outside villages were digitized (e.g. country lanes, field margins or strips along ditches). This dataset was intersected with potentially suitable butterfly habitats from the CORINE Land Cover Dataset (relevant for the study area: pasture, meadows and other permanent grasslands under agricultural use (code 231), natural grassland (code 321), moors and heathland (code 322), GeoBasis-DE / BKG, 2012).

2.4. Selection of explanatory variables

To reduce the number of variables according to the sample size and to avoid redundancy, a principal component analysis (PCA) after standardization (Quinn and Keough, 2014) was carried out for each of the main parameters (Figs. 2 and 3). In order to clearly represent the ecological relationships of individual variables and to facilitate the practical application of the model (survey of the variables in the field or

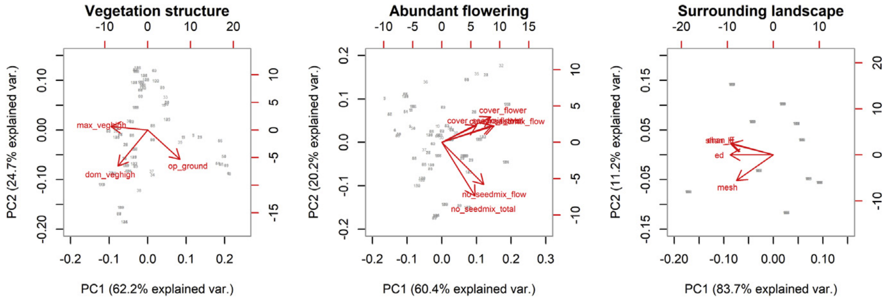

Fig. 2. Principal component analysis for potential fixed-effects of the three main parameters (vegetation structure, abundant flowering and surrounding landscape) for the model of flower strips (numbers indicate single study sites on individual investigations). For abbreviations of the variables see Table 3.

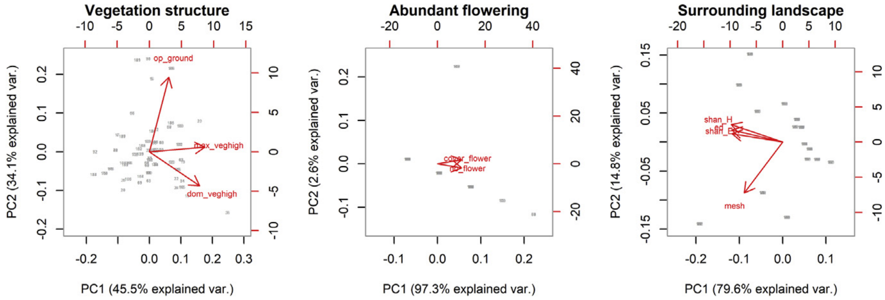

Fig. 3. Principal component analysis for potential fixed-effects of the three main parameters (vegetation structure, abundant flowering and surrounding landscape) for the model of field margins (numbers indicate single study sites on individual investigations). For abbreviations of the variables see Table 3.

implementation of the variables in practice), we chose individual, non-redundant variables of the different grouped variables and did not use the components of the PCA. Variables associated with the first and second component were selected (Supplementary data: Table B.1-B.6, Figs. 2 and 3). When groups of several variables showed association with one component (e.g. Fig. 2, Abundant flowering), the variable selected from each group was the one which could be surveyed in the field with least effort (e.g. number of flowering species rather than cover of flowering species). Therefore, we were able to exclude seven highly redundant variables for flower strips and four for field margins.

As the annual fluctuation of butterflies is crucial and as the life span (age) of flower strips can be controlled during the creation of flower strips, their influence was assessed as decisive. With regard to the results of the literature search (Table 2), the different widths of the field margins (Table 1) were also classified as relevant variables. The adjacent area of the field margins (maize or flower strip, Table 1) was crucial for evaluating the impact of flower strips on these areas. Therefore, once their influence was proved significant, the four variables (year and growing season for flower strips, width and adjacent area for field margins) were consistently included as fixed effects in the respective models.

Finally, eight variables were selected for the models of flower strips and seven variables for the models of field margins (written in bold and marked with '**X**' in Table 3 in columns FS or FM).

2.5. *Random-effects*

Some flower strips were examined in 2013 as well as in 2014 and they cannot be considered as independent variables without further criteria. Since the year of the investigation (fluctuation, weather conditions) has a decisive influence on the occurrence of butterflies (Table 2), it was used as a variable to define independent data. Furthermore, as the butterflies were recorded on blocked dates and against the background of phenological changes, the consecutive dates (defined as rounds) were taken into account in the statistical analyses. Therefore, we considered one study site for each round of the respective year of investigation as independent data basis for the models (Table 4). We thus included as random effects: the variance between study sites, the interaction of study site and year as well as the interaction of study site, year and round: $(1|\text{site}) + (1|\text{site:year}) + (1|\text{site:year:rd})$. Since the field margins were only examined in 2014, the year variable could be removed from the data structure of the random-effects in the models for field margins.

2.6. *Linear mixed-effects models*

We used linear mixed-effects models fit by maximum likelihood (ML) estimations. The exploratory graphics generated showed a right-skewed distribution. For the assumption of normally distributed data (residuals and random-effects), the number of species and individuals was log-transformed ($\log(y+1)$). Time-correlated measurements for the time series of the individual study sites were assumed (corAR1-structure).

The selection of the fixed effects was based on forward hierarchical selection (Kuckartz et al., 2013; Quinn and Keough, 2014), involving the sequential addition of the effects in a pre-defined way. The order was directed from local scale to that of landscape scale. Based on an ecological background, the main parameters that were expected to have the greatest influence on the butterflies were included first. By the order of inclusion, the additional effect of a variable could be tested. For model comparison and selection, likelihood ratio tests (LRT, Bolker et al., 2009; Zuur et al., 2009) and corrected Akaike information criterion (AICc) were used (Burnham and Anderson, 2002). 95% confidence intervals were computed for the fixed effect parameters of the final mixed effect models

Table 4
Overview of the random-effects.

Variable	Abbreviation	Description
Year	year	Year in which the surveys were carried out
Round	rd	The butterflies were recorded on blocked dates. The blocked appointments were summarized in time as rounds of 2–7 days
Study site	site	Name of the study site

fitted by restricted maximum likelihood (REML). For these final models, the assumptions (homoscedasticity, normality of residuals and random-effects) were visually inspected by residual plots and Q-Q plots. As compared to the untransformed data, the log-transformed data showed no or reduced deviations from normal distribution (QQ-normal-plot), and residual vs. fitted plots showed no heteroscedasticity.

Analyses were calculated in the R language and environment (RStudio Team, 2016). For linear mixed-effect models the package 'nlme' was used (Pinheiro et al., 2018). Post-hoc comparisons of means between different types of adjacent areas at pre-specified coavariate values (width) were performed using R package 'emmeans' (Lenth, 2018). AICc were calculated with the package 'MuMIn' (Kamil, 2018). Some graphics were created with 'ggplot2' (Wickham, 2016).

3. Results

3.1. Butterflies in flower strips and field margins

In total, we recorded 19 butterfly species and 1,795 individuals (Supplementary data: Table C.1-C.2). Only in the flower strips could all 19 butterfly species be detected. Seven species were solely documented here: *Agrodiaetus amandus*, *Colias crocea, Lycaena phlaeas*, *Pieris brassicae*, *Polygonum c-album*, *Polyommatus icarus*, *Vanessa cardui*). With 1,394 individuals compared to 401 individuals, three times as many individuals were observed in the flower strips as in the field margins. No endangered species were found (Reinhardt and Bolz, 2011) and only one grassland specialist according to Swaay et al. (2006), *Agrodiaetus amandus*, could be recorded. Considerable proportions of the recorded butterflies were classified as generalists at a European level (14 species) or as using a variety of biotopes (4 species).

3.2. Effects of habitat quality and surrounding landscape on butterflies

3.2.1. Interactions between selected explanatory variables

In general, we recorded a higher abundance of flowering species in the flower strips in the first growing season than in the second growing season. Though the medians were similar (first growing season: 4 species, second growing season: 3 species), the maximal number of species differed with 11 species recorded in flower strips in the first growing season compared to only 5 species in flower strips in the second growing season.

With an average width of 3 m (median), the field margins next to maize fields were much wider than those next to flower strips (median of 1.5 m; both, flower strips in the first and second growing season).

3.2.2. Impact of fixed-effects on butterflies in flower strips

Sequential testing of a total of eight explanatory variables in different model comparisons (Table 5) identified three variables which form well-supported predictors of the occurrence of butterflies (species richness and abundance) in flower strips: the growing season, the number of flowering species and the diversity of habitat types.

The model including the variables 'growing season' and 'year of investigation' showed significant influence on both the number of species and the number of individuals in contrast to the model including only the 'year of investigation' (Table 5, Test mod1s/mod1i vs. mod2s/mod2i). In both years the numbers of species and individuals were similar (median: 2 species (2013 and 2014), 7 individuals (2013) and 7.5 individuals (2014), range: 0–6 species (2013) and 0–8 species (2014), 0–35 individuals (2013) and 0–42 individuals (2014)). On account of this fact we tested the model without the influence of the year (mod3s/i): Excluding the 'year of investigation' showed no significant impact (Test mod2s/mod2i vs. mod3s/mod3i). For our investigation period it can

Table 5

Sequentially fitted linear mixed-effects models to analyze the occurrence of butterfly species (a) and individuals (b) in flower strips and the sequential likelihood ratio tests of added fixed effects (LRT: Test statistic of likelihood ratio test) with indication of significance (p-value, sign). Degree of freedom (df) and corrected Akaike information criterion (AICc) are provided for each fitted model. The selected variables/models used in the subsequent model comparisons (LRT, Test), as well as the models with lowest AICc (for the respective analysis step) are written in bold letters. The final model selected for use is underlined.

Flower strips

a) Response variable: Total number of butterfly species (log (1 + species))

Model	Variables	Test	LRT	p-value	sign.	df	AICc
Study design							
mod1s	~ year					7	236.4
mod2s	~ year + gro_sea	mod1s vs. mod2s	7.0198	0.0081	**	8	231.6
mod3s	**~ gro_sea**	mod2s vs. mod3s	2.0624	0.1510	n.s.	7	**231.4**
Abundant flowering							
mod4s	**~ gro_sea + no_flower**	mod3s vs. mod4s	30.9056	<.0001	***	8	**202.7**
mod5s	~ gro_seaf + no_flower + no_seedmix_flow	mod4s vs. mod5s	1.4260	0.2324	n.s.	9	203.6
Vegetation structure							
mod6s	~ gro_sea + no_flower + op_ground	mod4s vs. mod6s	2.5624	0.1094	n.s.	9	202.4
mod7s	~ gro_sea + no_flower + max_veghigh	mod4s vs. mod7s	2.4305	0.1190	n.s.	9	202.6
Surrounding landscape							
mod8s	**~ gro_sea + no_flower + shan_H**	mod4s vs. mod8s	5.4554	0.0195	*	9	**199.5**
mod9s	~ gro_sea + no_flower + shan_H + mesh	mod8s vs. mod9s	0.8519	0.3560	n.s.	10	201.0

b) Response variable: Total number of butterfly individuals (log(1+indiv))

Model	Variables	Test	LRT	p-value	sign.	df	AICc
Study design							
mod1i	~ year					7	405.4
mod2i	~ year + gro_sea	mod1i vs. mod2i	8.1659	0.0043	**	8	399.5
mod3i	**~ gro_sea**	mod2i vs. mod3i	0.7511	0.3861		7	**398.0**
Abundant flowering							
mod4i	**~ gro_sea + no_flower**	mod3i vs. mod4i	26.8662	<.0001	***	8	**373.4**
mod5i	~ gro_sea + no_flower + no_seedmix_flow	mod4i vs. mod5i	1.1671	0.2800	n.s.	9	374.5
Vegetation structure							
mod6i	~ gro_sea + no_flower + op_ground	mod4i vs. mod6i	2.5665	0.1092	n.s.	9	373.1
mod7i	~ gro_sea + no_flower + max_veghigh	mod4i vs. mod7i	1.5627	0.2113	n.s.	9	374.1
Surrounding landscape							
mod8i	**~ gro_sea + no_flower + shan_H**	mod4i vs. mod8i	7.8347	0.0051	**	9	**367.8**
mod9i	~ gro_sea + no_flower + shan_H + mesh	mod8i vs. mod9i	1.1399	0.2857	n.s.	10	369.0

Signif. codes: ***p < 0.001; **p < 0.01; *p < 0.05; ·p < 0.10; n.s. p ≥ 0.10.

therefore be concluded that the ‘growing season’ has a more decisive influence on butterfly occurrence than the ‘year’. Since the model including only the ‘growing season’ (mod3s/mod3i) had a lower degree of freedom and a lower AICc-value than the model including ‘growing season’ and ‘year’ (mod2s/mod2i), the model mod3s/mod3i was selected for the following model comparisons. Adding the ‘number of flowering species’ to the model showed a highly significant difference on both, number of butterfly species and individuals (mod4s, mod4i, $p < 0.0001$). In addition, this factor considerably improved the model quality in comparison to the previous model (AICc: 231.4 (mod3s) to 202.7 (mod4s); 398.0 (mod3i) to 373.4 (mod4i)). Neither the ‘number of flowering species of the seed mixture’ nor the vegetation structure (‘open-ground proportion’ and ‘maximum high of vegetation’) had a significant additional influence on the occurrence of butterflies (mod5s-mod7s; mod5i-mod7i). With regard to the surrounding landscape, including the ‘diversity of habitat types’ in the models (mod8s, mod8i) leads to a significant difference and to an improvement of the model quality compared to the previous models (mod4s, mod4i). The ‘effective mesh size’ had no significant influence neither on the number of species nor on the number of individuals (mod9s, mod9i).

The median number of species and individuals in flower strips in the first growing season (3 species, 8 individuals) was higher than the one in the flower strips in the second growing season (1 species, 3 individuals, Fig. 4). The number of butterfly species of flower strips in the first growing season decreased by a factor of 0.65 or increased by a factor of 1.20 (95% CI) in comparison to the flower strips in the second growing season. In terms of the number of individuals, the factor was 0.39–1.22 (95% CI).

Greater flowering resources increased species richness as well as abundances (Fig. 4). When the number of flowering species increased by 1, the number of butterfly species increased on average by 10–19% and the number of individuals by 17–36% (95% CI).

Here, the interaction between growing season and number of flowering resources has to be taken into account (Chapter 3.2.1). We recorded more butterflies (species and individuals) in flower strips with a high abundance of flowering species (Fig. 5). Furthermore, only the flower strips in the first growing season showed a high number of flowering resources with over 6 plant species. Overall, the flower strips in the first growing season were more species- and individual-rich than those in the second growing season in terms of butterflies and flowering resources (the latter only in the number of species).

The landscape heterogeneity had a negative, significant effect on butterfly occurrences. The Shannon-Index H could not be as clearly visualized with the raw data (Fig. 4), as this effect was estimated as an

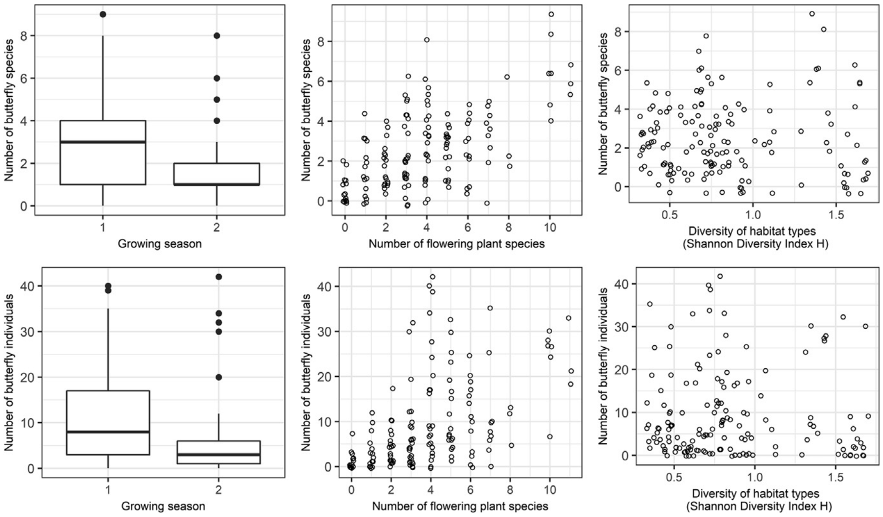

Fig. 4. Boxplots and scatterplots of the fixed-effects with significant influence of the number of butterfly species and individuals (Table 5) in flower strips (n = 150 observations: 8 inspections per study site in 2013, 5 study sites in 2013 and 11 inspections in 2014 per study site, 10 study sites in 2014, see Table 1). In order to make the graphic clearly legible, the dots in the scatterplots were jittered.

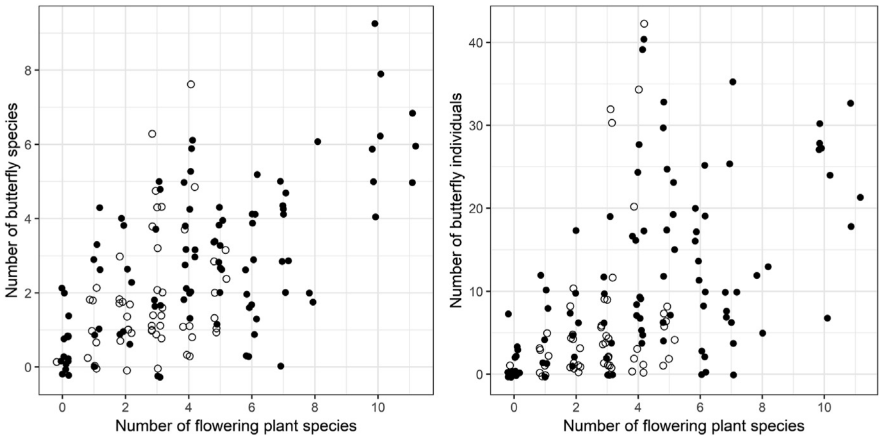

Fig. 5. Relation between the number of species or individuals in flower strips and the number of flowering species subdivided by the growing season of the flower strips (open circles = first growing season, closed circles = second growing season; n = 150 observations: 8 inspections per study site in 2013, 5 study sites in 2013 and 11 inspections in 2014 per study site, 10 study sites in 2014, see Table 1). In order to make the graphic clearly legible, the dots were jittered.

additional influence, i.e. after the influence of the effects previously included in the model - growing season, number of flowering plants - were calculated out of the data. The scatterplots indicate that high numbers of butterfly species and individuals accumulate at low Shannon-Index H values. However, some high species and individual numbers also occur at a high Shannon-Index H. Finally, if the Shannon-Index H increased by 1 unit, butterfly species decreased by 47% or remained almost the same with only a reduction of 1% (95% CI). Concerning the number of individuals, the negative effect was more evident by a factor decrease of 0.28–0.88 (95% CI). Because the Shannon-Index H itself encompassed only a very limited range (0.42–1.61), the increase in the slope of this variable by 1 was a substantial rise and so the CI varied in such a high range.

3.2.3. Impact of fixed-effects on butterflies in field margins

Sequential testing of a total of seven explanatory variables in different model comparisons (Table 6) identified three variables that are strongly associated with the occurrence of butterflies (species richness and abundance) in field margins: width, adjacent area and abundant flowering.

The field margins along the flower strips were significantly narrower than the field margins along maize fields (Chapter 3.2.1), requiring an examination of the interaction between ‘width’ and ‘adjacent area’. The interaction between ‘width’ and ‘adjacent area’ described the occurrence of butterflies (number of species and individuals) better than their additive inclusion (modAs/modAi vs modBs/modBi, Table 6). The inclusion of the ‘number of flowering species’ in these models with the interaction (modCs, modCi) showed a highly significant influence ($p < 0.0001$) and distinctly improved the model quality (the number of species and individuals). None of the further factors concerning the vegetation structure or the surrounding landscape indicated a significant difference or improvement of model quality compared to the model modCs or modCi.

The maximum number of species and in particular the number of individuals in field margins along flower strips (independent of the growing season) were higher than these in field margins along maize fields (Fig. 6). In comparison to field margins along flower strips in the first growing season, the number of observed species in field margins along maize fields differed by a factor of 0.72–1.97, the number of individuals by a factor of 0.57–2.69 (95% CI). For the comparison between the field margins along maize fields and the field margins along flower strips in the second growing season, the factor was 0.86–2.88 (number of species) or rather 0.70–4.56 (number of individuals). Furthermore, the field margins along flower strips in the first growing season were more species-rich and individual-rich than those along flower strips in the second growing season. These two types differed by a factor of 0.78–2.24 (species) or 0.64–3.28 (individuals).

The field margins next to the maize fields (width of 2–4 m) were much wider than the field margins along the flower strips (1–2 m, Fig. 7). Nevertheless, the highest numbers of butterflies (especially number of individuals) were recorded in the much narrower field margins along the flower strips.

The supply of flowering resources is strongly associated with butterfly abundance: A higher number of flowering plants attracted more butterfly species and individuals (Fig. 6). In average, with one additional flowering species the number of butterfly species increased by 14–44% and the number of individuals by 28–84% (95% CI).

4. Discussion

4.1. Species range of butterflies in flower strips and field margins

In the flower strips as well as in the field margins we have mainly recorded generalists. Other studies also indicated that flower strips usually promote generalists (e.g. Haaland et al., 2011). However, although no endangered species and only one grassland specialist could be detected in this study, this is not due to a minor effect of the flower strips or field margins. Rather, it has to be considered that the regional

Table 6

Sequentially fitted linear mixed-effects models to analyze the occurrence of butterfly species (a) and individuals (b) in field margins and sequential likelihood ratio tests of added fixed effects (LRT: Test statistic of likelihood ratio test) with indication of significance (p-value, sign). Degree of freedom (df) and corrected Akaike information criterion (AICc) are provided for each fitted model. The selected variables/models used in the subsequent model comparisons (LRT, Test), as well as the models with lowest AICc (for the respective analysis step) are written in bold letters. The final model selected for use is underlined.

Field margins

a) Response variable: Total number of butterfly species (log (1 + species))

Model	Variables	Test	LRT	p-value	sign.	Df	AICc
Study design							
modAs	~ width + adj_area					10	255.6
modBs	**~ width * adj_area**	modAs vs. modBs	7.6489	0.0218	*	8	**252.5**
Abundant flowering							
modCs	**~ width * adj_area + no_flower**	modBs vs. modCs	17.2564	<.0001	***	11	**237.5**
Vegetation structure							
modDs	~ width * adj_area + no_flower + op_ground	modCs vs. modDs	0.0003	0.9867	n.s.	12	239.8
modEs	~ width * adj_area + no_flower + dom_veghigh	modCs vs. modEs	0.0502	0.8228	n.s.	12	239.8
Surrounding landscape							
modFs	~ width * adj_area + no_flower + shan_H	modCs vs. modFs	0.0355	0.8506	n.s.	12	239.8
modGs	~ width * adj_area + no_flower + mesh	modCs vs. modGs	0.5813	0.4458	n.s.	12	239.3

b) Response variable: Total number of butterfly individuals (log(1+indiv))

Model	Variables	Test	LRT	p-value	sign.	df	AICc
Study design							
modAi	~ width + adj_area					8	370.8
modBi	**~ width * adj_area**	modAi vs. modBi	6.10398	0.0473	*	*10*	**369.2**
Abundant flowering							
modCi	**~ width * adj_area + no_flower**	modBi vs. modCi	21.3515	<.0001	***	11	**350.2**
Vegetation structure							
modDi	~ width * adj_area + no_flower + op_ground	modCi vs. modDi	0.1977	0.6566	n.s.	12	352.3
modEi	~ width * adj_area + no_flower + dom_veghigh	modCi vs. modEi	0.0405	0.8404	n.s.	12	352.5
Surrounding landscape							
modFi	~ width * adj_area + no_flower + shan_H	modCi vs. modFi	0.0049	0.9440	n.s.	12	352.5
modGi	~ width * adj_area + no_flower + mesh	modCi vs. modGi	0.5978	0.4394	n.s.	12	351.9

Signif. codes: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ·$p < 0.10$; n.s. $p \geq 0.10$.
Variables: * = Interaction between the two variables

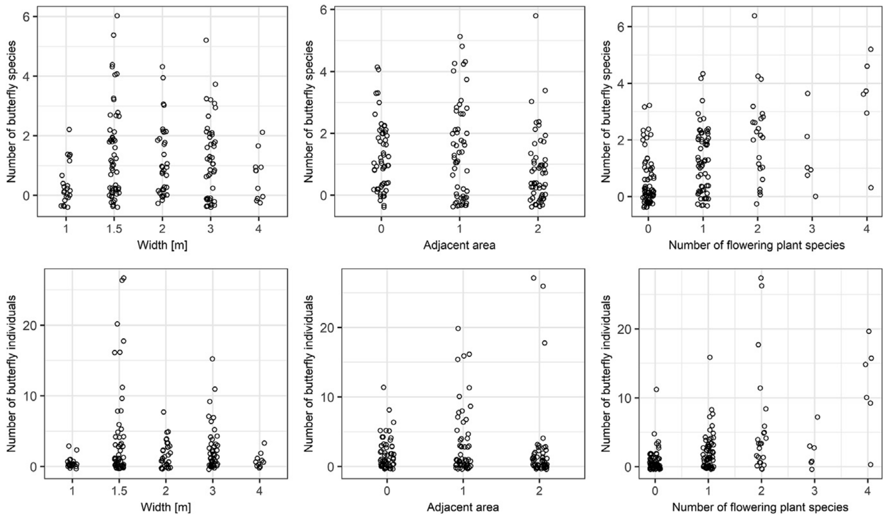

Fig. 6. Scatterplots of the fixed-effects with significant influence of the number of butterfly species and individuals (Table 6) in field margins (n = 165 observations: 11 inspections per study site, 15 study sites, see Table 1). In order to make the graphic clearly legible, the dots in the scatterplots were jittered.

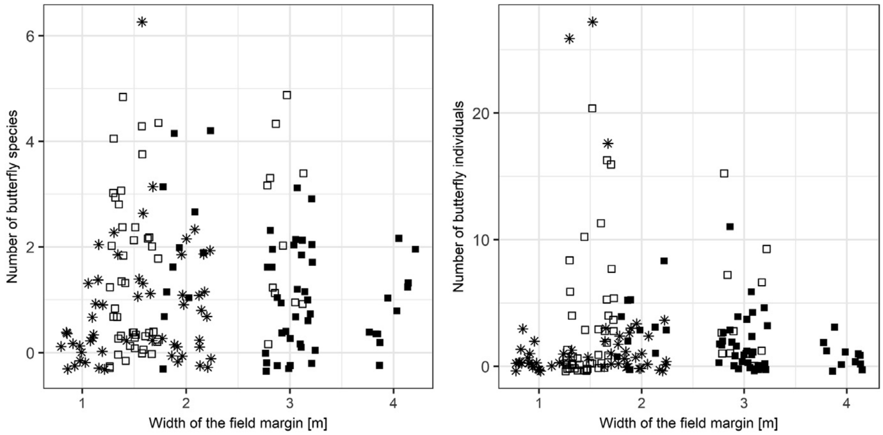

Fig. 7. Scatterplots of the number of species or individuals in field margins and the interaction between the width of the field margins and the adjacent area (closed squares = field margins next to maize field, open squares = field margins next to flower strips in the first growing season, asterisks = field margins next to flower strips in the second growing season; n = 165 observations: 11 inspections per study site, 15 study sites, see Table 1) In order to make the graphic clearly legible, the dots in the scatterplots were jittered.

species pool in a structurally simple agricultural landscape is limited. Furthermore, species of butterflies that were formerly widespread in the agricultural landscape have also been affected by population declines (Gaston and Fuller, 2007; Haaland et al., 2011; Wallisdevries et al., 2012).

4.2. *Factors determining butterflies in flower strips and field margins*

4.2.1. *Habitat quality*

Of all the investigated variables determining the occurrence of butterflies, a high number of flowering plant species was the key driver - both in flower strips and in field margins. Interestingly, neither the vegetation height nor the proportion of open-ground had a significant impact on butterflies in either habitats. However, this may be due to the fact that these variables only affect some species and we have considered the total number of species and individuals, or that our data set was too low to detect these effects.

The life span of flower strips can range from several months to several years (Haaland et al., 2011). In our study the flower strips in the first growing season were generally more species-rich (butterflies and flowering plants) and more individual-rich (butterflies) than those in the second growing season. Other studies also showed a reduction in flowering abundance with increasing age of the flower strips, as successional changes may result in an increased proportion of grasses (Frank et al., 2012; Huusela-Veistola and Vasarainen, 2000; Pywell et al., 2011a). However, a good selection of the seed mixture and a good germination rate and growth can slow down the progress of succession (Aviron et al., 2011). Therefore, the supply of flowering resources over several years must be ensured by a properly selected and planted seed mixture according to the respective soil characteristics (possibly in combination with specific management practices, Haaland et al., 2011).

4.2.2. *Landscape context*

Our study indicates that flower strips in landscapes with lower habitat diversity (Shannon Diversity Index H) are richer in species and individuals (Table 5). Hence, especially in structurally simple landscapes, which are dominated by arable land that still has a certain proportion of semi-natural habitats (SNH), the flower strips are of high relevance. This result is in line with that of previous studies which have shown that the effect of agri-environmental schemes (AES) is highest in structurally simple, rather than in cleared or in complex landscapes (inter alia for flower strips Scheper et al., 2013, for organic farming: Roschewitz et al., 2005, for local biodiversity conservation management in general Tscharntke et al., 2012). On the other hand, there are studies that have demonstrated the opposite, that biodiversity increases with higher diversity of the surrounding landscape (for field margins Sybertz et al., 2017, for farms Weibull et al., 2000). These conflicting results can be attributed to various causes, such as the differences in study design (survey of different habitats and on different levels (study site level or farm level)), the inconsistent definition of landscape heterogeneity

(Shannon-Index or percentage of different biotopes, varying radii for landscape characteristics) or variations in regional species pools in different landscapes. Above all, differing agricultural intensity of the landscapes seems to be decisive (Ekroos and Kuussaari, 2012; Scheper et al., 2013; Tscharntke et al., 2012). In structurally cleared landscapes (<1% SNH definition after Scheper et al., 2013) as well as in complex landscapes (complex landscapes: > 20% SNH), the effect of AES is low. However, in structurally simple landscapes (1–20% SNH), the SNHs are of great importance for species and their effects are strongest there (Scheper et al., 2013; Tscharntke et al., 2012). We could only detect a significant explanatory power of the habitat diversity of the surrounding landscape in the flower strips and not in the field margins. Obviously, SNH must have a certain quality to produce this positive effect. For a final explanation of the conflicting results concerning the influence of the habitat diversity on the surrounding landscape, more detailed data and analyses are required.

Contrary to our assumption, the connectivity of the landscape had no significant impact on the butterflies in our data set, neither in flower strips nor in field margins. One reason for this could be that the study sites were already sufficiently well connected to the surrounding landscape. Our study area is characterized by a rural environment, where several semi-natural habitats (like grassland, field margins, field paths or hedgerows) are present and provide a network for mobile species such as butterflies. Since for different European butterflies a mean daily displacement from 23-165 m (for sites <0.7 km) or 48–660 m (for sites >0.7 km) could be recorded by different multisite mark-release-recapture studies (Stevens et al., 2010).

The analyses of butterfly occurrences on field margins next to flower strips showed that flower strips positively affect adjacent areas: Butterflies were more abundant on field margins next to flower strips than on field margins next to maize fields. Wagner et al. (2014) also demonstrated this effect. They found a higher number of species and individuals on maize fields near flower strips than on maize fields further away from flower strips.

4.3. Conclusions: recommendations to improve the situation of butterflies in the agricultural landscape

Because of their particularly high supply of flowering resources, flower strips are a suitable measure to promote butterflies in the agricultural landscape. Moreover, many other insects can benefit from the creation of flower strips as well (Haaland et al., 2011; Ouvrard et al., 2018; Pywell et al., 2011b). It is crucial to ensure a high number of flowering species by a seed mixture suitable to site conditions and a proper seed bed preparation for germination rate and growth (Aviron et al., 2011).

For butterflies, it is additionally essential that the species composition of the seed mixture takes into account the requirements of the non-adult life stages (Feber et al., 1996; Haaland and Bersier, 2011; Pywell et al., 2011a). The two most frequently detected species in our study (*Artogeia rapae* and *Artogeia napi*) use brassicas as host plants and brassicas were abundant in the "Rotenburger seed mixture 2013" (Supplementary data: Table A.1). Furthermore, the time between sowing and ploughing of the flower strips should not be shorter than two growing seasons, as the non-adult life stages (e.g. the eggs deposited in the vegetation) will be destroyed when the flower strips are converted back into arable land after the first growing season (Haaland and Bersier, 2011).

The optimum age and management of the flower strips must be considered in connection with the seed mixture used. For example, an annual strip needs to be re-sown every year, while legume-dominated pollen and nectar mixtures (as in Pywell et al., 2011a) might last 3–5 years, and perennial wildflower mixtures (as in Aviron et al., 2011) might last up to ten years. Therefore, opinions differ on the optimal age of flower strips. Haaland and Bersier (2011) recommend a minimum life span of five years. Pywell et al. (2011a) showed that flower strips do not offer an optimal number of flowering species after more than three to four years. In contrast, there are results from Switzerland, where up to ten-year-old flower strips without significant influence on butterfly occurrence were found (Aviron et al., 2011). Aviron et al. (2011: 505) stated that ‘suitable soil conditions and management of WFS [wildflower strips] allow the maintenance of diversified vegetation over years’. However, Pywell et al. (2011a: 863) explained that flower strips ‘are only effective for 3–4 years despite intensive cutting management’ and recommended a re-establishment of flower strips after three years in order ‘to guarantee a continuity of pollen and nectar resources’. Another reason for the different recommendations could be the differing ecological conditions (i.e. climate, soil) of the study areas in Switzerland (Aviron et al., 2011) and Yorkshire, UK (Pywell et al., 2011a).

Flower strips have the greatest effect in structurally simple landscapes, so they should primarily be used in such landscape sections to counteract biodiversity loss (Scheper et al., 2013; Tscharntke et al., 2012). Flower strips of different growing seasons and with different ploughing periods should be planted next to each other (see also Korpela et al., 2013), because on the one hand, flower strips of different growing seasons have various plant species. On the other hand, the ploughing of the flower strips in an area should not take place in the same year, so that a sufficient supply of flowers is continuously available.

Considerably fewer butterflies were detected in the field margins than in the flower strips. However, the field margins also had a considerably lower number of flowering plant species (Figs. 4 and 6). But on the one hand, the grass-dominated field margins can promote other species than flower strips. In our study, the three most common species in the field margins (*Aphantopus hyperantus*, *Thymelicus lineola* and *Maniola jurtina*) depend on different grass species as host plants. Furthermore, knowing that the amount of flowering resources has a decisive influence on the occurrence of butterflies, the improvement of field margins towards a richer supply of nectar and host plants is particularly interesting. In this way, the field margins could offer a high diversity of flowering resources and also be permanently present in the landscape. So-called ‘improved field margins’, which are created by sowing a certain mixed seed mixture (annual, perennial herbs and native grasses), are part of the agri-environmental program in Switzerland (Eggenschwiler et al., 2013; Jacot et al., 2007). They should remain permanently in the landscape and develop into species-rich structural elements with a long-lasting abundance of flowers, for which the annual mowing of half of the strip is recommended. Thus, field margins certainly also have a high potential to counteract biodiversity loss in the agricultural landscape and they must also be considered in conservation measures (Aviron et al., 2011; Kuussaari et al., 2007).

Declarations

Author contribution statement

Nana Wix: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Michael Reich: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data.

Frank Schaarschmid: Contributed reagents, materials, analysis tools or data.

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Competing interest statement

The authors declare no conflict of interest.

Additional information

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