Agricultural intensification drives butterfly decline

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Abstract. 1. Severe losses of insects have taken place over major parts of Europe. This negative trend is assumed to be largely the result of agricultural intensification.

2. To analyse potential factors causing this loss of species, we assessed butterfly communities at 21 grassland patches. Seventeen of these were distributed across an agricultural landscape dominated by crop fields; four were embedded in two adjoining managed semi-natural grassland areas. We assessed environmental parameters such as patch size and habitat quality for each grassland patch. We further incorporated the surrounding land-cover considering different degrees of land-use intensity. We classified butterfly species into generalists and specialists according their ecological and behavioural characteristics.

3. As in the managed semi-natural reference grasslands, species richness and abundance were higher in patches surrounded by extensively used grasslands and unsprayed crop fields, and lower in patches surrounded by sprayed crop fields. Furthermore, blossom density positively affected butterfly occurrence.

4. Our data revealed that specialised butterfly species mainly occur in managed semi-natural grassland sites, and are largely absent from other grassland plots embedded in the agricultural matrix.

5. Our study underlines the negative impacts of intense conventional agriculture on butterfly species richness and abundance and reveals the urgent need for more nature-friendly cultivation methods. In situ experiments may help to understand and disentangle single drivers causing this negative trend.

Key words. Agricultural intensification, butterflies, insect decline, pesticides, semi-natural grasslands.

Introduction

Severe decreases of biodiversity are taking place across the globe (Dirzo et al., 2014). It is largely consensus that these declines are, to a large proportion, caused by the agricultural intensification starting after World War II (Robinson & Sutherland, 2002). If focusing on insects, existing studies have indicated losses in species richness and severe shifts in species community compositions, with most communities today being dominated by generalist species (Habel et al., 2016 with references therein). Furthermore, other studies indicate significant losses of biomass of flying insects (Hallmann et al., 2017), with cascading effects across trophic levels (Hallmann et al., 2014).

Potential factors causing these negative trends are manifold, but most of them are driven by agricultural industrialization (Thomas, 2016). Large-sized crop fields cause a
homogenization of landscapes and thus increases barrier effects for many species (Batáry et al., 2017; Hass et al., 2018). Subsequently, exchange of individuals among patches is restricted which diminishes long-term persistence of many taxa (Hanski, 1999; Krauss et al., 2003). In parallel, remaining habitats are often small and isolated and provide only limited resources and thus reduce the survival probability of species and local populations (Melbourne & Hastings, 2008). Atmospheric nitrogen influxes from traffic, industry and agriculture negatively impact habitat quality, especially in nitrogen-limited ecosystems such as semi-natural grasslands (Wallis de Vries & Van Swaay, 2006). Furthermore, pesticides are known to negatively impact insect diversity, either directly due to drifting insecticides (Geiger et al., 2010), or indirectly by the elimination of potentially important nectar sources and/or larval food plants with herbicides, showing a trade-off between weed control and insect occurrence (González-Varo et al., 2013).

Thus, drivers are manifold and often may synergise or, less frequently, antagonise each other. In this study, we assessed butterfly communities at 21 grassland patches in south-eastern Germany, with 17 study sites on grassland patches across an agricultural landscape with a high proportion of arable fields, and four study sites located in two larger areas of semi-natural grasslands, which are managed for nature conservation (the Dietersheimer Brenne and the Garchinger Heide). For each study site, we collected data on environmental parameters (such as size of the grassland and blossom density to express habitat quality). Furthermore, we considered the land-cover within a 200 m buffer, set around each study site, and did a detailed land-cover classification. We assigned butterflies into two groups, generalists and specialists, according to their dispersal behaviour (Bink, 1992). With our data, we address the following research questions:

1. Do butterfly community compositions differ between grassland patches managed for agriculture or conservation?
2. Which explanatory variables are of highest relevance explaining differences in butterfly species richness and abundance?

Material and methods

Data collection

Our study region is located east of Munich in south-eastern Germany. It represents an intensively used agricultural landscape dominated by arable fields, but two remaining larger semi-natural grassland sites, the Dietersheimer Brenne and the Garchinger Heide. For this study, we selected 21 grassland patches, which are scattered across this landscape, with 17 patches surrounded by agriculture and four patches located in the large semi-natural grasslands, managed for nature conservation. All patches selected were at least 300 m distant from each other. For each study patch, we assessed the following environmental parameters: grassland size (m²) (measured with a hand-held GPS-device, Garmin Etrex), and blossom density (number of blossoms per m², counted in five plots per patch, which were set randomly, and which was redone during each butterfly assessment). We counted the number of blossoms of all flowering plants. We classified the land-cover within a 200 m radius around each study patch. This 200 m radius coincides with frequently observed home range sizes of butterflies (see Settele et al., 2009; Clobert et al., 2012). For this land-cover assessment, we considered the following categories: Forest, extensively used grassland (i.e. hay meadows), sprayed crops, non-sprayed crops and others (e.g. buildings, streets, paths, water bodies). All land-cover data are given in Appendix S1.

For each study patch, we assessed all butterflies for about 10 min during five visits from May to July 2018. These assessments were done by transect walks: butterflies were observed or netted during good weather conditions (i.e. sunny, temperature ≥20 °C, moderate to no wind, see Pollard & Yates, 1993). Presence–absence and the abundance observed were recorded for each butterfly species. Species were identified either directly in the field while observing or by catching and using a field book (Settele et al., 2000), or by taking photographs (and determining the species based on these photographs afterwards). An overview of the data used is given in Table 1. An overview of the raw data of all butterflies assessed is given in Appendix S2.

Butterflies were classified into generalist and specialist species according to their ecological demands during the larval (monophagous, oligophagous, polyphagous, 1–3) and adult stage (one habitat, habitat complex, several habitat complexes, 1–3), as well as according to their dispersal behaviour (sedentary, mobile at the landscape level, migratory across landscapes, 1–3). This classification was derived based on data taken from Bink (1992), and slightly modified according local conditions in our study area. Subsequently, we created mean values across these three parameters considered (ecological demands during the larval and adult stage, and dispersal behaviour); values below 1.5 were considered as specialists; values above 1.5 as generalist species. All raw data for each species are given in Appendix S3.

Statistics

We used general linear and generalised linear (log-link function and Poisson error structure) models, and one-way ANOVA to relate landscape characteristics (predictors) to species richness, species abundance and the percentage of specialist species in a focal community (response variables). As we were particularly interested in the strength
of the effects of the predictors on the response variables, we focused on the general linear model approach that allows for a better interpretation of effect sizes (here we used partial $\eta^2$). To account for possible deviations from the constraints on general linear modelling (linear dependencies, normal error structure), we additionally provided respective results of the generalised linear model in Appendix S4: Table S4. Multicollinearity was moderate among predictors ($r < 0.5$) with the exception of the proportion of crops sprayed with pesticides (abbreviated: sprayed crop %) and the proportion of extensively used fields and grasslands (abbreviated: ext. use/grasslands %). These variables were negatively correlated ($r = -0.79$), which might have influenced parameter estimation.

Additionally, we used the Akaike model selection (AICc) to infer the most informative set of predictors (Table 2).

We studied potential differences of community composition using two approaches: First, we used the dominant eigenvector of a variance-covariance based principle components analysis (PCA1) to assess the variability in composition among study sites. This analysis was based on the abundance of butterflies. Second, we used unconstrained seriation to order species and study sites along the diagonal of the species × patches presence–absence matrix leading to a maximum change on community composition among study patches. Both orderings also entered the general linear and the generalised linear Table 1.

### Table 1. Basic data about the 21 grassland patches assessed in this study. Species abundance refers to the total abundance caught.

<table>
<thead>
<tr>
<th>Patch Nr.</th>
<th>Patch size [m²]</th>
<th>Blossom × m⁻²</th>
<th>Sprayed crop fields %</th>
<th>Ext. used fields/grasslands %</th>
<th>Species</th>
<th>Abundance</th>
<th>Proportion of specialist species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11 585</td>
<td>35</td>
<td>0.84</td>
<td>0.00</td>
<td>7</td>
<td>30</td>
<td>0.43</td>
</tr>
<tr>
<td>2</td>
<td>2843</td>
<td>5</td>
<td>0.52</td>
<td>0.00</td>
<td>7</td>
<td>27</td>
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</tr>
<tr>
<td>3</td>
<td>5300</td>
<td>10</td>
<td>0.68</td>
<td>0.11</td>
<td>7</td>
<td>20</td>
<td>0.43</td>
</tr>
<tr>
<td>4</td>
<td>3394</td>
<td>5</td>
<td>0.80</td>
<td>0.04</td>
<td>3</td>
<td>21</td>
<td>0.33</td>
</tr>
<tr>
<td>5</td>
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<td>0.49</td>
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<tr>
<td>6</td>
<td>363</td>
<td>5</td>
<td>0.41</td>
<td>0.05</td>
<td>4</td>
<td>14</td>
<td>0.25</td>
</tr>
<tr>
<td>7</td>
<td>1936</td>
<td>20</td>
<td>0.00</td>
<td>0.51</td>
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<td>104</td>
<td>0.54</td>
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<td>6263</td>
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<tr>
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<td>344</td>
<td>10</td>
<td>0.78</td>
<td>0.22</td>
<td>3</td>
<td>21</td>
<td>0.33</td>
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<tr>
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<td>0.97</td>
<td>0.00</td>
<td>1</td>
<td>2</td>
<td>0.00</td>
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<tr>
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<tr>
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<td>12 050</td>
<td>10</td>
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<tr>
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<tr>
<td>14</td>
<td>31 220</td>
<td>100</td>
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<tr>
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<td>0.85</td>
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<td>0.24</td>
<td>0.87</td>
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<td>113</td>
<td>0.60</td>
</tr>
<tr>
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<td>0.89</td>
<td>0.09</td>
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<td>40</td>
<td>0.43</td>
</tr>
<tr>
<td>18</td>
<td>6615</td>
<td>40</td>
<td>0.85</td>
<td>0.05</td>
<td>4</td>
<td>18</td>
<td>0.50</td>
</tr>
<tr>
<td>19</td>
<td>3002</td>
<td>25</td>
<td>0.87</td>
<td>0.05</td>
<td>7</td>
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</tr>
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<td>4403</td>
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<td>0.65</td>
<td>0.04</td>
<td>9</td>
<td>29</td>
<td>0.56</td>
</tr>
<tr>
<td>21</td>
<td>15 785</td>
<td>5</td>
<td>0.34</td>
<td>0.13</td>
<td>2</td>
<td>8</td>
<td>0.50</td>
</tr>
</tbody>
</table>

The four patches located in the two managed semi-natural grassland areas are marked in bold.

### Table 2. General linear modelling pointed particularly to blossom density and the proportion of extensively used fields and grasslands, but not to the proportion of sprayed crop fields and patch size as being main predictors of butterfly species richness, abundance, the proportion of specialist species and community composition as assessed from the dominant principal component PCA1 and the seriation order. Ln-transformed patch area served as covariate. Given are partial $\eta^2$ values.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Species richness</th>
<th>Abundance</th>
<th>Specialist species %</th>
<th>PCA1</th>
<th>Seriation order</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blossom density</td>
<td>0.23*</td>
<td>0.32*</td>
<td>0.14</td>
<td>0.25*</td>
<td>0.01</td>
</tr>
<tr>
<td>Sprayed crops %</td>
<td>0.11</td>
<td>0.06</td>
<td>0.11</td>
<td>0.01</td>
<td>0.06</td>
</tr>
<tr>
<td>ext. fields/grasslands %</td>
<td>0.06</td>
<td>0.49**</td>
<td>0.01</td>
<td>0.59***</td>
<td>0.01</td>
</tr>
<tr>
<td>log area</td>
<td>0.02</td>
<td>0.04</td>
<td>0.01</td>
<td>0.08</td>
<td>0.02</td>
</tr>
<tr>
<td>$r^2$ (model)</td>
<td>0.49**</td>
<td>0.81***</td>
<td>0.32*</td>
<td>0.81***</td>
<td>0.05</td>
</tr>
</tbody>
</table>

AICc selected variables are given in bold. Collinearity between predictor variables was moderate ($r < 0.50$) except for sprayed crops % and ext. fields/grasslands % ($r = 0.79$). Parametric significances: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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models as predictors. All calculations were done with Statistica 12.0 (StatSoft, Inc., Tulsa, OK).

**Results**

We observed 24 butterfly species and 864 individuals across all study patches (Table 1). Highest species richness was detectable for the four patches located in the two managed semi-natural grassland areas, the Dietersheimer Brenne and the Garchinger Heide, with on average 6.6 species per visit (ranging from 2.0 to 10.0 species per visit). In contrast, 2.7 butterfly species (ranging from 0.4 to 4.4 species per visit) were observed across all other patches. Mean abundance per visit was 22.7 individuals per patch at managed semi-natural grasslands (ranging from 3 to 35), and 6.7 individuals (ranging from 0.4 to 22.6) in patches across the agricultural landscape (Table 1; Fig. 2). The percentage of specialist butterflies was high at the four patches located in the two semi-natural grassland areas (46% in the Dietersheimer Brenne; 51% in the Garchinger Heide) and comparatively low at

![Fig. 1](image1.png)

**Fig. 1.** Species richness at 21 grassland patches did not depend on patch size (a: OLS linear regression, \( P > 0.5 \)), but increased with the abundance (b: OLS power function). Coefficients of variation (\( r^2 \)) and permutation based significance: \( *** R < 0.001 \). Black dots denote the four patches within the two semi-natural grassland areas. \( r^2 \) (plots) in (b) refers to a regression without the four semi-natural grassland patches.

![Fig. 2](image2.png)

**Fig. 2.** Dependence of species richness and abundance at 21 grassland patches on the proportion of sprayed crop fields (a, d), the proportion of extensively used fields and grasslands (b, e) and the density of blossoms within each patch (c, f). Coefficients of variation (\( r^2 \)) and permutation-based significances for OLS linear (a, b, d, e) and logarithmic (c, f) regressions: * \( P < 0.05 \); ** \( P < 0.01 \); *** \( P < 0.001 \). Black dots denote four patches within the two managed semi-natural grassland areas. \( r^2 \) (plots) in (c) and (d) refer to regressions without the four semi-natural grassland sites. The regressions are not significant at \( P < 0.05 \) in a, b, e and f without the four managed semi-natural grassland areas.

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all patches in the agricultural landscape (mean 20%, ranging from 0 to 38%).

Species richness was not significantly related to patch size (Fig. 1a), but was highly positively correlated with abundance (Fig. 1b). Species richness (Figs 2 and 3a–c) and abundance (Fig. 3d–e) significantly decreased with increasing proportion of crop fields sprayed with pesticides in the surrounding, and increased with the proportion of extensively used fields and grasslands in the surrounding, as well as with blossom density. This positive correlation between blossom density and butterfly species richness and abundance was also retained after excluding the four semi-natural grassland patches (Fig. 3c, d). The general linear model (Table 2) and the generalised linear model (Appendix S4: Table S4) pointed particularly to the proportion of extensively used fields and grasslands and blossom density as major factors determining butterfly species richness and abundance. The proportion of sprayed crop fields on the one hand and extensively used fields and grasslands on the other were significantly negatively correlated \( r = -0.79 \), permutation \( P < 0.001 \), a fact that might have influenced the partial \( \eta^2 \) values.

The four patches located in the semi-natural grasslands differed significantly in their species community composition from the remaining 17 patches in the agricultural landscape (Fig. 4). The composition changed along the gradients of the proportion of sprayed crop fields (Fig. 4a) and the proportion of extensively used fields and grasslands (Fig. 4b), but was not significantly linked with blossom density (Fig. 4c), except after excluding the four patches located in semi-natural grassland areas. Particularly, the four patches of semi-natural grassland contained a significantly higher proportion of habitat specialists than the 17 patches in the agricultural landscape [Table 1, Fig. 2, ANOVA \( F < 0.01 \)]. This difference was not significantly related to blossom density, the proportion of sprayed crop fields and the proportion of extensively used fields and grasslands (Table 2).

**Fig. 3.** Dependence of the dominant PCA eigenvector at 21 grassland patches on the proportion of sprayed crop fields a), the proportion of extensively used fields and grasslands (b), and the density of blossoms within each patch (c). Coefficients of variation \( (r^2) \) and permutation based significances for OLS linear regressions: * \( P < 0.05 \); ** \( P < 0.01 \); *** \( P < 0.001 \). Black dots denote the four patches located in the two managed semi-natural grassland areas. \( r^2 \) (plots) in c) refers to a regression without these four grassland sites.

**Fig. 4.** Dependence of the proportion of specialist species at 21 grassland patches on the proportion of sprayed crop fields (a), the proportion of extensively used fields and grasslands (b) and the density of blossoms within each patch (c). Coefficients of variation \( (r^2) \) and permutation based significances for OLS linear regressions: * \( P < 0.05 \). Black dots denote the four patches within the two managed semi-natural grassland areas.

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Discussion

Our data show that specialist butterfly species are mainly found in semi-natural grassland patches managed for conservations, and to a lower extent in grassland patches located in the agricultural landscape. This finding is in line with previous studies showing that butterfly species respond differently to environmental changes, such as agricultural intensification, and that specialised species have a lower ability to respond to environmental changes, such as decreasing habitat quality (Thomas, 2016). Consequently, those taxa are currently vanishing from major parts of our landscape (Filz et al., 2013; Habel et al., 2016). This situation becomes further aggravated by the fact that species with high ecological specialization are often sedentary and thus have limited potential to respond on habitat loss and increasing geographic isolation of the remaining habitats (Thomas, 2016). In consequence, in recent studies, temporal changes of butterfly communities indicated a vanishing of many butterfly species, and predominantly of specialist species, even from managed nature reserves (Wenzel et al., 2006; Habel et al., 2016). Thus, the preservation of high quality habitats and landscape permeability is essential to hold the major proportion of species in agricultural landscapes (see also Loos et al., 2015).

According to our data, butterfly species richness and abundance are determined by various parameters, such as blossom density and the surrounding environment. Species richness and abundance increased with the proportion of extensively used grassland in the surrounding. This coherence may document a classical species-area relationship (the larger a habitat, the more resources are available and the higher is the amount of ecological niches, fostering species richness and abundance) (Tews et al., 2004). Furthermore, our data show decreasing species richness and abundance at patches, which might be influenced by pesticides applied at the surrounding fields. Negative effects from pesticides on the viability of insects are known. Geiger et al. (2010) demonstrated that pesticides are one main driver of biodiversity loss in crop fields. Furthermore, the application of herbicides may diminish the occurrence of important (larval) food plants and nectar sources, with negative impact on insect diversity (Biesmeijer et al., 2006). Due to the fact that the proportion of sprayed crop fields on the one hand and the proportion of extensively used fields and grasslands on the other were correlated, we cannot distinguish between which of these two drivers (i.e. sprayed fields or extensive use/grasslands) is the major factor influencing community structure and composition (Table 2. Table S4). However, both factors express the level of agricultural intensification, which drives the vanishing of a major proportion of species and abundances. Hence, landscape context may shape communities, species richness and abundance considerably (see also Holzschuh et al., 2010; Krewenka et al., 2011; Ernst et al., 2017), but may affect species differently, depending on their ecology and behaviour (Kormann et al., 2015).

Despite the fact that our data were collected in a restricted region of south-eastern Germany and the resulting data set is limited (limited number of grassland patches, short time period of data collection), the obtained trends are clear and present an alarming signal, underlining the negative effects of intensive agriculture on biodiversity. Future in situ experimental research should focus on identifying drivers, such as pesticide applications and the impact of extensively used grasslands, and evaluate their relevance considering the dramatic biodiversity loss observed.

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Conflicts of interest

There are no conflicts of interest by any author.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Land-cover data assessed for 200 m landscape circles set around each grassland patch analysed.

Appendix S2. All butterflies and individuals for each species assessed at the 21 grassland patches.

Appendix S3. Ecological classification for each butterfly species, considering the larval and adult ecological requirements and the dispersal behaviour of each species.

Appendix S4. Generalised linear modelling (log link function, Poisson error structure) pointed particularly to blossom density and the proportion of extensively used fields and grasslands as being main determinants of butterfly species richness and abundance.

References


Butterfly loss in agricultural landscapes


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