

Sown wildflower fields create temporary foraging habitats for bats in agricultural landscapes

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ABSTRACT

While land-use change threatens insectivorous bats, there is a lack in conservation measures targeting bats in temperate agro-ecosystems. Further, there is no consensus on shared benefits of existing conservation measures either. To unravel the causal factors behind the failure and success of conservation measures, we studied whether sown wildflower fields create sufficient ecological contrast and adequate foraging habitats for insectivorous bats and if potential benefits depend on landscape context.

From June to September 2020, we simultaneously monitored insects and bats on paired wildflower and crop fields in landscapes with increasing complexity, here shares of semi-natural habitats such as hedgerows. We compared insect and specifically moth abundance as well as overall bat and foraging activity between wildflower and crop fields and studied effects of prey abundance on bat activity.

During summer, insect and moth abundances were two- to fourfold higher on wildflower than crop fields. On wildflower fields, insect abundances increased with wildflower cover, while moth abundances increased with shares of semi-natural habitats. Bat activity on wildflower compared to crop fields was higher during the beginning and lower towards the end of summer. Both bat and foraging activity increased with insect abundance and decreased with patch size of wildflower fields.

Wildflower fields seem to be a promising tool to provide adequate foraging habitats for insectivorous bats in agro-ecosystems but sufficient prey availability may be key, particularly during times of high food demand. Moreover, it seems vital to target complex landscapes and foster the retention and reintroduction of hedgerows in agro-ecosystems.

1. Introduction

Land-use change threatens insectivorous bats in agricultural landscapes, mainly through the loss of semi-natural habitats, which in particular, provide food resources in otherwise impoverished agro-ecosystems (Frick et al., 2020; Voigt and Kingston, 2015). While there is an overall lack in conservation measures that specifically target insectivorous bats in agricultural landscapes, there is no consensus on shared benefits of existing conservation measures either (Frick et al., 2020; Park, 2015). Hence, this study aims to unravel whether sown wildflower fields, aiming at insect conservation, provide sufficient ecological contrast and create adequate foraging habitats for insectivorous bats in agricultural landscapes and if benefits are mediated by landscape context.

The loss of insectivorous bats in agricultural landscapes is mainly

caused by land-use change and associated consequences for landscape composition, configuration and habitat quality (Frick et al., 2020; Mickleburgh et al., 2002; Voigt and Kingston, 2015). Predominantly, modern agricultural landscapes are characterized by an overall loss of semi-natural habitats and their connectivity at the landscape scale accompanied by successive habitat degradation of the surrounding agricultural matrix (Fischer and Lindenmayer, 2007). Consequently, species in agricultural landscapes are largely confined to remnants of semi-natural habitats isolated by a homogeneous and resource-poor agricultural landscape matrix (Tscharntke et al., 2012). As a result, bats face a shortage of foraging, roosting and breeding habitats as well as commuting corridors in agro-ecosystems (Frick et al., 2020; Voigt and Kingston, 2015). Yet, despite the persisting threat of land-use change, there is a lack in conservation measures specifically aiming at the protection of insectivorous bats in agricultural landscapes (Frick et al.,

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2020; Park, 2015).

While not targeting insectivorous bats per se, current conservation measures such as agri-environment schemes (AES), aiming at an overall increase in biodiversity, have been assumed to encompass shared benefits for insectivorous bats (e.g. MacDonald et al., 2012). In general, AES provide financial incentives for farmers to adopt environmentally-friendly farming practices in order to mitigate the environmental impact of modern agriculture, for example by enhancing habitat quality in agricultural landscapes (Science for Environment Policy, 2017). Shared benefits of AES have, for instance, been shown for birds and insects that both benefited from sown bird strips (Ouvrard and Jacquemart, 2018). However, previous findings suggest that among the studied AES neither field and water margins, nor hedgerows or species-rich grassland were beneficial to bats (Fuentes-Montemayor et al., 2011a). While this lack of benefits may be attributed to the field-scale application, studies at the farm-scale either confirmed the lack of benefits of AES for bats (Angell et al., 2019; MacDonald et al., 2012, 2019) or even found lower bat activity for certain species at farms under AES management (Angell et al., 2019). Empirical evidence, however, is scarce and studies so far are limited to the UK, which thus, precludes general conclusions on the efficacy of existing AES prescriptions for bat conservation (Angell et al., 2019, and sources therein; Lentini et al., 2013; Park, 2015). Hence, it is essential to advance our knowledge regarding the causal factors behind the failure and success of AES for effective bat conservation in agricultural landscapes (Angell et al., 2019; Frey-Ehrenbold et al., 2013; Frick et al., 2020; Lentini et al., 2013; Park, 2015).

Among others, previous studies identified the similarity of habitats and management practices between farms with and without AES as one of the key drivers for lacking benefits for insectivorous bats and their prey (Angell et al., 2019; Barré et al., 2018; MacDonald et al., 2019). Hence, similarity in resource availability and thus, local habitat quality with and without AES may limit the ecological contrast and thereby, diminish the benefits of AES (Kleijn et al., 2011; Scheper et al., 2013). In contrast to previously studied AES, sown wildflower fields have the potential to create large ecological contrast in agricultural landscapes and are considered high-quality habitats for a multitude of different taxa, particularly insects (Haaland et al., 2011; Scheper et al., 2013). While empirical evidence is scarce, sown wildflower fields may simultaneously promote crepuscular and nocturnal insects. For instance, species-rich grassland and field margins have been shown to benefit moths (Fuentes-Montemayor et al., 2011b; Merckx et al., 2009a), that are among the preferred food resources of insectivorous bats (Vesterinen et al., 2018). Hence, while sown wildflower fields have not explicitly been considered in context of bat conservation yet, this AES may provide foraging habitats and thereby, deliver pivotal benefits for bats, particularly in intensively managed agro-ecosystems (Heim et al., 2017).

Besides local prey availability, habitat selection by bats has been shown to be affected by the presence of linear features which function as corridors to commute, i.e. between roosting and foraging sites within the landscape (Boughey et al., 2011; Frey-Ehrenbold et al., 2013; Froidevaux et al., 2017; Heim et al., 2015, 2017, 2018; Park, 2015; Schaub and Schnitzler, 2007). Similarly, the presence of semi-natural habitats and woodland seemed to be stronger predictors for bat activity in agricultural landscapes than AES implementation (Froidevaux et al., 2017; Fuentes-Montemayor et al., 2011a). Consequently, bat activity and therefore, the efficacy of AES may be highest for wildflower fields embedded in complex landscapes characterized by a well-connected network of semi-natural habitats such as hedges (Downs and Racey, 2006; Frey-Ehrenbold et al., 2013; Fuentes-Montemayor et al., 2011a; Lentini et al., 2013; Russ and Montgomery, 2002).

Therefore, the aim of this study is to unravel (1) whether sown wildflower fields provide sufficient ecological contrast to promote crepuscular and nocturnal insects and (2) if increased prey availability on wildflower fields promotes bat activity and thereby, benefits insectivorous bats in agricultural landscapes. Specifically, we studied

whether insect and moth abundances as well as bat and foraging activity are higher on wildflower than crop fields and if landscape context, i.e. shares of semi-natural habitats, promote benefits of wildflower fields for bats. If proven successful, the contribution of sown wildflower fields to the conservation of insectivorous bats would support their multifunctional role in agro-ecosystems.

2. Methods

2.1. Study region and design

Our study region was in Schleswig-Holstein, a federal state in Northern Germany (Fig. 1) that is dominated by agricultural land-use (70%) interspersed by semi-natural habitats, such as hedges (Statistisches Amt für Hamburg und Schleswig-Holstein, 2020). The study region is characterized by warm temperate climate (Cfb after Köppen-Geiger; Kottek et al., 2006) with annual mean temperatures of 8.4 °C and annual mean precipitation of 770 mm (Fick and Hijmans, 2017).

The study sites ($n = 8$) consisted of a sown wildflower and an adjacent crop field separated by a hedge (Fig. 1; Table A.1). This paired design and the simultaneous monitoring of insects and bats on both habitat types allowed us to exclude confounding factors, such as abiotic conditions (i.e. temperature, wind velocity) and biotic factors (i.e. hedge characteristics, landscape context). Pairwise distances between the study sites averaged 39 km \pm 24 km (mean \pm standard deviation, hereafter).

To reliably identify benefits of sown wildflower fields for insect abundance and bat activity, we based site selection on a set of carefully composed criteria aiming at comparability of the chosen wildflower and crop fields (e.g. crop type), the hedges separating both field types (e.g. hedge structure and plant composition) and key features within the landscape across sites (e.g. distance to forests, urban areas and water bodies; Appendix B and C). To address the significance of landscape complexity, site selection further entailed the quantification of area shares of semi-natural habitats, i.e. hedgerows, single trees, tree rows, field margins and drainage ditches, within a radius of 500 m around the study sites. Environmental patterns at this spatial scale have been shown to drive responses of crepuscular and nocturnal insects (Fuentes-Montemayor et al., 2011b) as well as bat species responses in context with foraging activity (Dietz et al., 2007; Fuentes-Montemayor et al., 2011a; Heim et al., 2015; Nicholls et al., 2006). Moreover, shares of semi-natural habitats at the radius of 500 m were correlated with shares at higher spatial scales (Pearson's correlation; 1 km: p -value = 0.002, est. = 0.91; 1.5 km: p -value = 0.037, est. = 0.74). At the chosen radius, shares of semi-natural habitats at our study sites encompassed a gradient ranging from 2.4% to 8.4% averaging 5.0% \pm 1.7% (Fig. 1A; Table A.1). In addition to landscape context, we estimated the patch size of the sown wildflower fields, which ranged from 1.6 ha to 14.2 ha and averaged 7.4 ha \pm 3.8 ha (Fig. 1A; Table A.1). Finally, we did a vegetation survey for all wildflower fields and the hedges, separating the pairs of wildflower and crop fields, to exclude confounding effects (see Appendix C). We retained information on patch size, plant diversity and wildflower cover of the wildflower fields as covariates for the statistical analyses (Table A.1). In contrast, based on our hedge monitoring we inferred that all hedges in our study mirrored sympathetic hedgerow management (cf. Boughey et al., 2011; Froidevaux et al., 2019a, 2019b) and thus, did not include any of the characteristics in our statistical analyses. All spatial information were acquired using QGIS version 3.18.

2.2. Sampling design

We monitored insects and bats from June to September 2020 to capture the vegetation period of the sown wildflower fields and periods of high food demand for bats, i.e. peak reproduction and later on provisioning for hibernation or the onset of migration in autumn. Altogether, we monitored insects and bats five times per study site

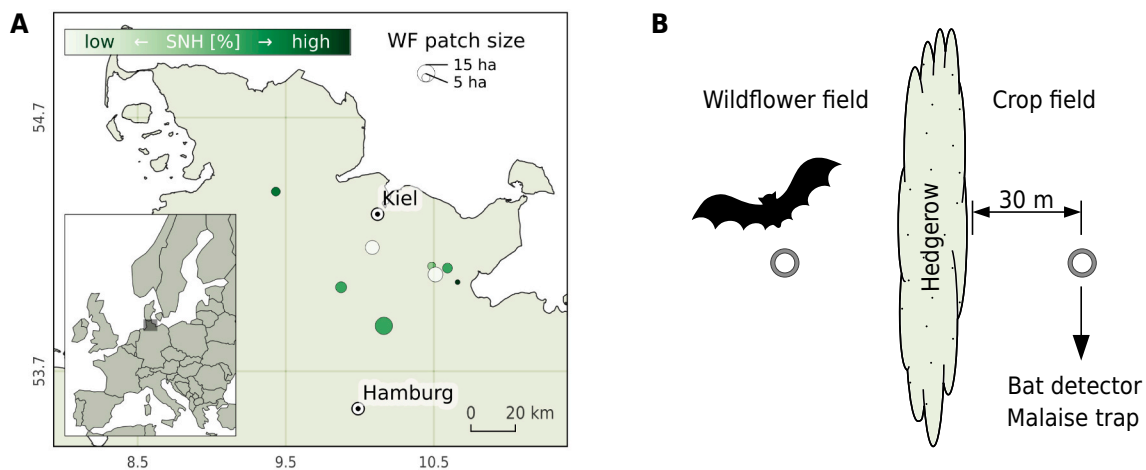


Fig. 1. (A) Study sites located in Schleswig-Holstein, Northern Germany. Shades of the points represent the shares of semi-natural habitats (SNH) from comparatively low (light green) to high proportions (dark green). (B) Insect and bat monitoring at the paired wildflower and crop field separated by a hedge. Bat detectors and malaise traps were positioned 30 m infield from the shared hedge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(monitoring periods, hereafter) with two nights each, resulting in ten nights per study site. Throughout the whole season, insect and bat monitoring commenced at sunset and continued for seven hours in order to capture peak activity following sunset as well as temporal activity patterns of all bat species.

To ensure comparability and exclude confounding factors (i.e. weather conditions), we always monitored pairs of wildflower and crop fields during the same night. Due to logistic constraints, however, we only monitored up to four sites simultaneously. For comparability across sites, bat and insect monitoring only took place at suitable weather conditions (no rain, wind velocity: Beaufort scale ≤ 2 , ambient air temperature $> 10^{\circ}\text{C}$). The five monitoring periods extended across multiple nights: (1) 16th June – 10th July, (2) 13th July – 24th July, (3) 27th July – 6th August, (4) 15th – 28th August and (5) 6th – 21st September (Fig. 2). Extended monitoring periods were particularly owed to moderate temperatures and high precipitation with partially heavy rain events from May until July 2020 (Fig. 2). Moreover, we aimed to avoid

potential bias due to moonlight and thus, monitoring beginning two nights before and ending two nights after full moon. While period three encompassed monitoring nights before and after full moon (Fig. 2), patterns of bat activity did not seem to change systematically during these nights and we thus, retained monitoring data from those nights.

2.3. Bat monitoring

To compare bat activity between the two habitat types, we did a stationary acoustic survey using calibrated, autonomous bat detectors (Elekon A+; Elekon AG, Switzerland). All bat detectors were set to high sensitivity ('crest advanced') while recording was triggered automatically (15 kHz to 155 kHz, crest factor ≥ 7 , post trigger time: 1 s). We placed one bat detector each at the wildflower and the crop field, at a distance of more than 60 m to each other, i.e. 30 m infield from the shared hedge, to avoid an overlap of the recording radius (Fig. 1B; Adams et al., 2012; Heim et al., 2018; Kelm et al., 2014). We attached the microphones to wooden poles at a height of about 2.5 m in order to reduce acoustical clutter echoes produced by vegetation (Schnitzler and Kalko, 2001). Throughout, microphones were attached pointing downwards and at an angle of 45° away from the hedge to reduce microphone damage from condensed water and the likelihood of detecting the same bat individual with both bat detectors. To validate that the range of the bat detectors on the paired fields did not overlap and thus, recorded the same individual, we matched recording information based on the timestamps for all pairs of wildflower and crop fields. Out of 17,295 recordings, we found 63 pairs that had the same timestamp but differed in call characteristics, i.e. mean, minimum and maximum peak frequency, suggesting the recorded calls are derived from different individuals. Due to the comparably low number of recordings with identical timestamps and the variance in call characteristics within each pair, we decided to retain these recordings in all further analyses. However, due to malfunctioning of some bat detectors, i.e. where recording paused in the middle of the night, we decided to exclude five monitoring nights totalling 155 observations (79 and 76 observations from the wildflower and crop fields, respectively). While this approach is highly conservative, i.e. recording took place during more than 80% of the night, it ensures comparability across study sites and between habitat types.

To analyse the bat recordings, we used the software BatExplorer (version 2.1). Despite recent advances, automated species identification by software is still prone to erroneous conclusions (Brabant et al., 2018; Russo and Voigt, 2016; Rydell et al., 2017). Therefore, we manually

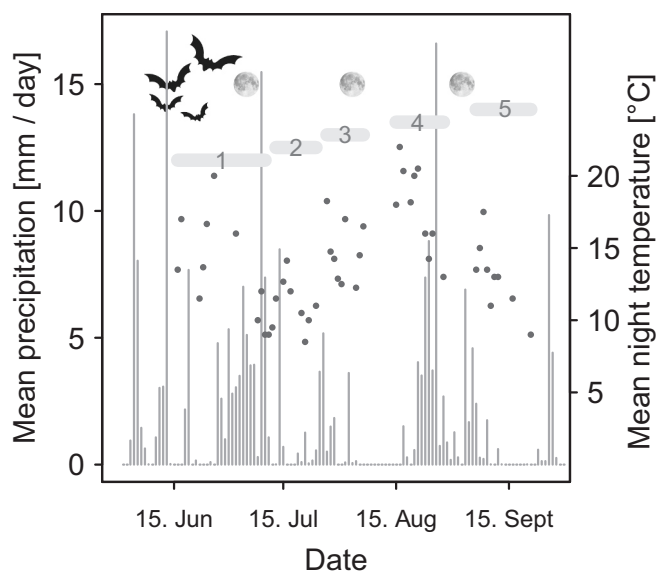


Fig. 2. Five monitoring periods from 16th June until 21st September 2020 along with daily precipitation (bars) and night temperature (points) averaged across the study sites. Additionally, moon phases are indicated by the full moon on top.

identified bats to species-level or assigned them to multi-species (*Myotis* spp.) or multi-genera groups (NEV: *Nyctalus leisleri*, *Eptesicus serotinus*, *Vespertilio murinus*) characterized by similar call characteristics, which do not allow reliable species identification.

We quantified bat activity as the number of bat passes (i.e. number of recordings with at least three calls) per night and study site for wildflower and crop fields, which enables comparability across studies (Kerbrouri et al., 2019). We only considered bat passes with at least three calls to reliably identify the species (group) and reduce the likelihood of counting commuting flights. Similar to bat activity, we quantified foraging activity as the number of feeding buzzes per night and study site for both field types. Since not all bat species are aerial hawkers and thus, exert feeding buzzes to catch their prey (Schnitzler and Kalko, 2001), we specifically studied effects on both bat activity and foraging activity.

2.4. Insect monitoring

In contrast to previous studies on nocturnal insects, we decided against the application of light traps for several reasons, e.g. artificial attraction of insects and bats or avoidance of light sources by bats (Appendix D; Adams et al., 2005; Froidevaux et al., 2018). In our study, we used malaise traps, since they have frequently been found to be appropriate for flight-active insects (van Achterberg, 2009), particularly Lepidoptera and Diptera, which are among the main prey items of insectivorous bats (Dietz et al., 2007; Montgomery et al., 2021; Ves- terinen et al., 2018).

Simultaneous with the bat monitoring, we placed one Townes-type malaise trap (Appendix D) each at the wildflower and crop field, perpendicular to the hedge (van Achterberg, 2009). To separate beneficial effects of the hedgerows from effects of the wildflower and crop fields, respectively, we placed the malaise traps next to each bat detector, between the bat detector and the hedge (Appendix D). We attached the malaise traps to wooden poles so that the bottom of the trap touched the vegetation while the main part of the trap was located above the vegetation. The collecting jar was filled with 70% ethanol and we identified individuals to order level, e.g. Diptera and Lepidoptera. Based on the samples, we counted the insects to estimate the abundance of insects and moths (Lepidoptera) per night and study site for the wildflower and crop fields as potential predictors for bat and foraging activity (Akasaka et al., 2009).

2.5. Statistical analysis

To compare insect and moth abundance as well as bat and foraging activity between wildflower and crop fields, we ran four generalized logistic mixed-effects regressions with betabinomial error distribution and logit link function ('glmmTMB'; Brooks et al., 2017). We chose mixed-effects regressions to account for non-independence of observations, i.e. spatial (paired design) and temporal pseudoreplication (insects and moths: 80 paired observations, bat and foraging activity: 75 paired observations), and used study site as the random effect. Logistic regressions enabled us to specifically compare observations within each pair of wildflower and crop field instead of a comparison of grouped observations, i.e. two sampling nights at eight sites and thus, 16 observations for each habitat type per monitoring period. Thus, we considered every event of bat activity (every bat pass) as a binary response of presence (1) or absence (0) above the wildflower field, where the latter is equivalent to the presence above the crop field (Ovaskainen et al., 2010). To identify shifts in the probability distribution, e.g. relative frequency of bat activity on wildflower and crop fields, across the five monitoring periods, we considered the monitoring period as a fixed effect and used a type-II Wald Chi-square test ('car'; Fox and Weisberg, 2019) to identify significant differences between monitoring periods. While it is worthwhile to consider interactive effects (e.g. with landscape context), we refrained to do so as the limited sample size

would have caused low statistical power. Throughout, we ran model diagnostics, i.e. to test for over- and underdispersion, zero-inflation as well as residual error distribution ('DHARMA'; Hartig, 2020).

To infer whether local field characteristics or landscape context affected insect and moth abundance, we ran separate generalized linear mixed-effects regressions to account for certain covariates that were recorded either for wildflower fields (e.g. plant diversity) or crop fields (e.g. crop type). We ran four generalized linear mixed-effects regressions with negative binomial error distribution and log link function ('glmmTMB'; Brooks et al., 2017), i.e. one model each for insect and moth abundance on either wildflower or crop fields. Throughout, we considered study site and monitoring period as random effects, while we added the shares of semi-natural habitats as well as the mean temperature per night and daily precipitation as fixed effects (Appendix E). Further, models for the wildflower fields contained patch size of wildflower field, plant diversity (Shannon diversity index) and wildflower cover as further covariates (Appendix C). In contrast, models for the crop fields contained crop type and harvesting state (pre- / post-harvest) as further covariates. Throughout, we standardized all continuous predictors to enable comparability among the predictors by centring and scaling. To find the best model, we first tested for multicollinearity based on the variance inflation factor ($VIF < 2$; 'performance'; Lüdtke and Waggoner, 2020) and subsequently, applied model selection based on the AICc, which is appropriate for small sample sizes ('MuMin'; Barton, 2020; Cavanaugh, 1997; Hurvich and Tsai, 1989). While we tested all combinations of predictors, we only allowed combinations of up to three predictors within a model to account for sample size and avoid over-parameterization. Moreover, if a set of candidate models had a $\Delta AICc \leq 2$ we chose up to three predictors that had the highest sum of Akaike weights ($\sum w_i$) and each $\sum w_i > 0.4$. For simplicity, we only present the most parsimonious model. Throughout the model selection process, we did the model diagnostics as described before.

To test for effects of insect and moth abundance on bat and foraging activity, we ran generalized linear mixed-effects regressions with negative binomial error distribution and log link function ('glmmTMB'; Brooks et al., 2017). Although bat and foraging activity showed a moderate correlation (linear mixed-effects regression: est. = 1.16, p -value < 0.001 , $R^2 = 0.58$, $n = 8$ with 155 observations), we decided to test effects on both variables to identify the factors that explain the specific variance of each response. For both regressions, we considered study site and monitoring period as random effects and further included insect and moth abundance, shares of semi-natural habitats, patch size of the focal wildflower field as well as the mean temperature per night as fixed effects. For each of the two regressions, we tested for multicollinearity, applied model selection and ran all model diagnostics as described before. All statistical analyses were done using the open software R version 4.0.4 (R Core Team, 2021).

3. Results

3.1. Insect and moth abundance

We captured 7358 insects dominated by Diptera (90.3%), followed by Lepidoptera (9.2%; exclusively moths), and Neuroptera (0.4%; Appendix F). Compared to crop fields, insect abundance on wildflower fields was higher (59% - 70%, hereafter, mean of the probability distribution on wildflower fields per period; Table 1, Fig. 3) for monitoring periods one to three and lower (40%) for monitoring period five (Table 1, Fig. 3, Appendix F). In contrast, moth abundance was higher (71% - 78%) on wildflower than crop fields for monitoring periods one to four (Table 1, Fig. 3, Appendix F).

On wildflower fields, insect abundance increased with wildflower cover, whereas moth abundance increased with shares of semi-natural habitats (Table 2, Fig. 4). Moreover, with only one exception, insect and moth abundance on wildflower and crop fields increased with temperature and decreased with precipitation (Table 2).

Table 1

Comparison of insect and moth abundance as well as bat and foraging activity on wildflower relative to crop fields across monitoring periods. (A) Probability distribution given by the log odds ratio (logit) as mean and standard error (SE), where positive (negative) values indicate, e.g. higher (lower) insect abundances on wildflower relative to crop fields. *P*-values indicate whether the log odds ratio significantly differed from 0, and thus, whether e.g. insect abundances significantly differed between wildflower and crop fields (shown in bold). Mean and standard deviation (SD) give the relative proportion of, e.g. insect abundance on wildflower relative to crop fields based on raw data. (B) Overall effect of the monitoring period on the probability distribution of e.g. insect abundance on wildflower relative to crop fields. df = degrees of freedom, R^2 = adjusted R^2 .

Monitoring period	Insect abundance			Moth abundance			Bat activity			Foraging activity		
	mean \pm SE	<i>P</i> -value	mean \pm SD [%]	mean \pm SE	<i>P</i> -value	mean \pm SD [%]	mean \pm SE	<i>P</i> -value	mean \pm SD [%]	mean \pm SE	<i>P</i> -value	mean \pm SD [%]
1	0.71 \pm 0.17	< 0.001	67.7 \pm 17.5	1.17 \pm 0.35	< 0.001	77.8 \pm 21.0	0.51 \pm 0.22	0.019	63.2 \pm 14.7	-0.29 \pm 0.40	0.465	46.9 \pm 34.9
2	0.82 \pm 0.17	< 0.001	69.6 \pm 11.5	1.34 \pm 0.33	< 0.001	75.2 \pm 27.7	-0.12 \pm 0.20	0.553	45.5 \pm 17.5	-0.46 \pm 0.46	0.310	37.4 \pm 38.2
3	0.37 \pm 0.15	0.014	59.3 \pm 14.2	1.07 \pm 0.30	< 0.001	70.6 \pm 29.4	0.10 \pm 0.19	0.582	53.1 \pm 17.9	0.00 \pm 0.36	0.996	47.9 \pm 38.4
4	-0.05 \pm 0.16	0.744	49.0 \pm 15.9	0.90 \pm 0.29	0.002	72.0 \pm 30.8	-0.38 \pm 0.19	0.041	40.5 \pm 16.0	-0.03 \pm 0.37	0.928	56.3 \pm 35.1
5	-0.48 \pm 0.16	0.002	39.7 \pm 19.0	-0.13 \pm 0.52	0.808	46.7 \pm 41.4	-0.20 \pm 0.19	0.285	44.3 \pm 23.1	-0.29 \pm 0.44	0.513	45.8 \pm 48.8

Monitoring period	df	Insect abundance			Moth abundance			Bat activity			Foraging activity		
		Chisq	<i>P</i> -value	R^2	Chisq	<i>P</i> -value	R^2	Chisq	<i>P</i> -value	R^2	Chisq	<i>P</i> -value	R^2
Monitoring period	4	47.09	< 0.001	0.47	6.86	0.144	-0.60	12.28	0.015	0.23	0.94	0.918	0.04

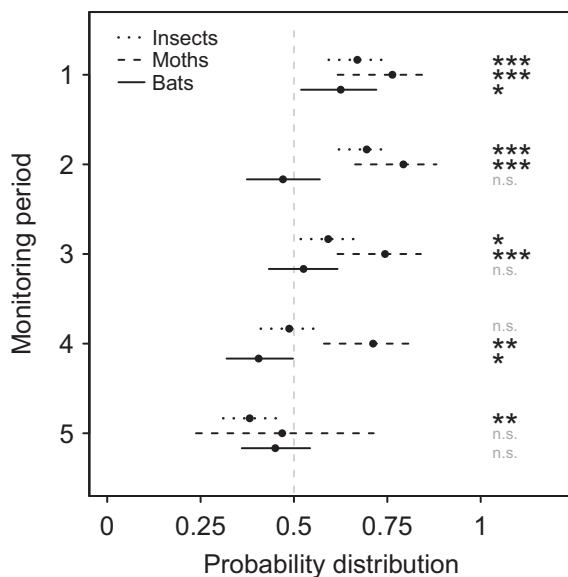


Fig. 3. Comparison of insect and moth abundance as well as bat activity (number of bat passes) on wildflower relative to crop fields, given as the probability distribution (inverse logit). Points and lines depict the mean and 95% confidence intervals, respectively. The grey dashed line represents equal proportions on both habitat types (inverse logit of log odds ratio 0, i.e. 0.5). Stars represent the significance level for the deviation from equal probability distribution between wildflower and crop fields: 0 < *** < 0.001 < ** < 0.01 < * < 0.05 \leq n.s. (not significant).

3.2. Bat and foraging activity

Across all study sites and sampling nights, bat activity amounted 17,295 bat passes and foraging activity totalled 622 feeding buzzes. Bat and foraging activity were largely dominated by the NEV group (*N. leisleri*, *E. serotinus*, *V. murinus*; 36.3% and 39.7%) and *N. noctula* (33.5% and 37.0%), followed by *Pipistrellus pipistrellus* (14.1% and 14.0%), *P. pygmaeus* (6.8% and 6.3%), *P. nathusii* (4.9% and 1.9%),

Myotis spp. (3.3% and 0.6%) and *Plecotus auritus* (0.7% and 0.5%; Appendix F). Compared to crop fields, bat activity on wildflower fields was higher (63%) during monitoring period one but lower (41%) during monitoring period four (Table 1, Fig. 3, Appendix F). In contrast, foraging activity did not differ between both habitat types (Table 1, Appendix F). Bat as well as foraging activity increased with insect abundance and decreased with patch size of wildflower fields (Table 3, Fig. 5).

4. Discussion

Insect and moth abundances were two- to fourfold higher on wildflower than crop fields during summer. On wildflower fields, insect abundance increased with wildflower cover, whereas moth abundance increased with shares of semi-natural habitats. Furthermore, bat activity on wildflower compared to crop fields was higher during early but lower towards end of summer. Finally, both bat and foraging activity increased with insect abundance.

4.1. Insect and moth abundance on wildflower and crop fields

Insect communities were strongly dominated by dipterans and moths, which is in line with other studies on effects of organic farming and AES, respectively (Froidevaux et al., 2019a; Heim et al., 2017). Across our study period, insect and moth abundances were two- to fourfold higher on wildflower than crop fields during summer, i.e. for a large part of the season. Since insect abundances actually increased with flower cover of the wildflower fields, habitat quality and thus, the significance of wildflower fields for insects seemed to be driven by the provisioning of floral resources. However, towards the end of summer, insect and moth abundances either did not differ between both habitat types or were lower on wildflower than crop fields. Comparable abundances on both habitat types may largely be explained by seasonal activity patterns as insect and moth abundances on wildflower fields dropped by about 55% and 95%, respectively, from summer towards autumn. Higher insect abundances on crop fields in autumn may be owed to harvesting activities and the application of manure preceding and during this time, which may have caused a temporary increase in

Table 2
Effects on insect and moth abundance on wildflower and crop fields.

	Wildflower fields								Crop fields							
	Insect abundance				Moth abundance				Insect abundance				Moth abundance			
	df	estimate	P-value	R ²	df	estimate	P-value	R ²	df	estimate	P-value	R ²	df	estimate	P-value	R ²
Temperature	1	0.42	< 0.001	0.57	1	0.47	0.002	0.74	1	0.64	< 0.001	0.66	1	0.53	< 0.001	0.53
Precipitation	1	−0.38	< 0.001		1	−0.24	0.066		1	−0.22	0.005			−0.54	0.014	
Flower cover	1	0.17	0.038													
SNH					1	0.49	0.002									

Significant effects are shown in bold. df = degrees of freedom; R² = adjusted R²; SNH = shares of semi-natural habitats.

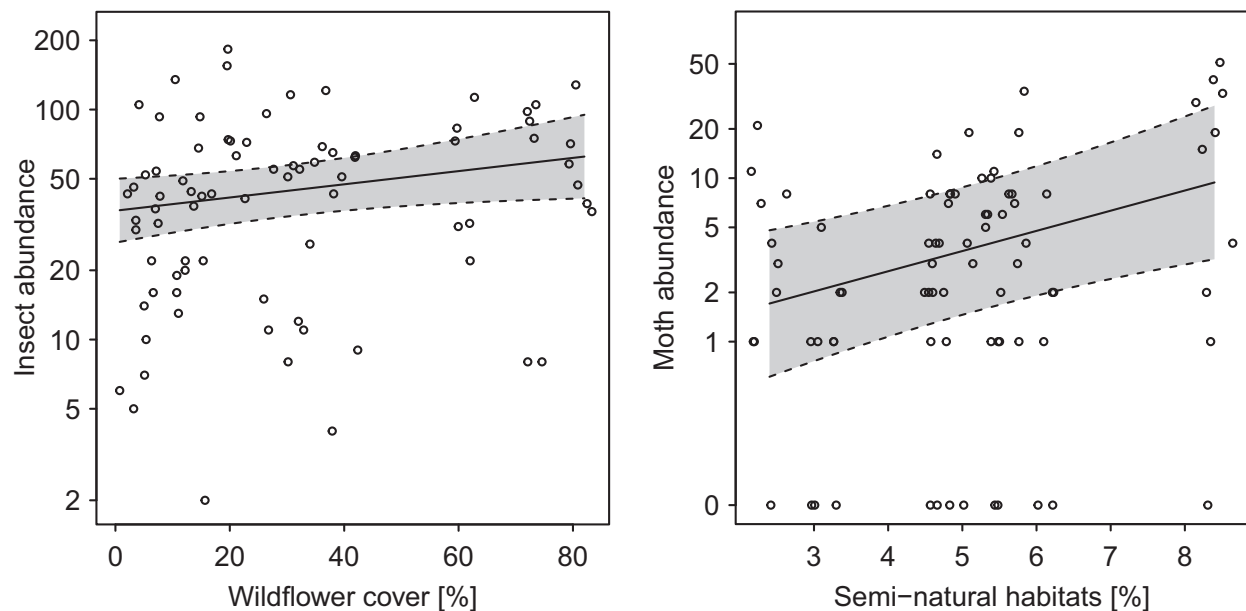


Fig. 4. Effect of wildflower cover on insect abundance (left) and effect of shares of semi-natural habitats on moth abundance (right) on wildflower fields. Solid lines represent the model fit and dashed lines the 95% confidence intervals. Points represent raw data (jitter to avoid overplotting).

Table 3
Effects on bat and foraging activity. Significant effects are shown in bold. df = degrees of freedom; R² = adjusted R²; WF = wildflower field.

	Bat activity				Foraging activity			
	df	estimate	P-value	R ²	df	estimate	P-value	R ²
Insect abundance	1	0.41	< 0.001	0.53	1	0.60	< 0.001	0.38
WF patch size	1	−0.34	0.008		1	−0.33	0.014	

insect abundances on crop fields (Heim et al., 2016; Pluciński et al., 2015). Altogether, despite phenological shifts in insect activity, sown wildflower fields seem to have the potential to provide high-quality habitats and thereby, create sufficient ecological contrast to promote crepuscular and nocturnal insects, which is in line with previous studies (Fuentes-Montemayor et al., 2011b; Merckx et al., 2009a).

Interestingly, while insect abundance increased with wildflower cover, moth abundance was not correlated with any measured characteristic related to wildflower fields but increased with shares of semi-natural habitats. Similarly, a study on the optimization of biodiversity gains from AES found hedgerow trees to be more important for moths than grassy field margins, particularly in landscapes with higher shares of this habitat feature (Merckx et al., 2009b). Among others, the ecological role of hedges for moths has been suggested to result from food provisioning across developmental stages, structural diversity, sheltered microclimate, functioning as dispersal corridors and finally, their temporal consistency compared to other habitat features in the agricultural matrix (Davies and Pullin, 2007; Maudsley, 2000; Merckx et al., 2009b, 2010).

In addition, the significance of hedges for moths confirms our assumption that the success of AES, here the sown wildflower fields, may depend on landscape context. In our study, sample size did not suffice to study whether benefits of wildflower fields relative to crop fields depend on landscape context. Nevertheless, moth abundances on wildflower fields increased with shares of semi-natural habitats. Hence, higher shares of semi-natural habitats, predominantly hedgerows, may have increased habitat connectivity and thereby, facilitated the dispersal and increased the populations of moths on wildflower fields (Merckx et al., 2009a, 2010). Thus, particularly with respect to less mobile species, a well-connected network of semi-natural features, such as hedgerows, can be beneficial when implementing AES, which is in line with studies that favour landscape- over farm-scale approaches (Froidevaux et al., 2019a; Merckx et al., 2009a, 2009b, 2010).

4.2. Bat and foraging activity

Patterns of bat species composition were very similar to findings of previous studies on bat activity above agricultural fields in North-East

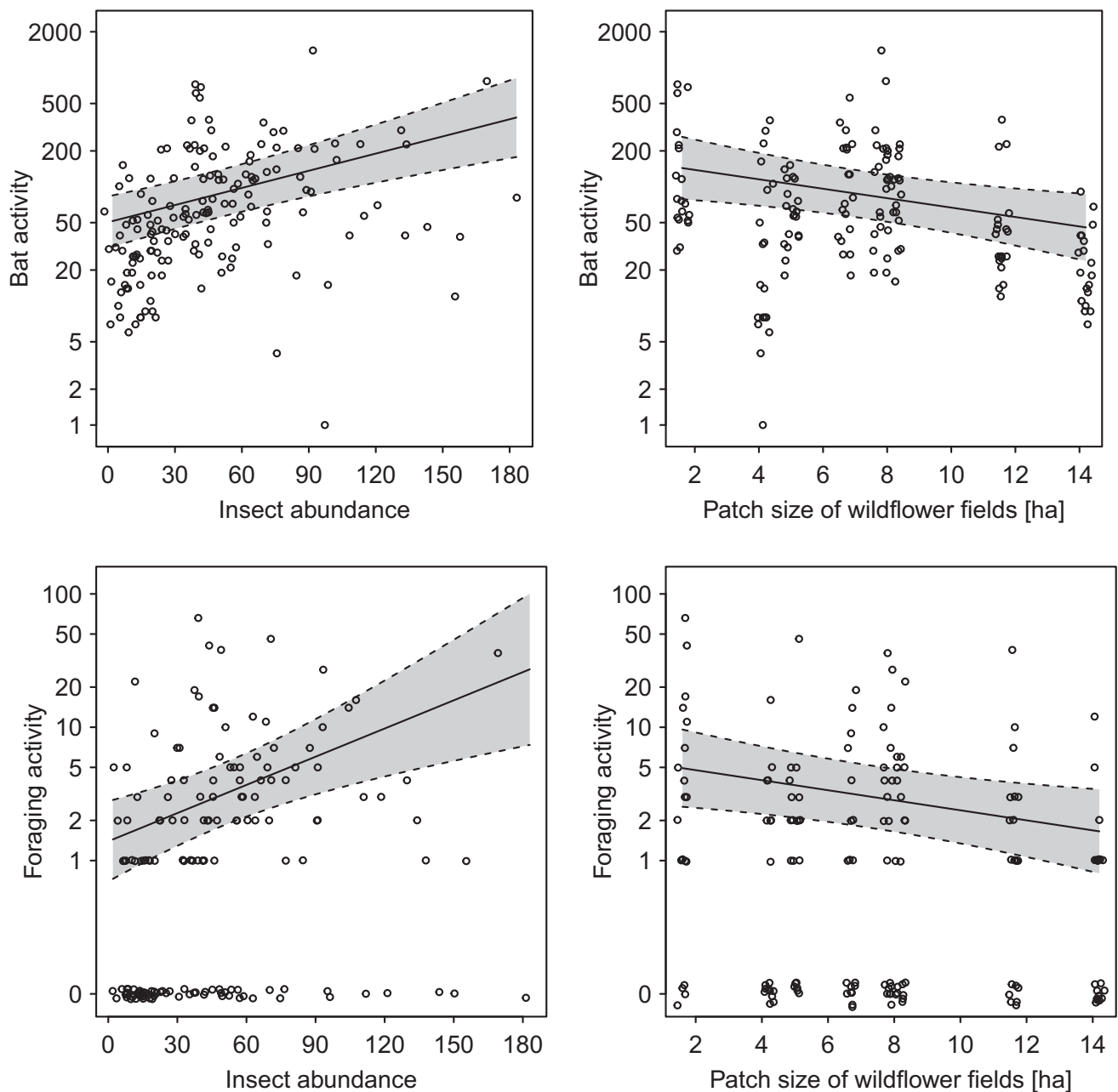


Fig. 5. Effect of insect abundance and patch size of wildflower fields on bat activity (top; number of bat passes) and foraging activity (bottom; number of feeding buzzes). Solid lines depict the model fit and dashed lines the 95% confidence intervals. Points represent raw data (jitter to avoid overplotting).

Germany, where *N. noctula* and pipistrelle bats were most frequently recorded (Heim et al., 2015, 2016, 2017; but see Adams et al., 2012). This pattern of bat activity largely mirrors species-specific habitat preferences of the prevailing bat species since all dominant species were either open-space (NEV group and *N. noctula*; about 70%) or edge-space foragers (pipistrelle bats; about 26%) and thus, common bat species in agricultural landscapes (Heim et al., 2016; Schnitzler and Kalko, 2001). In comparison, activity of narrow-space foragers (*Myotis* spp., *P. auritus*) was lower, which is in line with studies that found these species to rarely forage above arable fields (Heim et al., 2015, 2016; Schnitzler and Kalko, 2001). These patterns of activity distribution across the bat species largely matched patterns of foraging activity suggesting that in fact, bat activity above wildflower fields is mainly driven by their suitability as foraging habitats.

In our study, bat activity on wildflower compared to crop fields was higher during early but lower towards end of summer. Interestingly,

higher bat activity on either habitat type coincided with periods of highest activity levels considering all sites together (Fig. F.3, Appendix F). Hence, the likelihood of small-scale spatio-temporal aggregations of bats may increase with bat activity at the landscape scale. Since both bat and foraging activity increased with insect abundance, food availability in fact, seems to be one of the main drivers for spatio-temporal patterns of bat activity (Wickramasinghe et al., 2004). Hence, as a consequence of higher prey availability, wildflower fields seem to have the potential to provide suitable foraging grounds for insectivorous bats in agricultural landscapes.

Interestingly, moth abundance did not explain variation in neither bat nor foraging activity, which may largely be owed to the fact that bats do not solely rely on moths and, following the optimal foraging theory, adapt their dietary composition to current prey availability (Aizpurua et al., 2018). More generalist or opportunistic feeding behaviour may particularly coincide with periods of low prey availability or high food

demand, such as lactation and preparation for hibernation or the onset of migration (Vesterinen et al., 2016, 2018). This is also supported by the finding that bats seemed to prefer crop fields as foraging grounds towards autumn, where insect abundances temporarily increased, potentially as a result of harvesting and fertilizing activities. Comparable bat and foraging activity at both habitat types, however, may result from inter-patch movement or increased foraging on either side of the hedgerows, i.e. a trade-off between prey abundance and competition (Roeleke et al., 2018). Consequently, comparable activity patterns on wildflower and crop fields during the large part of the study period suggest that this AES may not necessarily introduce competition for insectivorous bats as natural pest control agents but facilitate the related ecosystem service within the adjacent agricultural landscape (Grab et al., 2017).

In addition, bat and foraging activity decreased with increasing patch size of wildflower fields, which at first, may seem counterintuitive but may largely be explained by avoidance or competitive exclusion while foraging (Arlettaz et al., 2000; Rydell, 1992). Hence, in order to simply avoid collision during prey pursuit, escape inter- and intraspecific competition and reduce sonar interference, i.e. jamming by conspecifics (Corcoran and Conner, 2014), bats may disperse across larger wildflower patches. For example, bats have been shown to change their flight trajectories, increase distances to conspecifics and the pursued prey in response to the emission of frequency-modulated social calls (Wright et al., 2014). The assumption of dispersal of bats across the whole wildflower patch, however, partly contrasts with studies that found a decrease in the activity of pipistrelle bats and *Myotis spp.* from the edge towards the centre of arable fields (Finch et al., 2020; Heim et al., 2018; Kelm et al., 2014). While this shift in bat activity has largely been attributed to higher prey availability at the interface between crop fields and hedges (Krauss et al., 2011; Nguyen and Nansen, 2018, and sources therein), edge effects for wildflower fields seem less likely, e.g. due to higher habitat quality and permeability and therefore, lower ecological contrast between wildflower fields and adjacent semi-natural habitats (Haaland et al., 2011; Nguyen and Nansen, 2018). Moreover, higher bat activity at the interface between crop fields and hedgerows has been attributed to the provisioning of shelter against wind and predators, particularly for edge- or narrow-space foragers since they comprise comparably small and slowly flying species (Schnitzler and Kalko, 2001). However, bat activity in our study was largely dominated by *N. noctula*, an open-space forager that is less susceptible to open landscapes (Finch et al., 2020; Heim et al., 2018; Kelm et al., 2014) and may have exploited this behavioural advantage and reduced competition while foraging (Roeleke et al., 2018).

Considering potential effects of landscape context, shares of semi-natural habitats such as hedgerows did not affect bat or foraging activity directly, possibly because bats rather select their foraging habitats based on prey availability, which in our study, was promoted by the availability of this landscape feature. Hence, our findings confirm that sown wildflower fields can play a significant role as foraging habitats for bats, particularly if implemented in complex landscapes characterized by a well-connected network of semi-natural habitats such as hedges. On a more cautious note, sown wildflower fields should not target areas with highly frequented infrastructure or wind turbines, as spatio-temporal aggregations of bats during foraging may increase mortality and wildflower fields may thus, become an ecological trap (Kelm et al., 2014; Tella et al., 2020).

4.3. Conclusions

In contrast to previous studies on benefits of AES, our findings suggest that sown wildflower fields provide sufficient ecological contrast and thus, are a promising tool to provide adequate foraging habitats for insectivorous bats in agricultural landscapes, which simultaneously, may sustain their valuable ecosystem service as biological pest control agents in agro-ecosystems. However, management prescriptions should

be tailored to the foraging behaviour of bats considering both the local habitat as well as the landscape scale. First, wildflower seed mixtures should aim at increased abundances of key components of the diet of insectivorous bats, particularly during times of increased food demand. Second, landscape complexity may facilitate benefits of wildflower fields which requires the reintroduction or restoration and appropriate maintenance of hedges in intensively managed landscapes. While further studies still need to corroborate our findings, it may be worthwhile to study synergies between wildflower fields and hedges and whether the proximity to woodland patches or water bodies may further promote benefits for insectivorous bats in agro-ecosystems.

CRedit authorship contribution statement

Franziska Peter: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Lisa Brucia:** Investigation, Formal analysis, Writing – original draft, Writing – review & editing. **Finn Carstens:** Investigation, Formal analysis, Writing – original draft, Writing – review & editing. **Matthias Götsche:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Tim Diekötter:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109364>.

References

- Adams, M.D., Law, B.S., French, K.O., 2005. Effect of lights on activity levels of forest bats: increasing the efficiency of surveys and species identification. *Wildl. Res.* <https://doi.org/10.1071/WR04060>.
- Adams, A.M., Jantzen, M.K., Hamilton, R.M., Fenton, M.B., 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods Ecol. Evol.* <https://doi.org/10.1111/j.2041-210X.2012.00244.x>.
- Aizpurua, O., Budinski, I., Georgiakakis, P., Gopalakrishnan, S., Ibañez, C., Mata, V., Rebelo, H., Russo, D., Szodoray-Parádi, F., Zhelyazkova, V., Zrnčić, V., Gilbert, M.T.P., Alberdi, A., 2018. Agriculture shapes the trophic niche of a bat preying on multiple pest arthropods across Europe: evidence from DNA metabarcoding. *Mol. Ecol.* <https://doi.org/10.1111/mec.14474>.
- Akasaka, T., Nakano, D., Nakamura, F., 2009. Influence of prey variables, food supply, and river restoration on the foraging activity of Daubenton's bat (*Myotis daubentonii*) in the Shibetsu River, a large lowland river in Japan. *Biol. Conserv.* <https://doi.org/10.1016/j.biocon.2009.01.028>.

- Angell, R.L., Langton, S.D., MacDonald, M.A., Skates, J., Haysom, K.A., 2019. The effect of a Welsh Agri-environment scheme on bat activity: a large-scale study. *Agric. Ecosyst. Environ.* <https://doi.org/10.1016/j.agee.2018.12.011>.
- Arlettaz, R., Godat, S., Meyer, H., 2000. Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). *Biol. Conserv.* [https://doi.org/10.1016/S0006-3207\(99\)00112-3](https://doi.org/10.1016/S0006-3207(99)00112-3).
- Barré, K., Le Viol, I., Julliard, R., Chiron, F., Kerbiriou, C., 2018. Tillage and herbicide reduction mitigate the gap between conventional and organic farming effects on foraging activity of insectivorous bats. *Ecol. Evol.* <https://doi.org/10.1002/ece3.3688>.
- Barton, K., 2020. *MuMIn: Multi-Model Inference*.
- Boughey, K.L., Lake, I.R., Haysom, K.A., Dolman, P.M., 2011. Improving the biodiversity benefits of hedgerows: how physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biol. Conserv.* <https://doi.org/10.1016/j.biocon.2011.02.017>.
- Brabant, R., Laurent, Y., Dolap, U., Degraer, S., Poerink, B.J., 2018. Comparing the results of four widely used automated bat identification software programs to identify nine bat species in coastal Western Europe. *Belgian J. Zool.* <https://doi.org/10.26496/bjz.2018.21>.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, Anders, Hans, J., Skaug, M.M., M.B., B., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *In: R J.*, 9, pp. 378–400.
- Cavanaugh, J.E., 1997. Unifying the derivations for the akaike and corrected akaike information criteria. *Stat. Probab. Lett.* [https://doi.org/10.1016/S0167-7152\(96\)00128-9](https://doi.org/10.1016/S0167-7152(96)00128-9).
- Corcoran, A.J., Conner, W.E., 2014. Bats jamming bats: Food competition through sonar interference. *Science*. <https://doi.org/10.1126/science.1259512>, 80.
- Davies, Z.G., Pullin, A.S., 2007. Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. *Landsc. Ecol.* <https://doi.org/10.1007/s10980-006-9064-4>.
- Dietz, C., von Helversen, O., Nill, D., 2007. *Handbuch der Fledermäuse Europas und nordwestafrikas*. Kosmos, Stuttgart.
- Downs, N.C., Racey, P.A., 2006. The use by bats of habitat features in mixed farmland in Scotland. *Acta Chiropterologica*. [https://doi.org/10.3161/1733-5329\(2006\)8\[169:TUBBOH\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2006)8[169:TUBBOH]2.0.CO;2).
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315.
- Finch, D., Schofield, H., Mathews, F., 2020. Habitat associations of bats in an agricultural landscape: linear features versus open habitats. *Animals*. <https://doi.org/10.3390/ani10101856>.
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.* <https://doi.org/10.1111/j.1466-8238.2007.00287.x>.
- Fox, J., Weisberg, S., 2019. *An R companion to applied regression*, 3rd edition. Thousand Oaks, CA.
- Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.12034>.
- Frick, W.F., Kingston, T., Flanders, J., 2020. A review of the major threats and challenges to global bat conservation. *Ann. N. Y. Acad. Sci.* <https://doi.org/10.1111/nyas.14045>.
- Froidevaux, J.S.P., Louboutin, B., Jones, G., 2017. Does organic farming enhance biodiversity in Mediterranean vineyards? A case study with bats and arachnids. *Agric. Ecosyst. Environ.* <https://doi.org/10.1016/j.agee.2017.08.012>.
- Froidevaux, J.S.P., Fialas, P.C., Jones, G., 2018. Catching insects while recording bats: impacts of light trapping on acoustic sampling. *Remote Sens. Ecol. Conserv.* <https://doi.org/10.1002/rse2.71>.
- Froidevaux, J.S.P., Boughey, K.L., Hawkins, C.L., Broyles, M., Jones, G., 2019a. Managing hedgerows for nocturnal wildlife: Do bats and their insect prey benefit from targeted agri-environment schemes? *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.13412>.
- Froidevaux, J.S.P., Broyles, M., Jones, G., 2019b. Moth responses to sympathetic hedgerow management in temperate farmland. *Agric. Ecosyst. Environ.* 270–271, 55–64. <https://doi.org/10.1016/j.agee.2018.10.008>.
- Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2011a. Pipistrelle bats and their prey do not benefit from four widely applied Agri-environment management prescriptions. *Biol. Conserv.* <https://doi.org/10.1016/j.biocon.2011.05.015>.
- Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2011b. The effectiveness of Agri-environment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach. *J. Appl. Ecol.* <https://doi.org/10.1111/j.1365-2664.2010.01927.x>.
- Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Sci. Rep.* 7, 45296. <https://doi.org/10.1038/srep45296>.
- Haaland, C., Naisbit, R.E., Bersier, L.F., 2011. Sown wildflower strips for insect conservation: A review. *Insect Conserv. Divers.* <https://doi.org/10.1111/j.1752-4598.2010.00098.x>.
- Hartig, F., 2020. *DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models*.
- Heim, O., Treitler, J.T., Tschapka, M., Knörnschild, M., Jung, K., 2015. The importance of landscape elements for bat activity and species richness in agricultural areas. *PLoS One*. <https://doi.org/10.1371/journal.pone.0134443>.
- Heim, O., Schröder, A., Eccard, J., Jung, K., Voigt, C.C., Schroeder, A., Eccard, J., Jung, K., Voigt, C.C., 2016. Seasonal activity patterns of European bats above intensively used farmland. *Agric. Ecosyst. Environ.* 233, 130–139. <https://doi.org/10.1016/j.agee.2016.09.002>.
- Heim, O., Lorenz, L., Kramer-Schadt, S., Jung, K., Voigt, C.C., Eccard, J.A., 2017. Landscape and scale-dependent spatial niches of bats foraging above intensively used arable fields. *Ecol. Process.* 6 <https://doi.org/10.1186/s13717-017-0091-7>.
- Heim, O., Lenski, J., Schulze, J., Jung, K., Kramer-Schadt, S., Eccard, J.A., Voigt, C.C., 2018. The relevance of vegetation structures and small water bodies for bats foraging above farmland. *Basic Appl. Ecol.* <https://doi.org/10.1016/j.baee.2017.12.001>.
- Hurvich, C.M., Tsai, C.L., 1989. Regression and time series model selection in small samples. *Biometrika*. <https://doi.org/10.1093/biomet/76.2.297>.
- Kelm, D.H., Lenski, J., Kelm, V., Toelch, U., Dziok, F., 2014. Seasonal bat activity in relation to distance to hedgerows in an agricultural landscape in Central Europe and implications for wind energy development. *Acta Chiropterologica*. <https://doi.org/10.3161/150811014X683273>.
- Kerbiriou, C., Bas, Y., Le Viol, I., Lorrilliere, R., Mougnot, J., Julien, J.F., 2019. Potential of bat pass duration measures for studies of bat activity. *Bioacoustics*. <https://doi.org/10.1080/09524622.2017.1423517>.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tschamtkke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2011.05.009>.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiger climate classification updated. *Meteorol. Zeitschrift* 15, 259–263. <https://doi.org/10.1127/0941-2948/2006/0130>.
- Krauss, J., Gallenberger, I., Steffan-Dewenter, I., 2011. Decreased functional diversity and biological pest control in conventional compared to organic crop fields. *PLoS One*. <https://doi.org/10.1371/journal.pone.0019502>.
- Lentini, P.E., Gibbons, P., Fischer, J., Law, B., Hanspach, J., Martin, T.G., 2013. Bats in a farming landscape benefit from linear remnants and unimproved pastures. *PLoS One*. <https://doi.org/10.1371/journal.pone.0048201>.
- Lüdecke, Makowski, Waggoner, Patil, 2020. Assessment of regression models performance.
- MacDonald, M.A., Cobbold, G., Mathews, F., Denny, M.J.H., Walker, L.K., Grice, P.V., Anderson, G.Q.A., 2012. Effects of Agri-environment management for cirl buntings on other biodiversity. *Biodivers. Conserv.* <https://doi.org/10.1007/s10531-012-0258-6>.
- MacDonald, M.A., Angell, R., Dines, T.D., Dodd, S., Haysom, K.A., Hobson, R., Johnstone, I.G., Matthews, V., Morris, A.J., Parry, R., Shellsell, C.H., Skates, J., Tordoff, G.M., Wilberforce, E.M., 2019. Have Welsh agri-environment schemes delivered for focal species? Results from a comprehensive monitoring programme. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.13329>.
- Maudsley, M.J., 2000. A review of the ecology and conservation of hedgerow invertebrates in Britain. *J. Environ. Manag.* <https://doi.org/10.1006/jema.2000.0362>.
- Merckx, T., Feber, R.E., Dulieu, R.L., Townsend, M.C., Parsons, M.S., Bourn, N.A.D., Riordan, P., Macdonald, D.W., 2009a. Effect of field margins on moths depends on species mobility: field-based evidence for landscape-scale conservation. *Agric. Ecosyst. Environ.* <https://doi.org/10.1016/j.agee.2008.10.004>.
- Merckx, T., Feber, R.E., Riordan, P., Townsend, M.C., Bourn, N.A.D., Parsons, M.S., Macdonald, D.W., 2009b. Optimizing the biodiversity gain from Agri-environment schemes. *Agric. Ecosyst. Environ.* <https://doi.org/10.1016/j.agee.2009.01.006>.
- Merckx, T., Feber, R.E., McLaughlan, C., Bourn, N.A.D., Parsons, M.S., Townsend, M.C., Riordan, P., Macdonald, D.W., 2010. Shelter benefits less mobile moth species: the field-scale effect of hedgerow trees. *Agric. Ecosyst. Environ.* <https://doi.org/10.1016/j.agee.2010.04.010>.
- Mickleburgh, S.P., Hutson, A.M., Racey, P.A., 2002. A review of the global conservation status of bats. *Oryx*. <https://doi.org/10.1017/S0030605302000054>.
- Montgomery, G.A., Belitz, M.W., Guralnick, R.P., Tingley, M.W., 2021. Standards and best practices for monitoring and benchmarking insects. *Front. Ecol. Evol.* <https://doi.org/10.3389/fevo.2020.579193>.
- Nguyen, H.D.D., Nansen, C., 2018. Edge-biased distributions of insects. A review. *Agron. Sustain. Dev.* <https://doi.org/10.1007/s13593-018-0488-4>.
- Nicholls, B., Racey, A., P., 2006. Habitat selection as a mechanism of resource partitioning in two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. *Ecography (Cop.)*. <https://doi.org/10.1111/j.2006.0906-7590.04575.x>.
- Ouvrard, P., Jacquemart, A.L., 2018. Agri-environment schemes targeting farmland bird populations also provide food for pollinating insects. *Agric. For. Entomol.* <https://doi.org/10.1111/afe.12289>.
- Ovaskainen, O., Hottola, J., Siitonen, J., 2010. Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. *Ecology* 91, 2514–2521. <https://doi.org/10.1890/10-0173.1>.
- Park, K.J., 2015. Mitigating the impacts of agriculture on biodiversity: bats and their potential role as bioindicators. *Mamm. Biol.* <https://doi.org/10.1016/j.mambio.2014.10.004>.
- Pluciński, T., Zmihorski, M., Pluciński, P., 2015. Impact of night-time crop harvesting on bat activity in agricultural landscape. *Zool. Ecol.* 25, 1–7. <https://doi.org/10.1080/21658005.2014.999501>.
- Roeleke, M., Johannsen, L., Voigt, C.C., 2018. How bats escape the competitive exclusion principle-seasonal shift from intraspecific to interspecific competition drives space use in a bat ensemble. *Front. Ecol. Evol.* <https://doi.org/10.3389/fevo.2018.00101>.
- Russ, J.M., Montgomery, W.I., 2002. Habitat associations of bats in Northern Ireland: implications for conservation. *Biol. Conserv.* [https://doi.org/10.1016/S0006-3207\(02\)00089-7](https://doi.org/10.1016/S0006-3207(02)00089-7).
- Russo, D., Voigt, C.C., 2016. The use of automated identification of bat echolocation calls in acoustic monitoring: a cautionary note for a sound analysis. *Ecol. Indic.* 66, 598–602. <https://doi.org/10.1016/j.ecolind.2016.02.036>.

- Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.* <https://doi.org/10.2307/2389972>.
- Rydell, J., Nyman, S., Eklöf, J., Jones, G., Russo, D., 2017. Testing the performances of automated identification of bat echolocation calls: a request for prudence. *Ecol. Indic.* <https://doi.org/10.1016/j.ecolind.2017.03.023>.
- Schaub, A., Schnitzler, H.U., 2007. Flight and echolocation behaviour of three vespertilionid bat species while commuting on flyways. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* <https://doi.org/10.1007/s00359-007-0269-z>.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of european Agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecol. Lett.* <https://doi.org/10.1111/ele.12128>.
- Schnitzler, H.-U., Kalko, E.K.V., 2001. Echolocation by insect-eating bats. *Bioscience* 51, 557. [https://doi.org/10.1641/0006-3568\(2001\)051\[0557:EBIEB\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2).
- Science for Environment Policy, 2017. Agri-environmental Schemes: How to Enhance the Agriculture-environment Relationship.
- Statistisches Amt für Hanburg und Schleswig-Holstein, 2020. Statistische Berichte. Hamburg.
- Team, R.Core, 2021. R: A Language and Environment for Statistical Computing.
- Tella, J.L., Hernández-Brito, D., Blanco, G., Hiraldo, F., 2020. Urban sprawl, food subsidies and power lines: an ecological trap for large frugivorous bats in Sri Lanka? *Diversity* 12, 94. <https://doi.org/10.3390/d12030094>.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* <https://doi.org/10.1111/j.1469-185X.2011.00216.x>.
- van Achterberg, K., 2009. Can Townes type Malaise traps be improved? Some recent developments. *Entomol. Ber.* 69 (4).
- Vesterinen, E.J., Ruokolainen, L., Wahlberg, N., Peña, C., Roslin, T., Laine, V.N., Vasko, V., Sääksjärvi, I.E., Norrdahl, K., Lilley, T.M., 2016. hat you need is what you eat? Prey selection by the bat *Myotis daubentonii*. *Mol. Ecol.* <https://doi.org/10.1111/mec.13564>.
- Vesterinen, E.J., Puisto, A.I.E., Blomberg, A.S., Lilley, T.M., 2018. Table for five, please: Dietary partitioning in boreal bats. *Ecol. Evol.* <https://doi.org/10.1002/ece3.4559>.
- Voigt, C.C., Kingston, T., 2015. Bats in the anthropocene: Conservation of bats in a changing world. In: *Bats in the Anthropocene: Conservation of Bats in a Changing World*. <https://doi.org/10.1007/978-3-319-25220-9>.
- Wickramasinghe, L.P., Harris, S., Jones, G., Jennings, N.V., 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. *Conserv. Biol.* <https://doi.org/10.1111/j.1523-1739.2004.00152.x>.
- Wright, G.S., Chiu, C., Xian, W., Wilkinson, G.S., Moss, C.F., 2014. Social calls predict foraging success in big brown bats. *Curr. Biol.* <https://doi.org/10.1016/j.cub.2014.02.058>.