



Effects of wildflower strips, landscape structure and agricultural practices on wild bee assemblages – A matter of data resolution and spatial scale?

Niels Hellwig^{a,*}, Lea F. Schubert^b, Anita Kirmer^b, Sabine Tischew^b, Petra Dieker^a

^a Thünen Institute of Biodiversity, Bundesallee 65, 38116 Braunschweig, Germany

^b Anhalt University of Applied Sciences, Department of Agriculture, Ecotrophology and Landscape Development, Strenzfelder Allee 28, 06406 Bernburg (Saale), Germany

ARTICLE INFO

Keywords:

Wild bees
Perennial wildflower strips
IACS
Landscape context
Land-use intensity
Habitat connectivity

ABSTRACT

Agricultural systems in Central Europe were redesigned during the last century to attain maximum yields. The results often lead to homogeneous landscapes with only few structures of ecological value and have concurrently exacerbated habitat fragmentation. Perennial wildflower strips have become a significant agri-environmental measure (AEM) to counteract the ecological consequences for wild bees and other pollinators in agricultural landscapes. The effectiveness of AEMs depends on the landscape context, but information about geodata sources and spatial scales relevant for the analysis of landscape effects on wild bees is lacking. This study uses data from various sources on land cover and agricultural practices to assess their applicability in an evaluation of perennial wildflower strips as AEM for wild bees in Saxony-Anhalt, Germany. We investigated the relationships of wild bee species diversity and abundance to the landscape context at spatial scales from 200 m to 10 km considering several factors: land cover/land use, protected areas, crop types, agri-environment schemes/greening, intensity of agriculture, and intensity of grassland farming. In general, our results revealed that landscape effects were more relevant for solitary than social wild bees on flower strips, pointing to a higher limitation of solitary wild bees in nesting resources as compared to social wild bees. Numbers of wild bee species and individuals benefitted from bare soil and ecological focus areas in the surroundings up to 3 km distance, whereas the share of Red List solitary bee species was positively influenced by a variety of factors (e.g., wood structures and grasslands) especially at large scales up to 10 km. The comparison of models based on different land cover data sources showed that the lack of geodata resolution can mask landscape effects on wild bees. Altogether, our results suggest a high potential of data from the Basic Digital Landscape Model (DLM), together with the Integrated Administration and Control System (IACS), to indicate effects of landscape structures and agricultural practices on the species composition and distribution of wild bee assemblages in Germany.

1. Introduction

Land-use change over the past six to seven decades has contributed significantly to the decline in biodiversity in agricultural landscapes (Stoate et al., 2009; Tschardt et al., 2005; Newbold et al., 2020). Intensive use of productive sites and agricultural abandonment on marginal lands have turned a diverse and rather nutrient-poor landscape into a homogeneous landscape, in which once typical elements can now only be found in fragments (Fartmann, 2017; Fischer and Lindenmayer, 2007). Several agri-environmental measures (AEMs) have been designed to maintain and promote biological diversity in agricultural landscapes over large areas (Batáry et al., 2015; Pe'er et al., 2019). Perennial wildflower strips are, for example, implemented to provide

food and nesting resources for insects, particularly pollinators, in agricultural landscapes (e.g. Ouvrard et al., 2018; Buhk et al., 2018; Haaland et al., 2011). Numerous scientific studies have so far evaluated flower strip effectiveness, examining the influence of their age, their spatial arrangement and management, and seed mixtures on wild bees and other pollinators (Schmidt et al., 2020; Nichols et al., 2019; Piqueray et al., 2019; Korpela et al., 2013). Schubert et al. (submitted) revealed that the attractiveness of perennial wildflower strips (established over four to five years) for wild bees depends on a combination of flower strip characteristics and landscape factors, e.g., wood structures and water body structures, making the availability and spatio-temporal resolution of such geodata a limiting factor in evaluating the effectiveness of flower strips for wild bee diversity and abundance at the landscape scale.

* Corresponding author.

E-mail address: niels.hellwig@thuenen.de (N. Hellwig).

Due to lacking monitoring schemes on pollinators and the effectiveness of AEMs, there is a need to assess suitable data sources and resolutions. Although the European INSPIRE Directive has already paved the way for the provision of geodata for scientific purposes, there are still challenges in the implementation of spatial data exchange infrastructures to overcome. From a wild bee perspective, high-resolution geodata are essential to capture flower and nesting resources at the local scale and to match the spatial scale of their home range, both on agricultural lands and beyond. Specifically, high-resolution geodata on land use, land-use intensity, landscape structures, and landscape heterogeneity (i.e. composition and configuration) are required across spatial and temporal scales to determine the connectivity of feeding and nesting habitats at the landscape scale, and thus the effectiveness of perennial wildflower strips.

Remote sensing data such as Sentinel and LiDAR data offer the opportunity to extract information about landscape structures and elements as well as the spatial configuration of croplands and grasslands (Weiss et al., 2020; Griffiths et al., 2020; Preidl et al., 2020). However, it is much more difficult to obtain the necessary temporally and spatially explicit information on feeding and nesting habitats for wild bees. For example, crop variety, crop rotations, grassland types, and land-use intensity (including mowing frequency, fertilisation, pesticide applications) are all well-known factors influencing the quality and connectivity of wild bee habitats, and thus their diversity and abundance in agricultural landscapes (Diekötter et al., 2014; Le Féon et al., 2010; Ekroos et al., 2020). These data are collected by the Integrated Administration and Control System (IACS), designed to manage payments to farmers within the European Union, yet researchers have only limited or even no data access in numerous member states such as Germany. Therefore, often data of low spatial extent, coarse spatio-temporal resolution or without any explicit spatio-temporal information (e.g. crop rotation) are used to model wild bee diversity and abundance to assess the effects of wildflower strips and their surrounding landscape (e.g. Ganser et al., 2021; Concepción et al., 2012; Scheper et al., 2015).

Here, we analysed different geospatial datasets to study the effects of perennial wildflower strips on wild bee species diversity and abundance at six different spatial scales. These reflect the variability of the flight distances of wild bees and include the regional landscape context. Building upon the study of Schubert et al. (submitted), we tested our geospatial approach to investigate the landscape effect with a dataset on the attractiveness of perennial wildflower strips across the federal state Saxony-Anhalt (Germany). Our study aims to answer the following research questions:

- Which environmental data (content and spatial resolution) are most critical to assess the influence of landscape structure and agricultural land-use practices (i.e., land-use type, crop rotation, land-use intensity) when evaluating the effect of perennial wildflower strips on wild bees?
- Which spatial scales must be analysed to understand the influence of landscape structure and agricultural land-use practices on the diversity and abundance patterns of solitary and social wild bee species on perennial wildflower strips?

Based on the study results, we discuss 1) which landscape information and at which spatio-temporal resolution should be considered in future monitoring schemes to evaluate the effectiveness of AEMs such as flower strips for wild bees, and 2) with which environmental data this information can be approximated.

2. Materials and methods

2.1. Study area

The study area covered the agricultural landscapes of the federal

state of Saxony-Anhalt (Germany). Across the study area, 30 sites were investigated: 20 sites on perennial wildflower strips and ten control sites on cereal fields without wildflower strips (Fig. S1). The study sites were selected covering a gradient of landscape heterogeneity in a 1 km radius, ranging from simple to complex agricultural landscapes (3–49% of semi-natural habitats, Table S1; Schubert et al., submitted). All wildflower strips were established by farmers in either 2014 or 2015, using prescribed seed mixtures of 30 native forbs from certified regional seed propagation (Table S2). Flower strip areas in the 1 km radius ranged from 0.4 to 11.2 ha (mean area 4.3 ha \pm 3.4 SD). At least one control site was selected per landscape unit in which the wildflower strips were located (arable plains, southern lowlands, river valleys and lowlands, mid-mountain forelands; Reichhoff et al., 2001). All 30 sites were at least 1 km apart, while the control sites were situated not more than 2 km from the wildflower strips (Schubert et al., submitted).

2.2. Wild bee data

Wild bee data used in this study were taken from Schubert et al. (submitted) (Tables S3–S4). The surveys were performed monthly in the fourth or fifth year after implementation of the wildflower strips from April to August 2019 using a semi-quantitative transect method. Bee transects were located 4 m from the field edge on the flower strip or control site and covered a length of 100 m and a width of 2 m. Each transect was traversed for 10 min and wild bees were caught with an aerial net by steady sweepings ('transect catches'). After that, for another 10 min, wild bees were captured by targeted sweepings outside the bee transect ('additional catches') to better estimate total bee species richness of the study sites (Schubert et al., submitted). Potential biases of sampling methods such as netting or using traps for wild bee monitoring have been compared in previous studies (O'Connor et al., 2019; Krahnert et al., 2021; Thompson et al., 2021).

Based on field surveys on the landscape structure in the 1 km radius of the study sites, Schubert et al. (submitted) showed that the attractiveness of wildflower strips for wild bees depended on the landscape habitat context. In particular, the findings from that study revealed that the occurrence of Red List wild bee species was related to various factors such as habitat diversity (Shannon landscape diversity index) and the proportions of wood structures, grasslands, and water body structures in the 1 km radius. In this study, we build upon those results focussing on several geodata sets to capture the landscape habitat context at several spatial scales.

As wild bees respond differently to foraging sources over time and space according to their sociality (e.g., Kratschmer et al., 2019; Bänisch et al., 2021), we divided the dataset into solitary, social and parasitic wild bees in accordance with Westrich (2019) and Scheuchl and Willner (2016), and analysed the effects of wildflower strips and surrounding landscape separately (Tables S3–S4). Due to low numbers in parasitic wild bee species and individuals, we only considered solitary and social wild bees for our analyses. The number of species of solitary or social wild bees is based on the data of transect catches plus additional catches. The number of individuals of solitary or social wild bees includes only the transect catches, as the additional catches covered only species that were not found in the transect catches. The share of solitary or social Red List wild bee species represents the Red List species of Germany (Westrich et al., 2011) and Saxony-Anhalt (Saure, 2020) (including categories 'near threatened' and 'threat of unknown magnitude') relative to the total number of solitary or social wild bee species per site.

2.3. Environmental data

Landscape structure and agricultural land-use practices of the study area were represented with several landscape factors (Table 1), differentiated in 86 individual factors (Table 2, Table S5). All individual factors were calculated as percentage values relative to the total extent of the analysed neighbourhoods at six spatial scales: 200 m, 500 m, 1

Table 1

Landscape factors tested for their relationship to wild bee diversity and abundance based on different data sources and spatial scales. See [Table S5](#) for details on all individual factors.

Landscape factor	Abbreviated factors	Explanation	Years	Data sources
Land cover/ Land use	DLM18	Land-cover classes	2018	Basic Digital Landscape Model (BKG, 2018)
Land cover/ Land use	fty15, gra15, imd15, swf15, waw15	High-resolution land-cover maps	2015	Copernicus Programme (CLMS, 2020)
Land cover/ Land use	fcir2009, lcir2009, pcir2009	Habitat types/Biotope types	2009	Biotope type mapping based on colour infra-red aerial photographs (LAU, 2020)
Protected areas	IUCN_N2000	Protected biotopes: Nationally designated areas and Natura 2000 areas	2019/20	EEA (2020a, 2020b)
Crop types	IACS14, IACS15, IACS16, IACS17, IACS18, IACS19	Agricultural floral resources as approximated by nectar and pollen indices	2014–2019	IACS data (MULE, 2020)
Agri-environment schemes/ Greening	IACS14, IACS15, IACS16, IACS17, IACS18, IACS19	Total areas under agri-environment schemes, flower strips and areas, ecological focus areas	2014–2019	IACS data (MULE, 2020)
Intensity of agriculture	IACS14, IACS15, IACS16, IACS17, IACS18, IACS19	Pesticide application index based on crop types	2014–2019	IACS data (MULE, 2020)
Intensity of grassland farming	mowing2017, mowing2018	Average number of mowing events in grassland areas	2017–2018	Sentinel-2 data (Schwieder et al., submitted)

Table 2

Details on selected individual factors (only factors correlated highly significantly to wild bee data, see [Table 3](#)). See [Table S5](#) for a list of all individual factors.

Factor	Explanation
DLM18_1020	Grassland: Code 1020 (AX Landwirtschaft/ Grünland) of Digital Basic Landscape Model (Basis-DLM)
DLM18_WoodStructures	Wood structures: Object type AX_Gehoeolz of Digital Basic Landscape Model (Basis-DLM)
gra15	Grassland cover based on high resolution layer: Grassland 2015
fcir2009_F	Unvegetated areas: Code F of biotope type mapping in 2009
fcir2009_G	Water bodies: Code G of biotope type mapping in 2009
fcir2009_H	Wood structures: Code H of biotope type mapping in 2009
fcir2009_K	Herbaceous vegetation: Code K of biotope type mapping in 2009
pcir2009_F	Unvegetated point objects: Code F of biotope type mapping in 2009
IACS14_nectar, IACS16_nectar	Combined nectar values of floral resources in 2014 or 2016 derived from IACS data of Saxony-Anhalt (details on calculation, see description of methods)
IACS15_aes, IACS16_aes, IACS17_aes, IACS18_aes, IACS19_aes	Total areas under agri-environmental schemes in the respective years 2015–2019 derived from IACS data of Saxony-Anhalt
IACS16_efa	Ecological focus areas in 2016 derived from IACS data of Saxony-Anhalt
IACS18_pesticides	Combined values of pesticide application in 2018 derived from IACS data of Saxony-Anhalt (details on calculation, see description of methods)
IUCN_N2000	Protected biotopes: Nationally designated areas and Natura 2000 areas
mowing2017	Average mowing frequency of grasslands in 2017

km, 3 km, 5 km, and 10 km, adding up to a total of 516 individual factors. Scales between 200 m and 3 km correspond to the variety in flight distances among wild bee species (Zurbuchen and Müller, 2012), whereas the 5 km and 10 km scales represent regional landscape influences.

Three different data sources were included for land cover/land use: the Basic Digital Landscape Model (DLM) of 2018 based on the official German land survey data compiled from land register maps, topographic maps, and orthophotos, with a target scale of 1:25,000 (BKG, 2018); high-resolution land-cover maps of Europe 2015 generated from satellite imagery in the Copernicus Programme with a pixel width of 20 m (CLMS, 2020); and a biotope type mapping of Saxony-Anhalt 2009 based on colour infra-red photography on the scale of 1:10,000 (LAU, 2020).

These three datasets were compared regarding their consistence in representing land-cover classes in the investigated surroundings of the study sites ([Table S6](#)). Due to the different data sources, the specification of land-cover classes was slightly variable (as defined in [Table S5](#)) and a potential source of disagreement. Additionally, all of the individual factors derived from those three datasets were included in the further analysis to investigate which of the individual factors were most closely related to solitary and social wild bee abundance and diversity, and thus how they differed in indicating land-use pressures on wild bees.

Agricultural floral resources were approximated by their specific nectar and pollen indices in a range from 0 to 4 ([Table S7](#)) (index values of Pritsch, 2018; MLR-BW, 2016; Stiftung Naturschutz Schleswig-Holstein, 2016; Apis e.V., n.d.; Verein Schweizer Wanderimker, 2012). Similarly, pesticide treatment indices of cultivated crops (Julius Kühn-Institut, n.d.; Roßberg and Hommes, 2018) were used to estimate the application of pesticides ([Table S7](#)). All index values were assigned to agricultural cultivation classes reported in IACS data (MULE, 2020) and spatially weighted according to their area shares of the total cultivated area reported by IACS.

2.4. Statistical analysis

Following Schubert et al. (submitted), we focussed on three target variables to analyse wild bee assemblages: the number of species, the number of individuals, and the share of Red List species, each separately for solitary and social wild bees. We did not detect any spatial autocorrelation for these variables in the empirical variograms ([Figs. S2–S7](#)). The one-to-one relationships between landscape factors ([Table 1](#)) and those wild bee variables were quantified by Pearson correlation analysis, both for the full dataset ($n = 30$) and for the sub-dataset on wildflower strips, i.e., exclusive of control sites ($n = 20$).

Based on the correlation analysis, multivariate effects of landscape factors on wild bees were analysed with generalised linear models (GLMs). Models were calculated separately for the wild bee variables at each of the six spatial scales. Number of species and number of individuals were modelled as negative binomial distributed random variables. Every model included all landscape factors significantly correlated to the respective wild bee variable at $p < 0.1$ ([Tables S8–S13](#)), with the site variant as an additional factor (wildflower strip or control site). Furthermore, separate models were calculated per land cover dataset to compare the effects of different data sources. In the data extraction for every model, landscape factors were checked for multicollinearity: Whenever two factors were intercorrelated with a correlation coefficient $|r| > 0.7$, the factor with a lower correlation to the target variable was excluded. Modelling consisted of a best subset selection of all model candidates from one to a maximum four landscape factors as predictors based on Bayesian Information Criterion (BIC). Considering

the best five model candidates, BIC model weights were calculated according to Buckland et al. (1997). We implemented all statistical analyses in R, version 4.0.2 (R Core Team, 2020).

3. Results

3.1. Correlations of wild bee assemblages to landscape factors

Of all 516 landscape factors, we identified 31 factors that were correlated highly significantly ($p < 0.001$) to at least one of the target variables (Table 3). Solitary bees were overall more correlated to the tested landscape factors than social bees, where only the number of individuals showed highly significant positive correlations ($p < 0.001$) to a local neighbourhood rich of water bodies, wood structures, and grassland (at 200 m distance, Table 3). The numbers of solitary wild bee species and individuals were the most positively correlated to wood structures at 200 m distance (fcir2009_H). Moreover, there were considerable positive correlations of the numbers of solitary wild bee species and individuals to the percentage of unvegetated areas at distances between 200 m and 3 km (fcir2009_F, pcir2009_F).

The share of Red List species of solitary wild bees on wildflower strips was linked to the surrounding landscape especially at scales from 3 km to 10 km (Table 3). The highest positive correlations were found to the percentages of grasslands/herbaceous vegetation (fcir2009_K,

Table 3

Factors with Pearson correlation coefficients r to target variables number of species (w_{sp}), number of individuals (w_{ind}), and share of Red List species (w_{red}) of solitary and social wild bees for wildflower strip sites ($n = 20$). Only factors correlated highly significantly at $p < 0.001$ are presented (correlation coefficients in bold), see Tables S8-S13 for all factors significant at $p < 0.1$ and for all sites ($n = 30$). Factor names are according to Table 2.

Factors	Solitary wild bees			Social wild bees		
	w_{sp}	w_{ind}	w_{red}	w_{sp}	w_{ind}	w_{red}
200 m						
fcir2009_F	0.76	0.83	-0.07	0.00	0.33	0.16
fcir2009_G	0.37	0.46	-0.01	0.20	0.87	-0.10
fcir2009_H	0.86	0.96	-0.07	0.09	0.71	0.07
fcir2009_K	0.27	0.48	0.36	0.15	0.76	-0.24
DLM18_WoodStructures	0.36	0.34	0.06	0.38	0.71	0.11
mowing2017	0.27	0.35	0.07	0.20	0.69	-0.08
500 m						
fcir2009_F	0.77	0.78	-0.07	0.05	0.30	0.25
pcir2009_F	0.76	0.83	-0.07	0.00	0.33	0.16
1 km						
pcir2009_F	0.75	0.69	-0.06	0.09	0.25	0.33
IACS19_aes	-0.31	-0.30	0.71	0.05	-0.08	-0.09
3 km						
fcir2009_K	-0.04	-0.23	0.78	0.35	-0.12	0.20
pcir2009_F	0.77	0.78	0.08	0.32	0.50	0.30
DLM18_1020	-0.15	-0.20	0.74	0.22	-0.05	-0.08
gra15	-0.18	-0.23	0.75	0.19	-0.06	-0.06
IACS18_pesticides	0.06	0.08	-0.70	-0.23	-0.02	-0.00
IACS19_aes	-0.14	-0.12	0.69	0.13	-0.03	-0.01
5 km						
IACS16_efa	0.58	0.77	-0.06	0.01	0.41	0.12
IACS18_aes	-0.26	-0.22	0.69	-0.03	-0.14	-0.12
IACS18_pesticides	0.04	0.16	-0.70	-0.29	-0.02	-0.12
IACS19_aes	-0.13	-0.13	0.69	0.12	-0.01	-0.04
10 km						
fcir2009_K	-0.18	-0.31	0.71	0.18	-0.17	0.03
DLM18_1020	-0.21	-0.27	0.74	0.13	-0.08	-0.10
gra15	-0.24	-0.26	0.73	0.13	-0.06	-0.13
IACS14_nectar	0.11	0.18	-0.77	-0.18	0.03	-0.14
IACS15_aes	-0.17	-0.17	0.69	0.05	-0.12	0.00
IACS16_aes	-0.15	-0.18	0.70	0.16	-0.09	0.06
IACS16_nectar	0.08	0.12	-0.69	-0.02	0.09	-0.01
IACS17_aes	-0.15	-0.17	0.69	0.13	-0.07	0.06
IACS18_aes	-0.18	-0.20	0.75	0.12	-0.08	-0.02
IACS19_aes	-0.16	-0.22	0.77	0.19	-0.04	0.00
IUCN_N2000	-0.02	-0.17	0.71	0.42	0.02	0.16

DLM18_1020, gra15) and areas under protection (IUCN_N2000) or under agri-environment schemes (e.g. IACS19_aes). Moreover, the share of solitary Red List wild bee species was negatively correlated to pesticide treatment indices and to nectar and pollen indices on arable land.

Comparing different significance levels from $p < 0.1$ to $p < 0.01$, the scale-dependent patterns of correlations between landscape factors and wild bee assemblages remained rather constant (Figs. S8-S9). The numbers of bee species and individuals were related to more local-scale influences (200 m to 1 km), whereas the share of Red List bee species was significantly correlated to more landscape factors at large scales (1–10 km).

3.2. Scale-dependent land cover effects per geodata set

The comparison of data sources revealed a high agreement of 84–91% between the corresponding land-cover classes of Basic DLM and the biotope type mapping (Fig. 1). The agreement was highest at the local scale, i.e. land-cover classes were especially consistent between the data sources in the 200 m surrounding of the study sites for wild bee sampling. Moreover, the available high-resolution land-cover layers from the Copernicus Programme also showed a similarly high agreement to the other data sources in the surroundings of most of the study sites (Figs. S10-S14).

The separately calculated models using data from the biotope type mapping detected land cover effects for all target variables except for the number of social wild bee species (Fig. 2). For the number of solitary wild bee species and individuals, these separate models found land cover effects at all spatial scales up to 3 km and 5 km, respectively, whereas the models based on data from the Copernicus Programme and the Basic Digital Landscape Model did not identify any land cover effects. The highest agreement in detected land cover effects among all datasets was found for the share of solitary Red List species. The distribution of social wild bee individuals and the share of social Red List species could be attributed to land cover effects in the Basic Digital Landscape Model and in the biotope type mapping at similar scales. On the contrary, in social wild bees, models using data from the Copernicus Programme detected only land cover effects for the share of Red List species on the 1 km scale.

3.3. Multivariate models

The model results highlight the positive effect of wildflower strips for solitary and social wild bee species. For all target variables, i.e., the numbers of species and individuals and the share of Red List species, the models had significant positive estimates for the site variant wild flower strips vs. control sites (Tables S14-S19). Furthermore, except for the number of social wild bee species, landscape effects largely contributed to the selected models, with significantly better models than the basic models including only the wildflower strip effect ($\Delta BIC > 15$). The number of social wild bee species showed no evidence of additional landscape effects as compared to the basic model testing only the

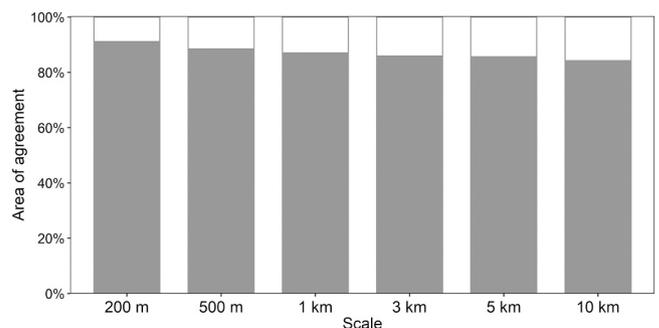


Fig. 1. Area of agreement (grey) between Basic Digital Landscape Model and biotope type mapping with regard to land-cover classes as given in Table S6.

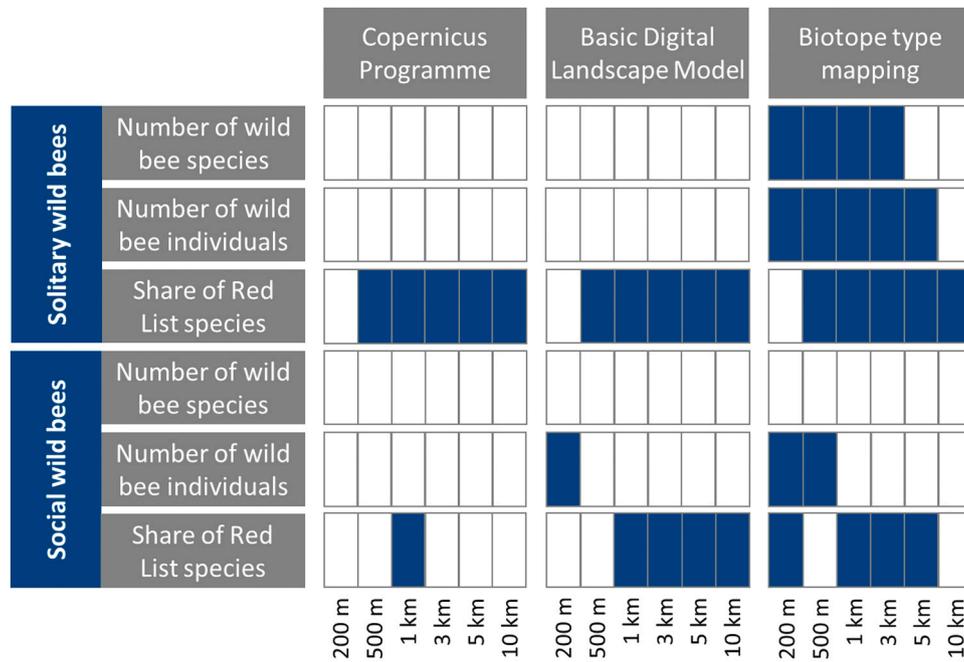


Fig. 2. Detected land cover effects per data source and scale. Segments are filled blue when separately calculated models performed significantly better than the basic models testing only the wildflower strip effect ($\Delta BIC > 2$).

wildflower strip effect ($\Delta BIC < 2$).

The most important landscape predictors in multivariate models are shown in Fig. 3. The presence of bare soil appeared to be important for wild bees across all target variables at scales from 500 m to 5 km (except

for the number of social bee species). The number of solitary wild bee species and the numbers of solitary and of social wild bee individuals were positively affected by wood structures up to 200 m distance. The share of solitary Red List wild bee species was mostly positively

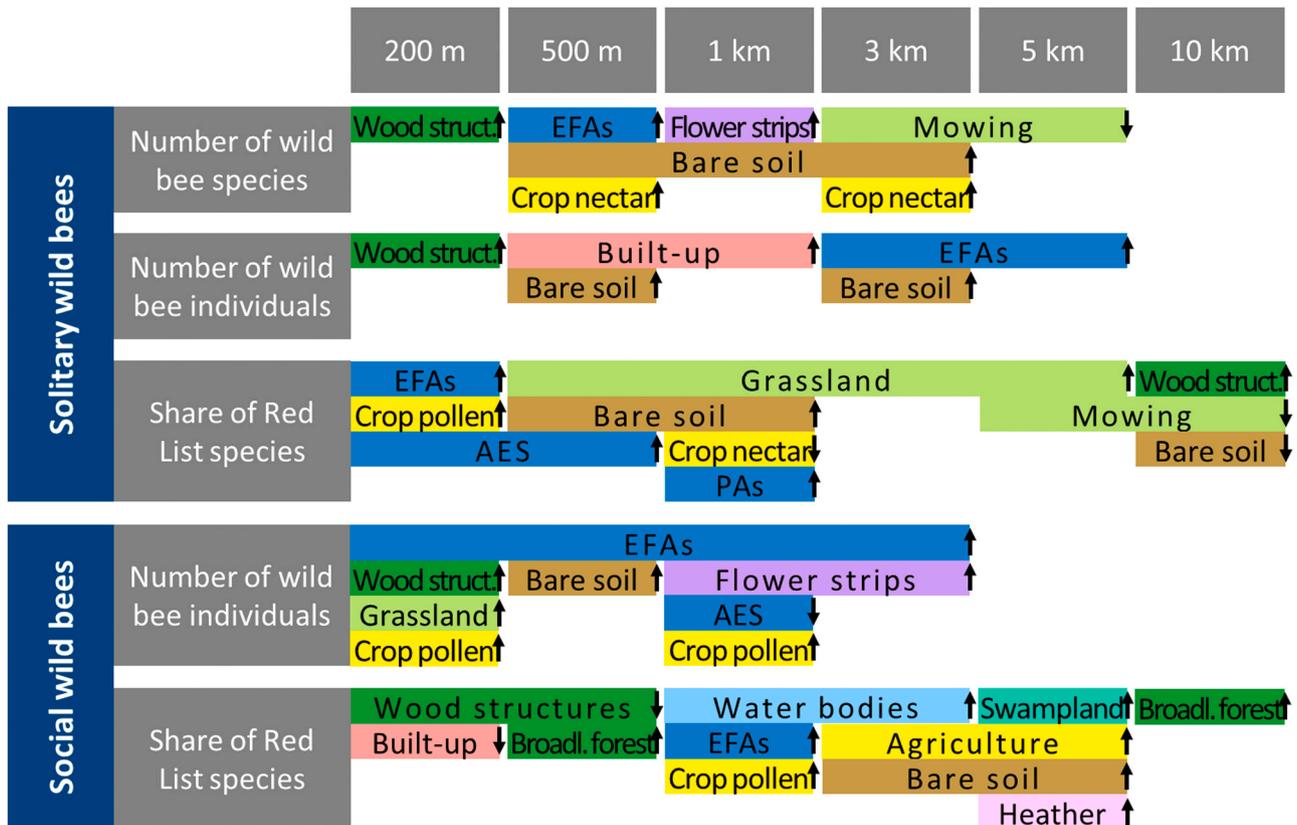


Fig. 3. Most important factors per target variable and scale in multivariate models. The figure includes all factors with cumulative BIC weights of 0.4 and larger based on the best five models according to Bayesian Information Criterion (positive/negative effects are marked with upwards/downwards arrows). Details on the underlying models are presented in Tables S14-S19.

influenced by the percentage of grassland, whereas social Red List wild bee species benefitted from a high landscape diversity at scales between 1 km and 10 km. In particular for solitary Red List wild bee species, mowing appeared to be a negative factor at large scale. For all target variables, the percentage of ecological focus areas on arable land was an important factor at different scales. All results from multivariate modelling are provided in detail in [Tables S14-S19](#).

4. Discussion

4.1. Spatial context determines effectiveness of wildflower strips for wild bees

In general, we found strong evidence that wild bee diversity and abundance on the study sites were related to landscape structure and agricultural practices ([Table 3](#), [Fig. 3](#)). However, the relationships between landscape factors and the target variables that we analysed to characterise wild bee assemblages were distinctly dependent on the spatial scale applied for landscape analysis.

The presence of perennial wildflower strips on the study sites supported a high species diversity of wild bees, which can be attributed to the variety of specific food resources from regional seed mixtures added to the agricultural landscape continuously over the flight period. The continuous provision of floral resources throughout the season is especially important for social wild bees such as bumblebees ([Guezen and Forrest, 2021](#); [Timberlake et al., 2019](#)). This fits to our model results, where the number of social wild bees other than solitary wild bees could be linked to the presence of wildflower strips rather than landscape factors. As a consequence, the diversity of social wild bees in the study area appears to be limited mostly by floral resources, whereas the diversity of solitary wild bees is limited by floral and nesting resources. Floral resources provided by perennial wildflower strips depend on their vegetational characteristics such as the numbers of forbs or the cover of grasses, which strongly influence wild bee assemblages ([Schubert et al., submitted](#)). Moreover, it is important to consider that four to five year-old wildflower strips can also offer valuable nesting habitats to wild bees.

In addition to the wildflower strips as such, multivariate models indicated a positive effect of the area-related nectar and pollen indices derived from cultivation classes on the numbers of solitary species and social individuals for scales up to 3 km. These results correspond to previous studies stating that different floral resources in agricultural landscapes complement each other in the provision of floral resources for pollinators (e.g., [Bänsch et al., 2021](#); [Marja et al., 2018](#), but see [Zamorano et al., 2020](#)). Mass-flowering crops, for example, have been previously shown to support colony growth of bumblebees ([Westphal et al., 2009](#)) and abundance of solitary generalist species ([Holzschuh et al., 2013](#)). Beside floral resources from agriculture, we found that the species diversity of solitary wild bees and the abundances of solitary and social wild bees also benefitted from unvegetated spots and wood structures in the surroundings up to 3 km ([Table 3](#), [Fig. 3](#)). Unvegetated spots, i.e., spots with open soil, and wood structures such as isolated trees, hedges, and groves represent valuable nesting sites within the agricultural landscape ([Harmon-Threatt, 2020](#)). Additionally, wood structures in agricultural landscapes are related to field margins, where spontaneous vegetation often provides further floral resources ([Kells et al., 2001](#); [Purvis et al., 2020](#)). The broad landscape context (> 3 km) appeared to be of minor relevance for wild bee species diversity and abundances on the whole ([Fig. 3](#), [Figs. S8-S9](#)).

The share of Red List wild bee species was related to a multitude of landscape factors ([Table 3](#), [Fig. 3](#)). This implies that wildflower strips alone are insufficient to support endangered species in the agricultural landscape. Our results show that solitary Red List species are supported by a landscape rich in grassland, especially when the number of mowing events is low. These findings are consistent with previous studies that identified grasslands as important habitats for rare and specialist wild

bees ([Banaszak and Twerd, 2018](#); [Le Provost et al., 2021](#)), with a lower species richness of wild bees in intensively used grasslands ([Ekroos et al., 2020](#)). Red List wild bee species are often oligolectic, i.e., they forage for specific flowers, or need specific nesting habitats. In agricultural landscapes, wetland habitats close to rivers, lakes or ponds can be important for rare wild bees ([Morón et al., 2008](#)). This is supported by our results, where high shares of social Red List species correspond to water bodies and swampland at scales between 1 km and 5 km ([Fig. 3](#)). Altogether, a high diversity of endangered species depends on a diverse landscape context on the large scale; thus, it is essential for them to sustain and improve habitat connectivity over wide areas. A thorough evaluation of the landscape context of potential wildflower strip locations is needed to assess and optimise the effects of wildflower strips on endangered wild bees. Although we did not include parasitic wild bees in our analyses, the effects of wildflower strips, landscape structure and agricultural practices on solitary and social bees can still be transferred to parasitic species, as these depend on their host bee species.

Our results imply that potential positive effects of perennial wildflower strips on wild bees in agricultural landscapes are generally dependent on the landscape context. Together with the results shown by [Schubert et al. \(submitted\)](#), this is in line with previous studies that reported spatial and temporal variations in wildflower strip effects, which were related to local and landscape factors ([Burkle et al., 2020](#); [Ganser et al., 2021](#); [Schepers et al., 2015](#); [Jönsson et al., 2015](#); [Korpela et al., 2013](#); [Schmidt et al., 2021](#)). As a consequence of the scale dependence in landscape factors relevant for wild bee assemblages on flower strips ([Fig. 3](#)), it is essential to conduct a multiscale landscape analysis to study habitat requirements of pollinator assemblages. Otherwise, important landscape effects on wild bees could be overlooked.

As landscape effects are species-dependent due to specific habitat preferences and requirements, future studies on the effectiveness of wildflower strips should also differentiate between further wild bee traits linked to the spatial scale of their habitats. For example, the findings by [Hofmann et al. \(2020\)](#) suggest that nesting sites for small bee species should be available within a distance of 150 m from wildflower strips to maximise their effectiveness for wild bees.

4.2. Data harmonisation and model uncertainties

We demonstrated that spatial landscape analysis is important for a thorough evaluation of AEMs. The effectiveness of wildflower strips for wild bee assemblages is significantly related to the surrounding landscape structures and agricultural practices. Hence, our results highlight the value of harmonised spatial data for the analysis of the landscape suitability as a habitat for wild bee species. We included datasets on land cover/land use that were different in terms of data sources, data types, spatial and temporal coverage and resolution, but all of them providing data rich in detail and thus being of great value for agroecological research. In previous studies, IACS data have shown their value for information on the effects of cultivated crops and implemented AEMs on biodiversity ([Lomba et al., 2017](#); [Jerrentrup et al., 2017](#)), although they are not collected for this purpose ([Tóth and Kučas, 2016](#)).

In the separate models based on the biotope type mapping, we detected land cover effects on species diversity and abundance of solitary wild bees, where we did not detect any effects with the other land cover datasets ([Fig. 2](#)). Nevertheless, land cover effects were detected relatively consistently among the datasets for the share of Red List species. As the numbers of species and individuals were more related to local-scale factors than the share of Red List species, these findings can be attributed to the higher spatial resolution of the biotope type mapping as compared to the other datasets. However, in dynamic parts of the landscape, the 10-year-old biotope type mapping could show some outdated land cover classes. Overall, the different datasets showed high areas of agreement in terms of land-cover classes ([Fig. 1](#)), but at local scales, we found distinct deviations (e.g., [Fig. S11](#)). It remains unclear

whether these are due to misclassifications or spatial inaccuracies, due to different resolutions between the datasets, or land-cover changes between the different periods of data acquisition of the land cover datasets. In general, land cover classification is variable and at different scales due to differing methods of data collection and different purposes. When harmonising geodata, it is always a challenge to balance content (based on different methods and sources of data acquisition), spatial resolution, and timeliness. Therefore, when using such datasets in an agroecological context, they should be evaluated either via a comparison of different data sources as in our study, or in a field survey, especially when the focus is on a site-specific local analysis.

Apart from inaccuracies inherent in the utilised datasets, there are also limitations regarding the applicability of the models. Due to a limited number of 30 study sites, the validity of the models is restricted to the investigated plots. This means that although the models reveal multivariate relationships between landscape influences and wild bees, they are not designed to derive predictions of wild bee diversity and abundance in sites not covered by the dataset of this study.

4.3. Implications for wild-bee monitoring

Although numerous studies have reported dramatic declines of wild bees and other pollinators in Central Europe and beyond (De Palma et al., 2017; Van Dooren, 2019; Wagner, 2020; Soroye et al., 2020; Zattara and Aizen, 2021), systematic large-scale monitoring programmes are still lacking (Schindler et al., 2013; Woodard et al., 2020). The recent concept for a pan-European Pollinator Monitoring Scheme (Potts et al., 2021) sets a promising framework for the implementation of a future large-scale monitoring of wild bees and other pollinators. The concept includes transect walks for flying insects, similar to the wild bee surveys of our study, and pressure indicators that correspond to some of the factors we calculated from geodata. Moreover, national monitoring programmes are under development in several countries (e.g., Dauber et al., 2019; Breeze et al., 2021). Considering the perspective of a wild bee on the landscape, large-scale, comprehensive monitoring approaches should not only target the state and change of species diversity and abundance, but also pressures on wild bees and their habitats as represented by changing environmental factors and intensifying land-use practices (Butchart et al., 2010; Smeets and Weterings, 1999; Wascher, 2004). On the one hand, wild bee habitat monitoring could be useful for future targeted monitoring, for example, in a large-scale evaluation of AEMs as enhancement of wild bee habitat quality. On the other hand, wild bee habitat monitoring would be a valuable part of future surveillance monitoring, for example, by reporting the trends in habitat quality through pressure indicators calculated from geodata.

Pressure mechanisms on wild bee habitats, i.e., how wild bees are affected by environmental changes, can be illustrated by dividing the landscape into the most relevant components for wild bees (“bee landscape” in Fig. 4). For example, we found that numbers of species and individuals were positively linked with high percentages of unvegetated areas and wood structures (Fig. 3), which provide wild bees with nesting sites in bare soil, deadwood, plant stems or cavities (Fig. 4). Furthermore, by analysing corresponding geodata, the combination of environmental factors relevant for wild bees (Fig. 4) needs to be considered in the development of a representative sampling design of a large-scale wild bee monitoring.

Our results on the high agreement of land-cover data from different sources imply that all of them can give valuable information on the location and heterogeneity of different land-cover classes (Fig. 1, Figs. S10-S14). Moreover, we found strong relationships between specific land-cover classes and wild bee diversity and abundance (Table 3, Fig. 3). Therefore, as the annually updated Basic DLM covers all of Germany (BKG, 2018), this will be an important source for future monitoring schemes to evaluate the effectiveness of AEMs at the landscape scale and potentially also for the planned nationwide monitoring to analyse the state and trends in wild bees and their habitats. Additionally, IACS data present an essential data source to account for agricultural practices and AEMs, which obviously affect species diversity and abundance of wild bees (Table 3). Future studies need to evaluate whether information on flowering crops, e.g., using the nectar and pollen indices derived from IACS data, are related more strongly to the composition of wild bee assemblages when samples come only from study sites without additional floral resources introduced by wildflower strips.

In general, a systematic monitoring of wild bees also needs to include an analysis of the spatial landscape context. This permits researchers to evaluate the state and trends in habitat quality and connectivity using modelling approaches (e.g., Gardner et al., 2020). Thus, apart from indicators of species diversity and abundance, future monitoring schemes should also be designed to report on indicators of the state and trends of wild bee habitats. Regarding the overall wild bee species diversity and number of individuals, our results suggest that the landscape context matters up to a distance of 3 km (according to the maximum of flight distances of most species). However, when monitoring the presence of specific species, especially Red List species, we also recommend considering the landscape context at substantially larger scales of at least 5–10 km.

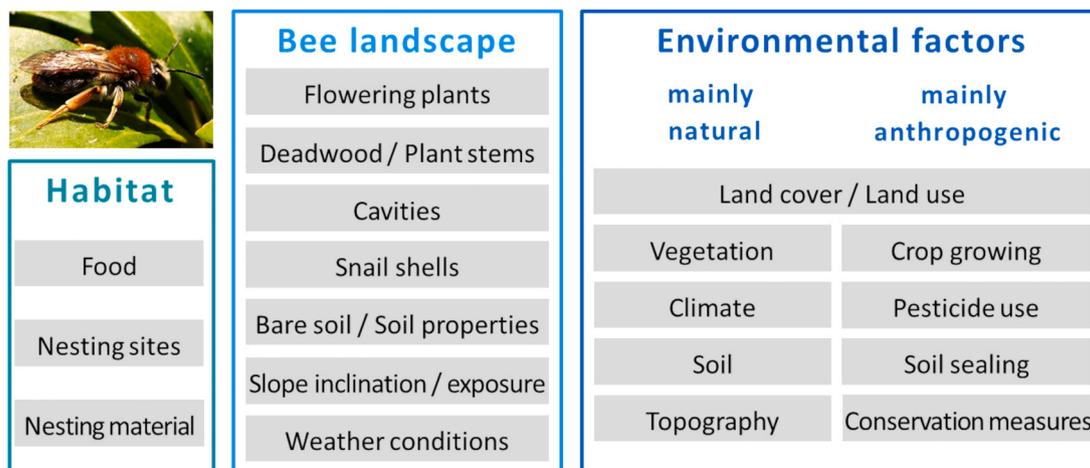


Fig. 4. Habitat requirements of wild bees, relevant landscape elements of the “bee landscape” and environmental influences. Picture: *Andrena haemorrhoea*.

5. Conclusions

Altogether, our findings suggest that data on land cover and agricultural practices are valuable not only to design ecological monitoring programmes and install representative sampling sites along landscape gradients. They are also essential for the analysis of wild bee data to understand spatial patterns and temporal trends in the context of habitat quality and connectivity as affected by land-cover changes and landscape heterogeneity. At the level of Germany, the Basic DLM, together with IACS data, are important data sources for future spatial analyses to evaluate effects of perennial wildflower strips on wild bees and, in general, to calculate pressure indicators on wild bees. The geospatial approach we used for the evaluation of wildflower strips can be also applied to assess the effectiveness of other AEMs for wild pollinators. Therefore, we stress the need to improve access to data on agricultural practices from IACS in accordance with the European INSPIRE Directive.

Wild bee assemblages proved to be considerably affected by the landscape context at various spatial scales. Numbers of wild bee species and individuals were positively related to landscape factors up to a distance of 3 km, especially the presence of bare soil and the presence of ecological focus areas. Red List wild bee species benefitted from a multitude of landscape factors such as wood structures and grasslands, especially at large scales up to 10 km. In conclusion, to assess the effectiveness of wildflower strips for high numbers of species and individuals on the one hand, and for a high diversity of endangered species on the other hand, the establishment of wildflower strips in agricultural landscapes needs to be linked to an analysis of the landscape context at different spatial scales.

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.

Acknowledgements

The presented study is part of the joint project ‘Monitoring of biodiversity in agricultural landscapes’ (MonViA; www.agrarmonitoring-monvia.de/en), funded by the German Federal Ministry of Food and Agriculture, and the project ‘Ecological effectiveness of perennial wildflower strips in Saxony-Anhalt for bees (Apidae)’, funded by the Ministry of Environment, Agriculture and Energy of Saxony-Anhalt (A 02/2019). We thank all students and colleagues for their help with field data collection and the State Institute for Agriculture and Horticulture Saxony-Anhalt as well as the State Institute for Environmental Protection Saxony-Anhalt for their excellent cooperation. Moreover, we thank Tom Breeze (University of Reading, UK) and one anonymous reviewer for helpful comments on earlier draughts of the manuscript and Dina Führmann for language corrections.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2021.107764](https://doi.org/10.1016/j.agee.2021.107764).

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