

Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes

Corina Maurer^{1,2}  | Louis Sutter³  | Carlos Martínez-Núñez¹  | Loïc Pellissier^{2,4}  |
 Matthias Albrecht¹ 

¹Agroecology and Environment, Agroscope, Zürich, Switzerland

²Landscape Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland

³Plant Production Systems, Agroscope, Conthey, Switzerland

⁴Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

Correspondence

Corina Maurer

Email: corina.m181@gmail.com

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Abstract

1. Semi-natural habitats provide important resources for wild bees in agricultural landscapes. Landscapes under management are dynamic and floral resources fluctuate in space and time. Thus, promoting different semi-natural habitat types within landscapes could be key to support diverse bee meta-communities throughout the season.
2. Here, we integrate analyses of α -diversity (species richness) and β -diversity and species-habitat networks to examine the relative contribution of all major semi-natural habitats to wild bee meta-communities in agricultural landscapes. We sampled extensively and conventionally managed meadows, flower strips, hedgerows and forest edges in spring, early and late summer in 25 landscapes in Switzerland.
3. Habitat types varied in their importance for wild bees throughout the season: While extensively managed meadows supported more rare species, habitat specialists and bee species overall than the other habitat types, flower strips were most important later in the season. Each of the five investigated habitat types harboured relatively unique sets of species with different habitats generally acting as distinct modules in the overall bee-habitat network.
4. Not only flower richness in a habitat per se, but also flower-habitat network properties (habitat strength and functional complementarity) were good predictors of wild bee richness. In addition to local floral richness, landscape composition and configuration interactively influenced β -diversity patterns across habitats.
5. *Synthesis and applications.* Our study highlights the value of pollinator-habitat network analysis to inform pollinator conservation management at the landscape scale, especially when combined with information on floral resources and flower-habitat networks. Maintaining different types of semi-natural habitats offers diverse and complementary resources throughout the season, which are crucial to sustain diverse wild bee meta-communities in agricultural landscapes. Particularly meadow extensification schemes can play a key role in safeguarding

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rare and specialist species in these landscapes. While locally a high flower richness promoted bee abundance and richness in general, our results indicate that increasing connectivity between habitat patches in landscapes dominated by arable crops appears to improve species exchange between local bee communities of different habitats, thereby possibly increasing their resilience to disturbances.

KEY WORDS

conservation, landscape complexity, pollinators, semi-natural habitat, species-habitat networks, wild bees, α -diversity, β -diversity

1 | INTRODUCTION

Wild bees provide essential pollination services to crops and wild plants (Potts et al., 2016; Wei et al., 2021), but are jeopardized by habitat loss and intensive agriculture (Goulson et al., 2015). To counteract declines in agricultural landscapes, management measures to conserve these semi-natural habitats (SNH) would ensure essential floral and nesting resources for wild bees throughout the season. Hence, agricultural landscapes with higher amounts of SNH are generally associated with an increased abundance and richness of pollinators (e.g. Holzschuh et al., 2010) and enhanced pollination services to crops (Garibaldi et al., 2011). The type, structure and floral composition of SNH may be critical drivers for different taxa of pollinators (Bartual et al., 2019), but our understanding of the relative contribution of different types of SNH and their floral composition to diverse pollinator meta-communities at the landscape scale is scarce. Some recent studies suggest that wild bee communities in agricultural landscapes of Central Europe may be more abundant and diverse in flower-rich grasslands than in woody habitats such as hedgerows and forest edges (e.g. Bartual et al., 2019; Rivers-Moore et al., 2020). Additionally, sown flower strips are locally contributing more to sustaining populations of generalist wild bee species than forest edges (Ganser et al., 2020).

In addition, the role of different SNH and floral resources can vary across the season, for example, due to distinct flowering phenologies of the dominant plant species in these habitats (Cole et al., 2017; Eeraerts et al., 2021). Some bumblebee species, for example, have been shown to track floral resources in different habitats throughout the season (Cole et al., 2017), shifting their main pollen source from woody plants mainly flowering in spring to herbaceous plants still abundantly flowering in summer (Bertrand et al., 2019). Thus, conservation management should consider how to promote resource continuity across landscapes (Schellhorn et al., 2015). Since different conservation target groups, such as rare or dominant crop pollinating bees, may rely on distinct key flowering plant species (Sutter et al., 2017), they may distinctively benefit from different habitat types over the season. Hence, different SNH in the landscape could provide complementary spatial and temporal niches, and combining them should support more diverse bee communities, partly due to enhanced β -diversity (Rivers-Moore et al., 2020). Therefore, information about the importance of different habitat

types throughout the season and underlying drivers at the local and landscape scale would allow developing tailored conservation measures to promote wild bees in agricultural landscapes.

A promising tool to evaluate the importance of habitat and landscape factors for species communities at the landscape scale are species-habitat networks (Marini et al., 2019). This approach applies the bipartite species interactions framework to species and habitats by considering the whole landscape as a unit and species in different habitat types as a meta-community. Hence, analysis of species-habitat networks can contribute valuable conservation relevant information about the roles of different SNH for the entire bee community and reveal how strongly the species are linked to certain habitats in a landscape (i.e. habitat specialists). This allows for example assessing the uniqueness of a habitat in terms of its contribution to the bee meta-community of a landscape.

Besides local drivers, such as resource quantity and quality provided by SNH (e.g. Sutter et al., 2017), landscape-level factors such as landscape composition (i.e. percentage of arable crop cover) and configuration (i.e. edge density) may be important drivers of wild bee communities in agricultural landscapes (Martin et al., 2019). In contrast to the generally positive relationships between the amount of SNH and wild bee diversity, findings for effects of landscape configuration are inconsistent (Hass et al., 2018; Holzschuh et al., 2010). A potential reason could be that the effect of landscape configuration on wild bees can depend on landscape composition (Martínez-Núñez et al., 2019; Maurer et al., 2020). Therefore, it is crucial to evaluate how landscape properties and their interactive effects influence important aspects of meta-community structure of wild bees such as β -diversity across different habitat types within a landscape.

In this study, we integrated species-habitat network and seasonal analyses to study the role of five different major SNH types in supporting diverse wild bee meta-communities in agricultural landscapes of varying composition and configuration. We analysed wild bee data from standardized transect surveys in extensively and conventionally managed meadows, flower strips, hedgerows and forest edges in 25 agricultural landscapes in Switzerland to address the following questions: (i) What is the relative importance of different SNH types in supporting diverse wild bee meta-communities? (ii) Does their importance vary throughout the season and (iii) for rare and dominant crop pollinating bees? (iv) Are flower-habitat network properties good predictors of bee richness? (v) How do

floral richness and landscape composition and configuration drive wild bee abundance and richness within—and β -diversity among—different types of SNH?

2 | MATERIALS AND METHODS

2.1 | Study design and sampling of wild bees

Data analysed here were collected in two different surveys in 2014 ($n = 17$) and 2020 ($n = 8$) in the northern Swiss lowlands (Figure 1a). Agricultural landscapes of 1 km radius were selected along a landscape composition and configuration gradient (17%–88% arable crop cover and 51–157 m/ha edge density), ensuring at least 3 km between landscape centres (except for two landscapes). They are considered as independent, since average foraging ranges of wild bees are typically <1 km (Greenleaf et al., 2007). A small-scaled mosaic of arable crops (few orchards and vineyards) and SNH such as permanent grasslands of different management intensity, hedgerows and forest dominated the landscapes. In each landscape, wild bees were sampled along transects in each of five major SNH types (hereafter habitats): (i) conventionally managed meadows (intensive meadows), (ii) extensively managed meadows ('biodiversity promoting area': no fertilizer application; first cut after 15th of June), (iii) sown flower strips, (iv) hedgerows (inclusive herbaceous border) and (v) forest edges (Figure 1b).

In the 2014 survey, wild bees were sampled in one habitat patch per type (wherever possible, see Appendix S2, Table S1) in each landscape along a 100 m transect (2 m width; see Bartual et al., 2019 for details). In the survey conducted in 2020, wild bees were, analogous to the 2014 survey, sampled along 2 m wide transects in the same five major habitat types. However, a 1 km transect was subdivided into sections proportional to the amount of these different habitat types in a landscape (similar to Cappellari & Marini, 2021). These sections were randomly placed in different patches of the corresponding habitat types in each landscape (including flowering crops, not analysed here). In both surveys, three sampling rounds in April, May/June and July were conducted between 9 am and 6 pm during dry and warm weather conditions (min. 14°C) with low wind. Transects within a habitat type of a landscape were not fixed but were allowed to vary across sampling rounds. When present in the landscape, each of the five habitat types was sampled once per round within each landscape (see Appendix S2, Table S1 for an overview). During standardized transect walks, 3 min were used for recording flower visiting bees in a 25 m section, pausing the clock for catching and processing the samples. Back in the laboratory, the samples were stored in 70% ethanol in 2014 and at -80°C in 2020 until insect identification. In 2014, experts determined bees morphologically, while in 2020, bees were determined by barcoding the cytochrome oxidase subunit I gene region by the company Microsynth Ecogenics GmbH (Balgach, Switzerland). Identified bees were classified into

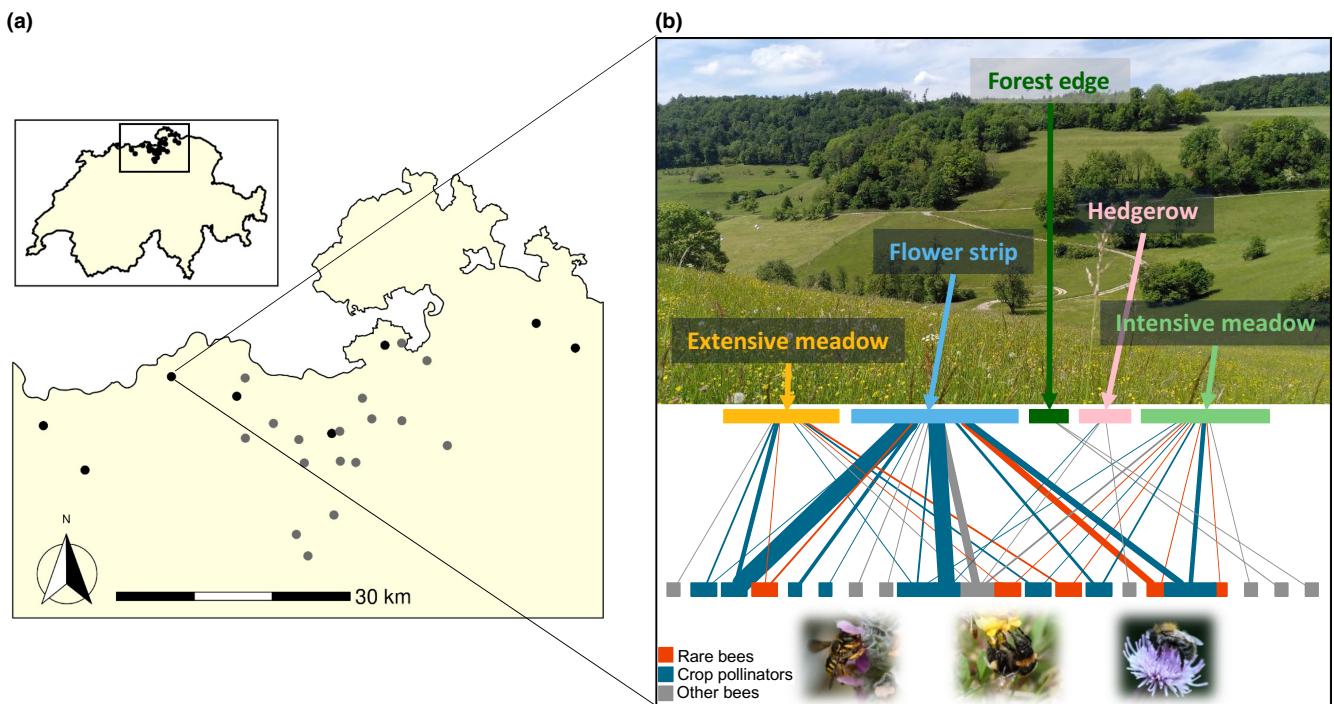


FIGURE 1 (a) Location of the 25 study landscapes in Northern Switzerland (grey: 2014; black: 2020). (b) Example of a bee species-habitat network (pooled across sampling rounds for illustration). Size of nodes and links are proportional to number of links; colours depict the different studied habitat types (yellow: extensively managed meadow; blue: flower strip; pink: hedgerow; green: intensively managed meadow; dark green: forest edge) and bee groups (red: rare bees; dark blue: dominant crop pollinating bees; light grey: other bees). Photo credits: Landscape: Corina Maurer; bees: Kai Bachofner.

two conservation target groups: as rare when they were listed on the most recent available Swiss Red List of bees as 'vulnerable', 'endangered' or 'critically endangered' (Amiet, 1994; to be interpreted with adequate caution due to its age); or as dominant crop pollinators when they were listed as dominant crop pollinating wild bees of Central Europe provided by Kleijn et al. (2015). We excluded the managed honeybee *Apis mellifera* L. in all analyses since its presence is strongly attributed to beekeeping in the surrounding. This study did not require permission do to fieldwork, nor ethical approval for sampling wild bees.

2.2 | Floral resource survey

In the 2014 survey, floral resources were assessed as described in Bartual et al. (2019). Similarly, in 2020, 10 plots (2 m × 0.5 m) were randomly placed along transects (10 plots per 100 m; horizontally for herbaceous flowering vegetation; vertically along woody vegetation of hedgerows and forest edges). In both surveys, flower abundance per m² was estimated for each vascular flowering plant species as the number of single flowers multiplied by flower area. Flower area was calculated as area of a circle, and radii of single flowers (or inflorescences in the case of Asteraceae and *Plantago* sp.) for each species were retrieved from the following trait databases: Casanelles-Abella et al. (2021), Info Flora (<https://www.infoflora.ch/de/>), PlantNET (<https://plantnet.rbgsyd.nsw.gov.au/>) and Naturegate (<https://luontopointti.com/>). Flower richness was calculated as the number of flowering species per transect section.

2.3 | Landscape descriptors

Using a geographic information system (ArcGIS Pro version 10.7, ESRI), we classified landscape composition in each landscape (1 km radius) into the following categories: Arable crop, orchard, vineyard, hedgerow, forest, meadow, urban green (>25% green areas) and urban space (<25% green areas). Based on the resulting raster maps (pixel size: 1 × 1 m), we calculated the percentage of arable crop cover and total edge density (m/ha) for each landscape, using the R package LANDSCAPEMETRICS (Hesselbarth, 2021). These two metrics inform about landscape simplification and configuration in each landscape and are widely used proxies (e.g. Albrecht et al., 2020; Hass et al., 2018).

2.4 | Species-habitat networks

We built bee-habitat and flower-habitat networks for each landscape and sampling round, with habitats and wild bees or flowers as nodes and wild bee or flower abundance in each habitat as links (Marini et al., 2019). In this framework, we considered bees found in different habitats within a landscape as a meta-community, where the local communities are likely linked through dispersal (Leibold

et al., 2004). To assess to what extent the bee or flowering plant community depends on a specific habitat type (i.e. habitat specialists), we calculated the strength of each habitat (Collado et al., 2019; Marini et al., 2019). The strength of a habitat is the sum of dependencies (fraction of appearances) of all bee or flower species to a particular habitat type (Bascompte et al., 2006). Compared to traditional measures such as species richness, which treats all species equally, strength provides complementary information, contributing to a more complete picture about the importance of a habitat for bee conservation from a landscape perspective. To assess complementarity of habitats in flower species composition (pooled sampling rounds), we further calculated functional complementarity as the total branch length of a dendrogram based on qualitative differences in flower species assemblages between habitats (Devoto et al., 2012). To investigate whether bee community composition differs across habitat types, we assessed network modularity (Cappellari & Marini, 2021). In modular networks, certain bee species and habitats share more links than others and thereby form modules (Olesen et al., 2007). If certain species are mostly found in certain habitats, modules should correspond to different habitats. Then, species' roles can be identified by calculating z (standardized number of links within the same module, within-module degree) and c values (level to which the species is linked to other modules, among-module connectivity; Olesen et al., 2007). Here, species with a high z value show a strong preference for the specific habitat, while species with a high c value can be considered as habitat generalists. Strength, functional complementarity and modularity were not related to the number of habitats in a network (Appendix S2, Table S2). All network analyses were performed using R package BI-PARTITE (Dormann et al., 2008).

2.5 | Statistical analysis

First, we assessed sampling completeness of each habitat and both survey years (see Appendix S1 for details). Results showed that sampling completeness and coverage was satisfactory and that it did not differ between the surveys or habitats, respectively (see Appendix S1 and Appendix S2, Figure S1). Therefore, we analysed data of both survey years together and habitats can be compared without bias.

2.5.1 | Relative importance of habitats for wild bee communities throughout the season

To examine how different habitats support bee communities across sampling rounds, we calculated wild bee abundance and richness for each transect and strength for each habitat type and sampling round. We fitted generalized linear mixed models with negative binomial error distribution for abundance and richness, while strength (square-root transformed) was fitted with a Gaussian distribution. Habitat type and its interaction with sampling round were used as explanatory variables and habitat type nested within landscape ID

as random effects. We applied Tukey post-hoc tests to test for significant differences among habitat types (within sampling rounds). To evaluate whether the importance of habitat types differs among bee groups (rare, dominant crop pollinator, other), we fitted negative binomial models with bee abundance and richness as response variables and sampling round, habitat type and bee group, and the two-way interaction between habitat type and bee group as explanatory variables (using the same random structure as described above).

2.5.2 | Uniqueness of habitats in bee species composition

To investigate variation in bee species composition across different habitat types and their relative importance in terms of unique contributions to the landscape meta-community (i.e. uniqueness), we pooled data of the three sampling rounds. In a first step, we calculated the local contribution to beta diversity (LCBD) of each habitat type with the 'beta.div' function of the R package *ADESPATIAL* (Dray et al., 2021; see Appendix S1 for details). We examined differences in LCBD values (square root transformed) among habitat types with a linear mixed effects model and habitat type as explanatory variable and landscape ID as random factor. In a second step, we calculated total β -diversity within a landscape and disentangled its components according the method proposed by Legendre (2014) based on a quantitative (abundance-weighted) Jaccard index, using the function 'beta.div.comp' of the *ADESPATIAL* package. This method quantifies the relative contribution of species turnover or nestedness to variation in species composition among different habitats. We tested for significant differences in the contribution of the two groups (turnover and nestedness) with a Wilcoxon rank sum test. In a third step, we tested the hypothesis that each habitat supports relatively different sets of species and hence the bee-habitat network should be more modular than expected by chance, and modules correspond to the different habitats. Modularity of the overall bee-habitat network was calculated using DIRTLPAb+ algorithm in *bipartite* (Beckett, 2016). The observed value was compared to values obtained from 1000 null models representing random visits to any habitat type, while controlling for bee abundance (Patefield algorithm; Dormann et al., 2014). We calculated within-module degree z and among-module connectivity c values for each species to determine species' roles using critical thresholds ($c = 0.62$; $z = 2.6$) according to Olesen et al. (2007).

2.5.3 | The roles of floral diversity and landscape drivers

To evaluate the effects of flower richness and landscape context on bee abundance, richness, habitat strength, total β -diversity and modularity of species-habitat networks in each landscape, we fitted five models. Flower richness (in each habitat, averaged over sampling rounds) and the interaction between arable crop cover and edge density entered the model as explanatory variables. Flower

abundance and richness were positively correlated (coefficient $|r| = 0.64$) and as models with flower richness showed a lower AIC and thus a better fit than models with flower abundance, we used flower richness in these analyses. In the first three models, wild bee abundance and richness (log-transformed) and strength (square root transformed) per habitat were fitted using linear mixed effects models and landscape ID as random factor. In the fourth and fifth model, total β -diversity within a landscape and modularity (z-scores) in each landscape (sampling rounds pooled) were fitted using a linear model. Modularity was calculated the same way as described above, but for each landscape separately, and standardized to z-scores using 1000 null models (Patefield algorithm; Dormann et al., 2014). Moreover, we explored how well alternative descriptors of floral resources to flower richness, such as flower-habitat network based properties like habitat strength and functional complementarity, explained bee richness in separate models (Appendix S2, Table S3). Since these flower-habitat network properties mainly describe availability of different niches, we only explored their influence on bee richness. We included sampling year as additional fixed factor in all models to account for possible differences between the 2 years.

All statistical analyses were performed with the software R version 4.1.1 (R Core Team, 2021). Models were fitted with the package *LME4* (Bates et al., 2015) and model assumptions were checked by inspection of residual plots using R package *DHARMa* (Hartig, 2022). All continuous explanatory variables were standardized to improve convergence of the model algorithms.

3 | RESULTS

All together, we recorded 2072 wild bees of 104 species (530 flower-visiting bees of 61 species in April, 744 bees of 60 species in May/June and 798 bees of 62 species in July). Of those, 24 species were classified as rare and 21 species as dominant crop pollinators. See Appendix S2, Table S4 for a list of sampled bee species.

3.1 | Relative importance of habitats for wild bee communities throughout the season

Overall, extensively managed meadows supported the highest abundance and richness of wild bees, but the relative importance of habitats changed throughout the season (significant interaction between habitat type and sampling round for both wild bee abundance and richness; Table 1; Figure 2a,b). In April, wild bee abundance was similar in all habitat types, while richness was significantly higher in extensive meadows than in flower strips and forest edges. Similarly, in May/June, extensive meadows generally supported the highest abundance and richness of wild bees, while in July, flower strips became as important as extensive meadows (Table 1; Figure 2a,b). Wild bee abundance and richness in woody habitats (forest edges and hedgerows) were generally lower. Results were qualitatively identical and very similar when analyses were repeated with estimated species richness

TABLE 1 Summary of (1) results of linear (LMM) and generalized linear mixed effect models (GLMMs) testing for the importance of habitats across the season (three sampling rounds) and (2) for different target groups for bee conservation (rare bees, dominant crop pollinators, others)

Model	Fixed effects	df	F value	LRT	p value	R ² _M	R ² _C
(1) Wild bee abundance	Habitat: round	8		37.30	<0.001	0.25	0.39
	Habitat	4		41.23	<0.001		
	Round	2		0.44	0.80		
	Sampling year	1		0.18	0.67		
(1) Wild bee richness	Habitat: round	8		26.22	<0.001	0.23	0.36
	Habitat	4		37.30	<0.001		
	Round	2		0.44	0.80		
	Sampling year	1		0.002	0.96		
(1) Strength of a habitat ^a	Habitat: round	8	3.63		<0.001	0.35	0.51
	Habitat	4	12.72		<0.001		
	Round	2	0.16		0.85		
	Sampling year	1	5.93		0.02		
(2) Wild bee abundance	Habitat: bee group	8		24.87	0.002	0.40	0.54
	Habitat	4		34.98	<0.001		
	Bee group	2		257.44	<0.001		
	Round	2		0.15	0.93		
	Sampling year	1		11.1	<0.001		
(2) Wild bee richness	Habitat: bee group	8		20.94	0.007	0.35	0.45
	Habitat	4		34.12	<0.001		
	Bee group	2		146.99	<0.001		
	Round	2		1.17	0.56		
	Sampling year	1		11.38	<0.001		

Note: Denominator degrees of freedom (df), F value for F-tests (LMM) or differences in log-likelihood for χ^2 -tests (LRT; GLMMs), p values and marginal and conditional R-squared are shown. Significant p values ($p < 0.05$) are shown in bold.

^aSquare root transformed.

(Appendix S2, Table S5, Figure S2). Consistently, we found the same patterns and seasonal shifts for habitat strength (i.e. the capacity of a habitat to support habitat specialists; Table 1; Figure 2c). Results for strength were also robust when analysed with a reduced dataset (Appendix S2; Table S6). Relative importance of habitats differed for the two studied conservation target groups of bees (abundance and richness of rare bees and dominant crop pollinators): while extensive meadows were of highest relative importance in supporting rare bee species, dominant crop pollinators were additionally supported by flower strips (Table 1; Appendix S2, Figure S3).

3.2 | Uniqueness of habitats in bee species composition

The studied habitat types did not significantly differ in their local contribution to β -diversity of bees (LCBD: $F = 0.99$, $p = 0.42$; marginal $R^2 = 0.03$, conditional $R^2 = 0.32$). However, within landscape β -diversity was mainly due to species turnover ($70\% \pm 5\%$, mean \pm SE), rather than nestedness ($30\% \pm 5\%$; one-tail Wilcoxon Rank Sum Test: $W = 103$, $p < 0.001$), indicating that each habitat type harboured

unique species to a relatively large extent. In fact, on average 17% of the species were exclusively found in a specific habitat type (unique species; Appendix S2, Table S7). Among these, extensive meadows supported the highest number of unique species classified as rare (5 rare species; Appendix S2, Table S8).

Modularity (Q) of the entire bee-habitat network was 0.2, and thus the network significantly more modular than expected by the null models (one-tail Z test: $p < 0.001$; Appendix S2, Figure S4). The algorithm detected four modules corresponding to (1) extensive meadows, (2) flower strips, (3) hedgerows and intensive meadows and (4) forest edges (Figure 3), corroborating findings that different habitat types harboured different sets of wild bee species. Eighteen species exceeded the thresholds for within-module degree z and/or among-module connectivity c (Appendix S2, Table S9, Figure S5).

3.3 | The roles of floral diversity and landscape drivers

Floral richness had a significant positive effect on wild bee abundance, richness, habitat strength and within landscape β -diversity

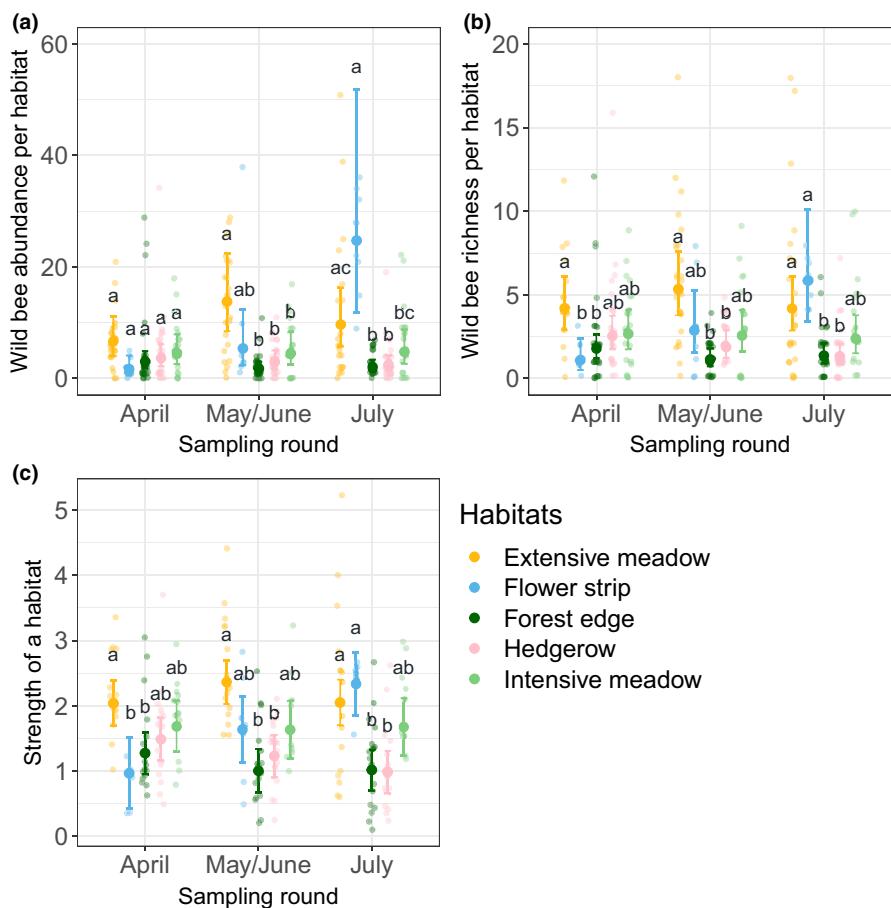


FIGURE 2 Effect of habitat type across different sampling rounds during the season on (a) wild bee abundance, (b) richness and (c) strength of a habitat. Mean estimates of the fitted model and 95% confidence intervals are given. Points show raw data. Different letters indicate significant differences ($p < 0.05$) between habitat types within one sampling round, tested using Tukey post-hoc tests. Square-root transformed values are shown for habitat strength.

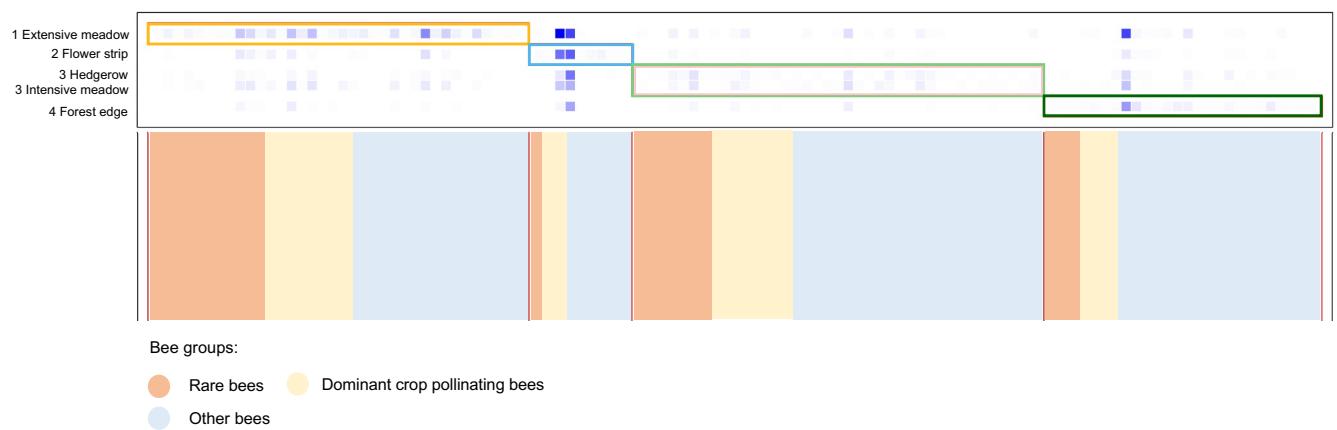


FIGURE 3 Modules of the overall bee-habitat network, corresponding to (1) extensively managed meadows, (2) flower strips, (3) hedgerows and intensively managed meadows and (4) forest edges. Darker squares indicate a higher number of observed interactions. The colour depicts the different bee groups of sampled bee species occurring in each module, and the width of the bars corresponds to the number of species in each group.

(Table 2). Bee species richness was also positively related to the flower-habitat network properties habitat strength (linear relationship) and functional complementarity (when an outlier was excluded; hump-shaped relationship, Appendix S2, Table S3). Moreover, β -diversity and bee abundance, but not bee richness or habitat strength, were positively affected by arable crop cover, and β -diversity by an interactive effect of crop cover and edge density

(Table 2). Bee communities in different habitats within a landscape were more similar in well-connected (high edge density) than in less connected (low edge density) landscapes, but only at moderate to high levels of landscape simplification (high arable crop cover; >50%; Table 2, Figure 4). In contrast, standardized modularity was not significantly influenced by flower richness or landscape drivers (Table 2).

TABLE 2 Summary of results of linear mixed effect models of landscape drivers on wild bee abundance, richness, strength of a habitat, and linear model results for within-landscape β -diversity and modularity

Model	Fixed effects	Estimate	SE	t value	p value	R^2_M	R^2_C
Wild bee abundance ^a	Flower richness	0.56	0.08	7.10	<0.001	0.37	0.38
	Arable crop cover	0.23	0.10	2.30	0.02		
	Edge density	0.03	0.08	0.33	0.74		
	Arable crop cover: edge density	-0.01	0.09	-0.08	0.93		
	Sampling year	-0.85	0.2	-4.37	<0.001		
Wild bee richness ^a	Flower richness	0.43	0.05	8.64	<0.001	0.45	0.46
	Arable crop cover	0.13	0.06	2.04	0.06		
	Edge density	0.03	0.05	0.56	0.58		
	Arable crop cover: edge density	0.02	0.05	0.36	0.73		
	Sampling year	-0.57	0.12	-4.64	<0.001		
Strength of a habitat ^b	Flower richness	0.43	0.07	6.55	<0.001	0.34	0.36
	Arable crop cover	0.09	0.08	1.08	0.28		
	Edge density	0.07	0.07	0.94	0.35		
	Arable crop cover: edge density	0.07	0.08	0.92	0.36		
	Sampling year	-0.09	0.18	-0.52	0.60		
Total β -diversity	Flower richness	0.01	0.007	1.85	0.08	0.56	-
	Arable crop cover	0.05	0.02	2.66	0.02		
	Edge density	-0.0004	0.0002	-1.97	0.06		
	Arable crop cover: edge density	-0.0004	0.0002	-2.34	0.03		
	Sampling year	-0.006	0.02	-0.36	0.72		
Modularity (z-scores)	Flower richness	0.88	0.81	1.09	0.29	0.16	-
	Arable crop cover	0.96	0.75	1.27	0.22		
	Edge density	-0.19	0.62	-0.31	0.76		
	Arable crop cover: edge density	-0.41	0.63	-0.66	0.52		
	Sampling year	-2.72	0.63	-1.40	0.18		

Note: Mean estimates \pm standard error, t value, p value and marginal and conditional R-squared are shown. Significant p values ($p < 0.05$) are shown in bold.

^aLog-transformed.

^bSquare root transformed.

4 | DISCUSSION

Here, we integrated different methodological approaches to shed light on habitat-level and landscape-level factors shaping wild bee communities in different types of semi-natural habitats (SNH) in agricultural landscapes. We demonstrate that extensively managed meadows sustained consistently high abundance and diversity of wild bees during the entire growing season, particularly many habitat specialists and rare species. At the same time, the importance of flower strips increased gradually from April to July, mainly sustaining dominant crop pollinators rather than rare species. We further show that each habitat harboured a relatively unique set of species, highlighting that all SNH types provide complementary niches and contribute to diverse wild bee meta-communities in agricultural landscapes. These results emphasize the need for pollinator conservation management to take a landscape perspective and to consider the relative importance of specific habitats and their temporal

dynamics during the season for different conservation target groups of wild bees. Floral richness, and properties of flower-habitat networks, drove the local diversity patterns within habitats, while interactive effects between landscape composition and configuration additionally influenced species turnover between habitats.

While extensively managed meadows—and to a lesser extent conventionally managed meadows—sustained high wild bee abundance, richness and habitat specialists during the whole season, flower strips gained in importance late in season. Extensively managed meadows provide continuously high floral richness from early to late season compared to other habitats (Appendix S2, Figure S6). This is essential for sustaining a diverse suite of bee species (Albrecht et al., 2007), especially rare species, since one fifth of all detected rare species in our study was uniquely found in these extensively managed meadows, similar to Ekoos et al. (2020). In contrast, sown flower strips often offer only few floral resources early in the season, when most bee species are active and resources are crucial, particularly for colony

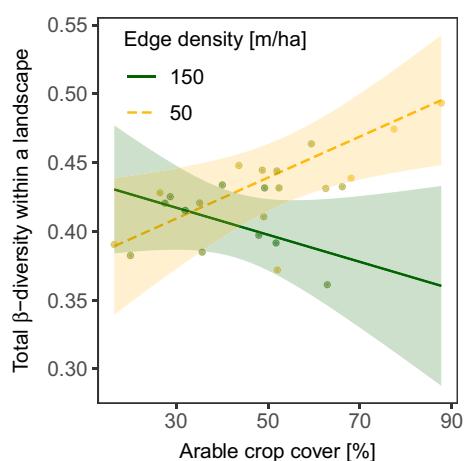


FIGURE 4 Relationships of arable crop cover and within landscape β -diversity predicted for high (150 m/ha) and low (50 m/ha) edge density (1000 m radius). Model predictions and 95% confidence intervals are shown; points show partial residuals. When arable crop cover is high and edge density is low (presumably low connectivity among habitats), the communities in the different habitats within a landscape are more dissimilar compared to landscapes with high edge density (high connectivity).

building of bumblebees (Williams et al., 2012). However, they provided important floral resources in times of resource scarcity – when most meadows have been mown—in summer (Ouvrard et al., 2018). Our results indicate that flower strips enhance mainly dominant crop pollinators, but not rare species (e.g. Albrecht et al., 2021; but see Schubert et al., 2022). In fact, assuring resource continuity during periods of floral resource scarcity should be particularly important for pollinators with long active periods such as bumblebees (Rundlöf et al., 2014), which are among the most important crop pollinators in the study region. In line, flower strips have been shown to support more social than solitary bees (von Königslöw et al., 2021). Interestingly, our analysis of flower-habitat networks corroborates that not only local floral species richness and habitat strength but also functional complementarity of floral resources across habitats drives bee meta-communities at the landscape scale, although the exact underlying patterns and mechanism require further study. Thus, meadow extensification schemes, in addition to establishing flower strips, have a high potential for wild bee conservation in agro-ecosystems (Ekroos et al., 2020; Ganser et al., 2020).

Despite the important roles of extensively managed meadows and flower strips, each habitat can contribute to wild bee β -diversity within a landscape (Pfiffner et al., 2018). This is shown by the high turnover in species composition among habitats and high modularity of the network in our study, which implies that each habitat harboured a relatively unique set of species. Therefore, our findings support evidence from other ecosystems (Penado et al., 2022) that sustaining different habitat types within an agricultural landscape is essential for conserving diverse wild bee meta-communities. For example, the oligoleptic longhorn bee *Eucera nigrescens* was strongly associated with the module consisting of intensively managed meadows and hedgerows (high within-module degree z and low

among-module connectivity c). In fact, its preferred forage plant species in the study region, *Vicia sepium* L. (Westrich, 2019), can be typically found along the herbaceous borders of hedgerows and rather nutrient rich and generally intensively managed meadows. Although the bumblebee *Bombus pascuorum* and the sweat bee *Lasiglossum malachurum* showed an association with forest edge or extensively managed meadows, respectively, they were less specialized to their apparently preferred habitats and also regularly found in other habitats (high within-module degree z and high among-module connectivity c). Simultaneously, a series of other species were identified to use many habitat types (low within-module degree z and high among-module connectivity c). Even though this analysis cannot make any direct inference about the factors determining a species' association to a particular habitat, it evaluates if a species is using mainly one particular or several habitat types (and which). This can be especially useful to develop targeted conservation measures (Cappellari & Marini, 2021). We would like to note, however, that as almost inevitably in most studies assessing pollinator species composition across habitats, under-sampling could lead to an overestimation of uniqueness, which therefore needs to be interpreted with adequate caution. However, our analyses suggest that sampling completeness and coverage was satisfactory in our highly replicated study across 25 agricultural landscapes. Moreover, many of the unique species were rare Red List species, which can inherently only be expected at low abundances.

Besides local resources, landscape composition and configuration can influence α - and β -diversity of species (Hendrickx et al., 2007). In contrast to previous findings (e.g. Hass et al., 2018; Holzschuh et al., 2010; Lami et al., 2021), landscape factors such as arable crop cover and edge density did not influence bee richness, habitat strength for bees and modularity of the species-habitat networks in our study, except from arable crop cover that was positively related to bee abundance. However, they influenced β -diversity of bees among habitats within a landscape: at moderate to high levels of arable crop cover, bee communities in the different habitats within a landscape were more similar in well-connected landscapes than in landscapes, where remaining SNH patches are less connected through field edges and other linear elements. Because bees are central-place foragers with restricted foraging ranges (Greenleaf et al., 2007), the often relatively high specialization to certain habitats can result in relatively high community turnover within a landscape, as shown by our findings. A higher amount of SNH in the landscape could dampen this community turnover (Beduschi et al., 2018). Consequently, a more structurally rich landscape with a connected network of SNH and high edge density enhances species turnover and thereby could facilitate dispersal among habitats (Hass et al., 2018). This might increase community resilience after a disturbance, since better-connected habitats may be re-colonized faster (Tscharntke et al., 2012). At the same time, high flower richness at the local habitat level and high resource complementarity across habitats offers more niches and thereby increases bee α - and β -diversity across habitats. Therefore, structurally and flower species-rich

agricultural landscapes with connected patches of SNH should be promoted to support resilient bee communities.

5 | CONCLUSIONS

Our study illustrates that pollinator species-habitat networks, especially when combined with information about floral resources and flower-habitat network analyses, are valuable tools to assess the relative importance of habitats for wild bee species during the season. This provides an important baseline for informed management recommendations. In fact, flower-habitat network properties were good predictors for variation in bee richness besides flower richness, providing valuable complementary insights relevant for pollinator conservation at the landscape scale. Combining species-habitat network analysis with traditional community descriptors (α - and β -diversity), we show that promoting different types of SNH in agricultural landscapes is essential to sustain diverse wild bee meta-communities. Especially habitats with different flowering phenologies, such as extensive meadows and flower strips, are shown to complementarily benefit bees. Locally, the value of habitats for bees, in particular for habitat specialists, can be further promoted by maintaining and ideally increasing flower richness. Our findings highlight that particularly meadow extensification schemes can play a key role in safeguarding rare and specialist species. At the landscape level, especially in simple landscapes, increasing connectivity between habitat patches through enhanced edge density (e.g. smaller field sizes and a more dense network of green infrastructure such as SNH or areas under agri-environment schemes) seem to facilitate species exchange between bee communities of different habitats, possibly increasing their resilience to disturbances. Actions based on these management recommendations should not only help sustaining diverse bee communities in agroecosystems, but likely also associated pollination services to wild plants and crops (Albrecht et al., 2020).

AUTHOR CONTRIBUTIONS

Corina Maurer and Matthias Albrecht conceived the ideas; Corina Maurer, Louis Sutter and Matthias Albrecht designed the methodology and collected the data; Corina Maurer, Carlos Martínez-Núñez and Matthias Albrecht analysed the data; Corina Maurer led the writing of the manuscript; Loïc Pellissier and Corina Maurer conceived ideas for visualization of the results. All authors contributed critically to the drafts and gave final approval for publication. Our study brings together authors from two countries and includes scientists based in the country where the study was carried out.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.9cnp5hqn3> (Maurer et al., 2022).

ORCID

Corina Maurer  <https://orcid.org/0000-0001-8103-4111>

Louis Sutter  <https://orcid.org/0000-0002-2626-216X>

Carlos Martínez-Núñez  <https://orcid.org/0000-0001-7814-4985>

Loïc Pellissier  <https://orcid.org/0000-0002-2289-8259>

Matthias Albrecht  <https://orcid.org/0000-0001-5518-3455>

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SUPPORTING INFORMATION

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