



Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes

Lolita Ammann^{a,*}, Alette Bosem-Bailod^{a,b}, Felix Herzog^a, David Frey^c, Martin H. Entling^d, Matthias Albrecht^{a,**}

^a Agroscope, Agricultural Landscapes and Biodiversity, Reckenholzstrasse 191, CH-8046 Zürich, Switzerland

^b Research Institute of Organic Agriculture FiBL, Ackerstrasse 113, CH-5070 Frick, Switzerland

^c Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

^d Institute for Environmental Sciences, University of Koblenz-Landau, Fortstrasse 7, D-76829 Landau, Pfalz, Germany

ARTICLE INFO

Keywords:

Agri-environment schemes
Biodiversity
Floral food resources
Functional habitat maps
Habitat management
Landscape composition
Mass-flowering crops
Pollination services
Pollinator conservation
Semi-natural habitats

ABSTRACT

Targeted conservation and promotion of wild bees in agroecosystems requires understanding of relationships between different groups of bees and available floral resources across land-use types during the season and at the landscape scale. Here, we quantified floral resource amount and diversity across habitat types at different times during the season at the scale of entire landscapes (500 m radius) across 20 different agricultural landscapes. Moreover, we examined whether floral resource metrics obtained from these high-resolution floral resource maps are more suitable to assess and predict abundance and species richness of different bee pollinator groups, including rare species and important crop pollinators, sampled in these agricultural landscapes compared to traditional land-cover metrics. Floral resource availability shifted from flower-rich woody vegetation early in the season to herbaceous vegetation such as grasslands and crops later in the season, which was associated with a ten-fold decline in overall floral resource availability. Forest edges had highest per-area floral contributions in spring, whereas floral diversity of grasslands, in particular if extensively managed, was continuously high. Total wild bee species richness, as well as rare species richness and abundance of important crop pollinators, increased with floral resource availability and/or diversity contributed by forest edges and floral diversity of permanent grasslands. Rare bee richness was also positively related to floral resource amount provided by crops. Total bee richness and important crop pollinator abundance, but not rare bee richness, were positively related to overall floral resource amount, but not floral diversity, in the landscape. Floral resource maps based on floral resource supply by major habitat types early or late in the season predicted wild bee species richness ($R^2 = 0.61$) better than traditional descriptors of landscape composition such as proportion of semi-natural habitat. The pronounced temporal shifts in floral resource availability for pollinators from woody towards herbaceous vegetation during the season highlights the importance of taking a landscape-scale perspective on pollinator conservation. Our findings indicate that both rare bees and important crop pollinators benefit from complementary floral resources of forest edges and grasslands in agroecosystems. This reveals a potential synergy between the conservation of endangered species and the landscape scale management to promote pollination services. Our study also highlights that floral resource maps are useful tools in supporting more targeted pollinator conservation and pollination service management at the landscape level.

1. Introduction

Wild bees play a vital role as pollinators of both wild flowering plant species and crops in agroecosystems (IPBES et al., 2016; Klein et al., 2007; Kleijn et al., 2015; Ollerton et al., 2011). Beyond their functional

importance for pollination, wild bees are of high intrinsic value as they contribute to agroecosystem's biodiversity. However, several studies have reported strong declines of wild bee populations, as well as bee diversity in several regions of Europe and North America during the last decades (Biesmeijer et al., 2006; Carvalheiro et al., 2013). Wild bees are

* Correspondence to: Software Competence Center Hagenberg GmbH (SCCH), Softwarepark 21, 4232 Hagenberg, Austria.

** Corresponding author.

E-mail addresses: lolo.ammann@gmail.com (L. Ammann), matthias.albrecht@agroscope.admin.ch (M. Albrecht).

<https://doi.org/10.1016/j.agee.2023.108754>

Received 16 May 2023; Received in revised form 15 September 2023; Accepted 18 September 2023

Available online 25 September 2023

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therefore of high conservation concern (Potts et al., 2016).

Loss and degradation of habitats providing nesting and in particular suitable floral food resources (pollen and nectar) is considered to be among the major drivers of bee decline (Potts et al., 2016; Scheper et al., 2014). Hence, a prerequisite for successful bee conservation in agroecosystems is (i) an improved understanding of the importance of different descriptors of landscape-level floral resource availability (e.g., floral abundance and diversity) in their contribution to sustain wild bee pollinators during different times of the year (Dicks et al., 2010). Moreover, (ii) quantitative knowledge on floral resources provided by different habitat types in agricultural landscapes and their importance for different groups of bee pollinators is required (Baude et al., 2016; Guezen and Forrest, 2021; Ogilvie and Forrest, 2017; Timberlake et al., 2019; Woodard and Jha, 2017). Importantly, also (iii) a better understanding of the temporal dynamics of floral resources provided by different habitats during the season and the role of potential spatio-temporal complementarity of floral resource availability across different habitat types during different times of the year is needed (Jachula et al., 2021; Mallinger et al., 2016; Mandelik et al., 2021; Timberlake et al., 2019, 2021). Such knowledge allows to identify times of floral resource scarcity in agricultural landscapes (Jachula et al., 2021; Ogilvie and Forrest, 2017) and how this affects different wild bee groups. Importantly, such improved understanding helps to identify the specific habitats and floral resource species that are most promising to focus on through targeted measures aimed at mitigating floral resource scarcity during certain time periods in the year and increasing continuous supply of floral resources in agroecosystems (Guezen and Forrest, 2021; Jachula et al., 2021; Mallinger et al., 2016; Ogilvie and Forrest, 2017; Timberlake et al., 2019, 2021). A better understanding of such temporal dynamics in floral resources and their role for different important management target groups of bees will be particularly helpful to achieve major bee pollinator conservation goals such as promoting overall wild bee diversity, rare bees of particular conservation concern or important crop pollinators (Sutter et al., 2017; Timberlake et al., 2019). This requires a landscape perspective on pollinator conservation and pollination service management (e.g. Marini et al., 2019; Ogilvie and Forrest, 2017; Tscharnitke et al., 2012). Traditional approaches using coarse landscape composition properties based on land-cover maps ignoring the generally highly varying amount, diversity and quality of floral resources across and within such land use classes may fail to achieve these goals (Bartual et al., 2019; Hellwig et al., 2022; Holland et al., 2016). Here, functional habitat maps considering different metrics of floral resource availability quantified for entire landscapes and across the season may provide a more promising approach to achieve these goals (Timberlake et al., 2021).

Likely not at least due to the logistical challenges and efforts required to collect data on floral resource availability across major habitat types, most previous studies have either mainly focused on floral resource use by bees in local habitat elements (Cole et al., 2017) or on effects of landscape-level floral resources availability on a single bee species (Williams and Kremen, 2007; Williams et al., 2012), but see e.g. Guezen and Forrest (2021); Mallinger et al., 2016; Scheper et al. (2015)). Moreover, while many studies have focused on floral resources provided by herbaceous vegetation, likely partly because quantification of floral resources is methodologically more straightforward in herbaceous than in woody vegetation, a better understanding of the role of flowering trees and shrubs during different times of the season for different important groups of wild bees is needed (Bertrand et al., 2019; Mallinger et al., 2016; Timberlake et al., 2019).

In the present study we therefore quantified different metrics of floral resources across all major habitat types on the scale of entire landscapes. Moreover, we assessed their importance for overall wild bee diversity and different functional groups of bees (important crop pollinators and rare bees) during different time periods as a prerequisite to inform targeted landscape management decisions to promote them. Potential trade-offs are conceivable as these management target groups

may vary in their spatio-temporal requirements of floral resources. Rare bees are often characterized by specific resource and habitat requirements and diversity of such specific key floral resource plants is expected to play a key role (Senapathi et al., 2015; Sutter et al., 2017), while important crop pollinating wild bees are expected to use habitat and floral resources more opportunistically and thus the availability and continuity of flowering crops and mass-flowering wild plants across different habitats during the main activity period may be more important (Bertrand et al., 2019; Westphal et al., 2003). Alternatively, different groups of bee pollinators may overlap to a large extent in their reliance on floral resources provided by certain habitat types. An improved understanding of such potential trade-offs or synergies is essential to enhance the effectiveness of targeted measures, and can inform management strategies for win-win situations: both for the conservation of rare pollinator species, and to promote important crop pollinators and their pollination services (Ekroos et al., 2014; Kleijn et al., 2015; Senapathi et al., 2015). Such knowledge is highly relevant to guide future agricultural policy to better support wild pollinators in agroecosystems (Cole et al., 2020).

Improving our understanding of the relationships between floral resource composition of landscapes across habitat types should also help to refine models to predict impacts of habitat change on pollinator communities (Lonsdorf et al., 2009). However, landscape-scale floral resource mapping (i.e., the spatially and temporally explicit quantification of floral resources at a landscape scale at different points in time) is a highly time and resource-intensive task. An important question is therefore whether more easily obtained land-cover maps may be sufficient to predict certain groups of bees, and to what extent more refined “functional habitat maps”, e.g. based on spatially and temporally resolved quantification of floral resources, can improve predictions (Lausch et al., 2015; Vanreusel et al., 2007).

In this study, we quantified landscape-scale floral resource availability provided by a range of major herbaceous and woody habitats (including grasslands, forest edges, semi-open habitats and crops), and we assessed their role for different groups of wild bees, sampled through standardized methods at different locations (grassy edges/field boundaries) within a landscape, across 20 agricultural landscapes in Switzerland. We were mainly interested in the following wild bee groups and response variables: overall wild bee diversity (major interest from a pollinator biodiversity conservation perspective); rare (Red List) bee species richness (main interest for the conservation of threatened wild bees) and abundance of important crop pollinators (main target group for landscape management to promote crop pollination services). We therefore address the following research questions:

- (1) What is the contribution of different habitat types to floral resources for bees in agro-ecosystems during different times of the year?
- (2) Are abundance and species richness of bees, including rare bees and important crop pollinators, driven by landscape-scale abundance and diversity of floral resources?
- (3) What is the relative importance of floral resources provided by different semi-natural habitat types and crops for rare bees and important crop-pollinating bees?
- (4) Does the relative importance of floral resources provided by these habitats for different bee groups shift during the season?
- (5) Do floral resource maps better predict richness and abundance of bees than land-cover maps, and are predictions improved by accounting for seasonal availability of resources?

2. Materials and methods

2.1. Study design

A total of 20 landscape sectors of 500 m radius each (hereafter ‘landscapes’) with varying proportions of different land-cover types

were randomly selected in the north eastern Swiss Plateau (Fig. S1). The studied agricultural landscapes of this region are mainly characterised by a relatively small-scaled mosaic of crops, grasslands, forest patches, hedgerows and traditional high-stem orchards (see also Table S1). The landscape radius of 500 m was primarily chosen according to the relevant average foraging ranges of most sampled bee species. Although maximum foraging ranges of some of the most mobile bees (e.g. bumblebees) can sometimes be larger, the average foraging ranges even of such mobile taxa are typically restricted to a few hundred meters (Greenleaf et al., 2007; Osborne et al., 2008; Zurbuchen et al., 2010). In the small-scaled mosaic type agricultural landscapes characterizing our study region, typically even shorter foraging distances have been observed (Albrecht et al., 2007a; Ganser et al., 2020). Moreover, this radius represents the maximum scale, at which floral resources could be mapped with such high precision (spatial and temporal resolution) in all 20 landscapes, ensuring high replication, given the enormous logistic and time effort required.

To be able to compare the suitability of different mapping strategies, four different maps of varying precision and content were compared: (i) simple dichotomous land-cover maps only distinguishing semi-natural habitat from the surrounding crops; (ii) more detailed land-cover maps distinguishing between crops (including arable areas and horticulture) and major types of semi-natural habitats: forest edges, semi-open habitats (i.e. hedgerows, traditional orchards and single trees) and permanent grasslands (meadows and pastures, managed intensively or extensively); (iii) simple functional resource maps with information of floral resources pooled at the landscape scale and (iv) functional resource maps with detailed information on the floral resources present in the above mentioned four major land-cover types. Land-cover types were mapped based on aerial photographs, ground-truthed in the field and subsequently digitalized in ArcGIS (version 10.6, ESRI; see Supplementary S1 for detailed information on habitat categorisation and landscape variables).

2.2. Flower mapping and estimation of floral resource availability

2.2.1. General approach

Assessments of landscape parameters and bees were carried out in 20 sectors of 500 m radius agricultural landscapes of the Swiss lowlands (Fig. S1). Floral resources of four major habitat types were assessed: grasslands, crops, semi-open habitats and forest edges. Neither floral resource availabilities nor floral diversities among these four habitat types were strongly correlated (Pearson correlation: all $|r| < 0.34$ or < 0.25 , respectively) (Zuur et al., 2007; Fox, 2018).

To obtain functional floral resource maps, floral resource availability and floral diversity (Simpson diversity index) of flowering plants were estimated for each habitat type from the beginning of April to end of June 2018 (Table S2). All entomophilous flowering plants but excluding wind-pollinated plants according to the BiolFlor plant trait database (Klotz et al., 2002) were considered. Floral resource availability was calculated based on recorded flower numbers in three-dimensional sampling plots (cubes) considering species-specific flower volumes of different species (which was found to be positively related to the floral resources a flower provides) as well as flowering duration (see detailed description below). Species-specific floral resource availability of different habitat elements was then pooled to floral resource availability per habitat and landscape, allowing subsequent calculation of flower diversity in the respective habitats.

Floral resources were assessed in each habitat type in each landscape based on the sum of the floral resource availabilities of all sampled entomophilous flowering plant species. The floral resource availability of a species (F_{species}) was estimated as the product of the average number of flowers of the species per volume (flower density D_{species} , [flowers m^{-3}]; see detailed description in 2.2.2; considering also variation in flower volume across species), which was found to be positively related to the amount of floral resources provided by a flower (S_{species} ; see Section 2.2.3

and Fig. S4) of the flowering parts of the vegetation in a habitat, e.g. the flowering tree crown and the volume (V_{species} , [m^3]; see detailed description in Section 2.2.4) occupied by the flowering parts of the plant species in a habitat and landscape. To account for variation in the duration of flowering periods of different species this product was multiplied by the flowering period of the species (e.g., the estimated average number of days the species was flowering; T_{species} ; see detailed description in Section 2.2.5).

$$F_{\text{species}} = S_{\text{species}} \times D_{\text{species}} \times V_{\text{species}} \times T_{\text{species}}$$

$$F_{\text{veg.type}} = \sum_{\text{species}} F_{\text{species}}$$

$$F_{\text{habitat}} = \sum_{\text{veg.type}} F_{\text{veg.type}}$$

For the estimation of formula parameters vegetation specific protocols were used. Protocols account for differences in structure and floristic composition of the different vegetation types. Details on parameters and their estimation are described in the following sections.

2.2.2. Flower density (D_{species})

Flower density (D_{species}) describes the number of open flowers in the flowering parts of the species during its flowering period. To estimate flower density, the four habitat types were split into sub-categories based on distinct vegetation characteristics for flower mapping in the field (Table S1). In these habitat sub-categories, flower density was differently assessed for woody vegetation, grasslands and arable flowering crops.

Flower density of woody vegetation (trees and shrubs of forest edges, hedgerows, orchards and single trees; Table S1) was assessed in the flowering parts (flower bearing volume, see Section 2.2.4 below) for each tree and shrub species separately. To this end, the number of flowers were counted within 20 cubes (each 1 m^3 ; two randomly selected cubes each in each of ten randomly selected individual plants per species) during the species' flowering period. Flower densities in tree crowns and shrubs within a specific species did not strongly or systematically vary among different landscapes, but species composition and relative abundance of flowering tree and shrub species in woody habitats strongly varied across landscapes. Hence, to obtain robust estimates of flower densities of woody vegetation, we combined these estimates of flower density of each tree and shrub species with spatially highly resolved information about the relative abundance of each individual tree and shrub plant of each flowering species in each element or patch of woody vegetation of each habitat sub-category across the studied 20 landscapes (based on precise mapping of individual tree and shrub plants; see detailed descriptions in Section 2.2.4). Wherever woody habitats also comprised herbaceous flowering plants in adjacent grassland strips along hedgerows or forest edges, these were quantified according to the description of for flower density for grasslands in the following section.

Flower densities in the four grassland sub-categories (Table S1) were assessed in each landscape over the entire bee sampling period at roughly three-week intervals (five sampling rounds). Flower density of each entomophilous flowering species was counted within ten randomly located cubes (each 1 m^3) in two randomly chosen grassland areas of each category, if present. This resulted in a total of 6060 individual cubes of 1 m^3 in which flower density was estimated in grasslands across the 20 landscapes from beginning of April until end of June (20 cubes of each category; four sub-categories) in each of the 20 landscapes per sampling round (five sampling rounds). Flower density in crops, which were very homogeneously flowering, were counted in ten randomly placed cubes of 1 m^3 size in two randomly selected fields per crop species during the peak flowering period.

2.2.3. Species' flower volume ($S_{species}$)

Inflorescences and single flowers greatly vary in size and volume, which is likely to be related to the amount of offered floral resources. In fact, our findings show that flower (inflorescence) volume was closely positively related to the amount of nectar and pollen it produces; significant positive linear relationship of flower volume and the amount of nectar and pollen (see Fig. S2). We therefore considered flower volume in the formula to obtain an even more accurate estimation of floral resource availability instead of simply using flower counts. A detailed description of how flower (inflorescence) volume was calculated is provided in the Supplementary (Fig. S2 and method description in figure caption).

2.2.4. Flower bearing plant volume ($V_{species}$)

To quantify flower bearing plant volumes, approaches optimised for the different habitat types were applied. In grasslands and arable crops, the height of the flower bearing part of the vegetation never exceeded one meter, and $V_{species}$ was directly available from the sample 1 m^3 cubes and the meadow or field size. To estimate the floral resource contribution of tree and shrub species, however, the entire flower bearing part of woody vegetation (forest edges, hedgerows, single trees e.g. in high-stem orchards) of all entomophilous tree and shrub species of woody vegetation was estimated (not only within the selected 1 m^3 cubes as described above for herbaceous grasslands and crops, see also Fig. S4). For the linear woody vegetation categories forest edges and hedgerows, this was done for the entire length of all forest edges and hedgerows in each landscape (c. 38 km total length mapped in the field). To this end, the entire assessed forest edge and hedgerow vegetation of each landscape was split into three-dimensional segments of two meters length and the entire width of the woody vegetation in the case of hedgerows, or a width of ten meters in the case of forest edges. Within each of these segments, the presence of all woody species was recorded and the volume of the flowering parts of each of these species were estimated, separately for the upper crown layer, the middle crown layer (for trees) and the shrub layer (for an illustration and detailed description of the calculation of flower bearing volumes of trees and shrubs see Fig. S4). To calculate floral resource availability in woody vegetation sub-categories, this estimated flower bearing plant volume of a flowering shrub or tree species within a woody habitat sub-category in each landscape was combined with the estimated flower density in the 20 cubes (1 m^3) of each flowering tree and shrub species as described in Section 2.2.2, accounting for a species' flower volume (see Section 2.2.3) and a species' flowering period (see Section 2.2.5).

2.2.5. Estimation of flowering period ($T_{species}$)

The flowering period of flowering herbaceous plants in grasslands was determined based on the continuous floral assessments at different dates within and across the five major sampling periods during the season within the total of 6060 sampled cubes of 1 m^3 . A species' flowering period was defined as the period from the first to the last day it was recorded flowering in any of these sampling cubes. Very rare flowering herbaceous species that occurred in less than 1% of all sampling cubes (22 species) were excluded from further analyses, as they did not allow to reliably estimate flowering periods. Flowering periods of crops were estimated based on field observations. For each flowering tree and shrub species, its flowering stage (peak flowering, flowering but not peak flowering, not flowering) was recorded repeatedly. These observations allowed to reliably estimate peak flowering, but not the exact start and end date of flowering of each tree and shrub species. However, although flowering periods of these trees and shrubs vary between species, variation appeared to be not huge but generally relatively similar for the dominant flowering tree and shrub species in the study region, with an average duration of approximately 21 days (see also Bock et al., 2014 for similar estimations). We therefore used this approximation of average flowering period around the observed peak to approximate the flowering period, i.e. to estimate the start and end date

of flowering of these tree and shrub species in the study region.

2.3. Sampling of bees

In each landscape, bees were sampled with four traps constructed as a combination of a passive window intersection trap component together with a large (42.5 cm upper diameter) funnel-shaped pan trap component ("combi traps"; the intersecting plexiglass windows are fixed above the opening of the large funnel-shaped pan trap; Duelli et al., 1999). Combi traps have been demonstrated to be highly effective for quantifying bees and other flying insects in agricultural landscapes, and they are less biased towards certain taxa compared to traditional pan trapping (Duelli et al., 1999). As they combine passive sampling through window trapping with very large pan traps, they have been shown to reflect bee and other flying insect communities beyond the immediate local sampling site, and they are less prone compared to traditional pan traps to the potential influences of the very local flower availability on sampling efficiency (Duelli et al., 1999; Kovács-Hostyánszki et al., 2011; Westerberg et al., 2021). This potential influence was further minimized by establishing combi-traps on flowering plant species poor grassy edges /boundaries with relatively similar plant composition across landscapes as a "standardized" local sampling location (four locations per landscape). A further critical advantage of this sampling method to address the objectives of this study compared to alternative methods, such as transect walks, is that the method is not constrained to specific vegetation types, such as herbaceous or only lower heights of woody vegetation that can be reached with a net. Thus, combi traps are considered a highly adequate standardized method to sample bees beyond local habitats in the agricultural landscape (e.g., Duelli et al., 1999). Combi traps consisted of two plexi-glass windows (50 cm x 42 cm) arranged cross-wise over a large yellow funnel-shaped pan trap. The pan trap (12 litre volume) was filled with water and a drop of soap to reduce surface tension and enhance trapping success. Traps were set up along grassy field margin and grassland edges at least 150 m apart but as close to the centre of a landscape as possible. Bees were sampled from early April until late June 2018, and traps were emptied weekly. Samples of the four traps were pooled per landscape for analysis. Bees were stored in 70% ethanol until pinning and identification by experts. We excluded managed *Apis mellifera*, the Western honeybee, and the two solitary bee species *Osmia cornuta* and *O. bicornis* from further analyses because they are often managed in high numbers for the pollination of fruit orchards in the study region. Bees were categorized according to their conservation status (vulnerable, endangered or critically endangered) based on the Red List of bees of Switzerland (Amiet, 1994) and important crop pollinators were categorised according to Kleijn species listed as dominant wild crop pollinators for Europe) et al. (2015), respectively (see Table S2 for an overview of the assignment of bee species to groups).

2.4. Statistical analysis

Linear model analyses were used to test the effects of landscape explanatory variables (i.e., floral resource and land-use descriptors) on bee response variables (pooled bee samples of the four traps per landscape). Landscape-scale species richness and sampling effort adequacy were visualised and estimated in R using package iNEXT version 2.0.20 and vegan package v. 2.5-7 (Fig. S4; Hsieh et al., 2016; Oksanen et al., 2019). Response and explanatory variables were centred and scaled prior to analysis to be able to directly compare parameter estimates of different models. Explanatory variables in a model were not highly correlated (VIF <3) (Zuur et al., 2007). The adjusted- R^2 was used to compare the goodness-of-fit of different models. Statistical inference was based on full models.

To test the effects of landscape-scale floral resource availability and floral diversity on the studied bee response variables (research question 2) linear models for overall wild bee diversity (total species richness), species richness of rare bees and abundance of important crop

pollinators were run. Separate linear models were also used to explore variation explained by floral abundance and diversity contributed by each of the four habitat types (forest edge, semi-open habitat, grassland and crops) for these bee response variables; research question 3).

To explore variation explained by season-specific (early or late) contributions of the four habitat types on bees, models with early or late floral resource availability or diversity provided by each habitat as explanatory variables and total species richness of bees active in the corresponding season (early or late) as response variables were run. Effects of early floral resource contributions were also tested for bees active late in the season.

To test whether floral resource maps accounting for seasonal availability of floral resources in a landscape better predict richness of bees than land-cover maps (question 4) the amount of explained variation (R^2) and goodness-fit (adjusted R^2) of the models described above with early or late floral resource contributions (floral abundance or diversity) of the four major habitat types were compared to the models with classical areal proportions covered by the four habitat types.

All statistical analyses were performed using the software R (version 3.4.1); R Core Team (2017)).

3. Results

3.1. Seasonal contribution to floral resources availability by different habitat types

The relative importance of different habitat types in terms of floral abundance and diversity varied strongly over the season (Fig. 1; Fig. S5).

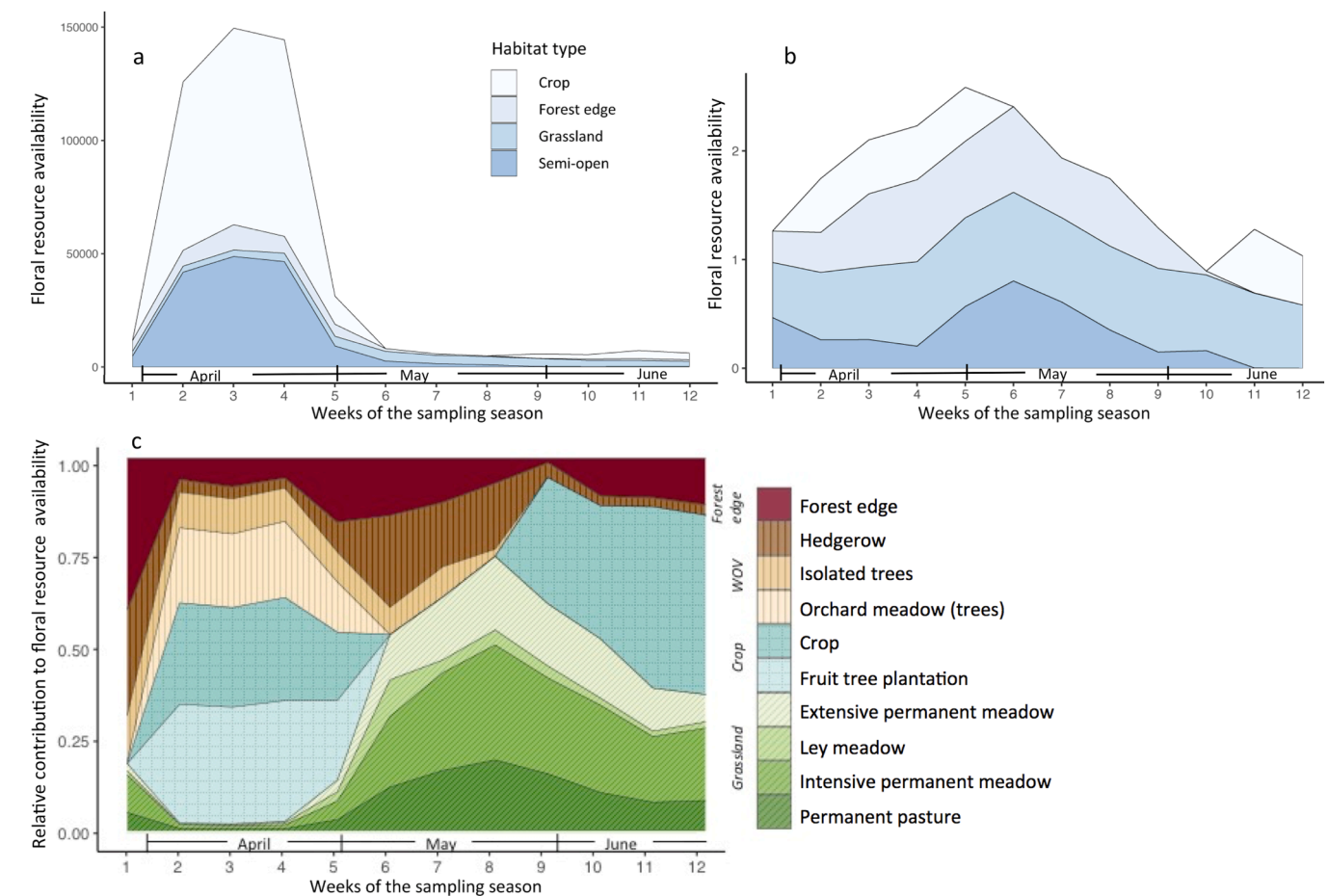


Fig. 1. Temporal shifts in the contribution of major habitat types (crops, grasslands, forest edges and semi-open habitat (i.e., hedgerows, traditional orchards and single trees) over the season (12 sampling weeks from April to end of June) in terms of a) floral resource abundance b) flower diversity (Simpson diversity) and c) the relative contribution to floral resource availability over time.

Floral resource availability was highest early in the season (April), with highest relative contributions of semi-open habitat and crops. Flowering trees and shrubs belonging to the genera *Prunus*, *Pyrus* and *Malus* (Rosaceae) in forest edges and hedgerows, in traditional orchards, as single trees and in intensive orchards made large contributions to flower availability (Fig. 1). The relative contribution of grasslands to floral resource availability increased towards mid-season, reaching almost 75% by the end of May. Explorative analyses showed that in particular meadows that were extensively managed according to the prescriptions of the Swiss agri-environment scheme for grasslands contributed to the high floral diversity of grasslands: it was on average 31% higher in extensively compared to intensively managed grasslands ($t = 3.02$, $df = 37.4$, $P = 0.005$). Flower diversity peaked in mid-May, mainly due to semi-open habitat (Fig. 1). Floral species richness and diversity of forest edges and semi-open habitat declined strongly from spring to end of June, while grasslands provided high floral diversity throughout the season (Fig. 1; Table S3). Crops exhibited generally low floral diversity (Fig. 1; Table S3).

3.2. Floral resources contributed by different habitats driving wild bees

Over the entire sampling period 4742 wild bees have been sampled, comprising 108 species. The genera most commonly collected were *Andrena* (47.4% of collected specimens), *Lasioglossum* (29.3%), *Bombus* (12.4%), *Colletes* (5.8%) and *Halictus* (3.0%). A total of 45.5% were classified as important crop pollinating wild bees, and 6.3% as rare bees (Table S2). Total bee species richness and the abundance of important crop pollinators increased with landscape-level floral resource

availability, but not landscape-level floral diversity, while rare bee richness tended to increase with landscape-level floral resource availability (Fig. 2; Table S4).

Regarding the relationships of wild bees with floral resources contributed by different habitats, total bee species richness increased with floral resource availability and diversity contributed by forest edges and flower diversity of grasslands (Table 1). The relative importance of different floral metrics slightly varied for rare bees and important crop pollinators across specific habitat types (Fig. 3), but both groups were positively related to flower metrics of forest edges and grasslands (Fig. 3; Table S5): Species richness of rare bees increased with floral resource availability of forest edges, whereas abundance of important crop pollinating was also positively correlated with their floral diversity (Fig. 3; Table S5). Moreover, floral diversity, but not floral abundance, of grasslands was positively related to the abundance of important crop pollinators and species richness of rare bees (Fig. 3; Table S5). No significant relationships between floral resource availability or diversity of semi-open habitat was found with any of the studied bee groups (Fig. 3; Tables S5).

3.3. Seasonal shifts of floral resources driving bee abundance and richness

More bee individuals and species were sampled in the first half of the sampling period (beginning of April to mid-May; 72.8%) than in the second half of the period (mid-May to end of June). Early floral diversity of grasslands was positively related to early and late bee species richness, and late grassland diversity was positively related to late bee species richness (Fig. 4). Early crop floral resource availability but not early semi-open habitat had a positive effect on late bee species richness (Fig. 4; Table S6).

3.4. Do floral resource maps predict bees better than land-cover maps?

Floral resource maps performed equally well or better than land-cover maps, with varying importance of different habitat types and temporal subsets (Table 1). A significant improvement of floral resource maps over land-cover maps was achieved when floral resource maps

accounted for season-specific floral resource contributions (61% of variation explained for wild bee richness compared to 31% variation explained by land-cover maps; Table 1; Table S6).

4. Discussion

4.1. Spatio-temporal contribution of habitats to floral resources in agricultural landscapes

The present study is among the first providing a landscape-scale assessment of the spatio-temporal availability of floral resources across major habitat types in agricultural landscapes. Notably, while most previous studies have mainly focused on floral resources provided by herbaceous vegetation, or less of often on floral resources provided by shrubs, we quantified individual trees and shrubs of each flowering species and estimated their floral resources for each studied woody habitat element during different times in the year across the 20 studied agricultural landscapes. Our findings reveal a strong decline in overall landscape-level floral resource abundance during the main activity period of most bee species from early April to late June in the agricultural study region. Especially high-stem fruit trees of traditional orchards and arable crops (74% of early flower availability) and to a lesser extent forest edges and hedgerows (12%) contributed to a more than ten-fold higher overall floral abundance early in the season (April) compared to later time periods. Thus, habitat types supporting flowering trees and shrubs, such as forest edges, hedgerows and traditional orchards, and to a lesser extent intensively managed orchards, contributed substantially to the high floral resource availability in early spring (more than 70%), but also mass-flowering arable crops such as oilseed rape. However, there was a strong decline in the contribution of woody plants to floral resource availability later in the season and a pronounced shift towards herbaceous plants contributing to landscape-level floral resource availability in summer (52% mainly provided by flowering plants of grasslands), a general pattern that may not be confined to the studied Central European agroecosystems but appears to apply also for e.g. North-American agricultural landscapes (e.g. Mallinger et al., 2016). In fact, floral resource abundance per area (i.e., floral density;

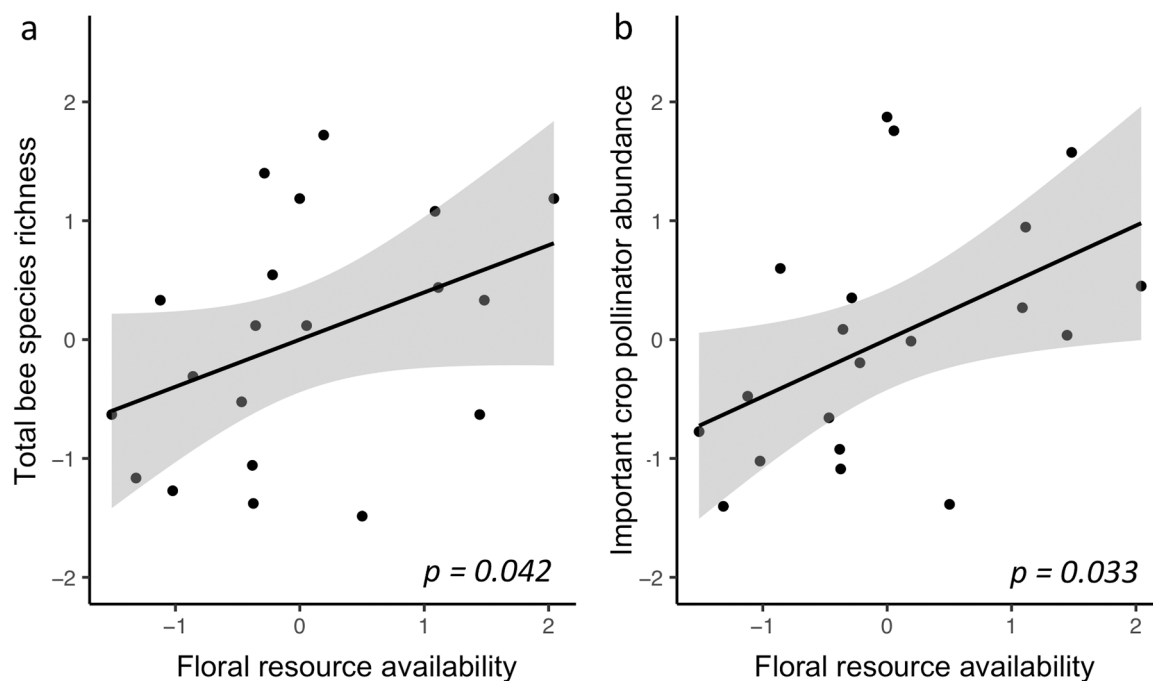


Fig. 2. Significant ($P \leq 0.05$) relationships between (a) species richness of all wild bees and (b) the abundance of important crop pollinators and landscape-scale floral resource availability (scaled). Grey areas indicate 95% confidence intervals. Summary statistics of all models are provided in Table S4.

Table 1

Summary of linear model analysis of the effect of habitat proportion and floral resources (floral abundance or diversity) of the four major habitats on wild bee species richness. Parameter estimates (slopes) of regression models with scaled variables are provided. Significant effects ($P \leq 0.05$) are indicated in bold (d.f. = degree of freedom; Adj. R^2 = Adjusted R^2 ; SE = standard error). SNH: semi-natural habitat.

| Predictor variable | d.f. | R^2 | Adj. R^2 | Habitat type | Estimate | SE | P-value |
|---------------------------|------|-------|------------|---|-------------|-------------|--------------|
| Coarse habitat proportion | 17 | 0.087 | 0.037 | SNH (semi-open, forest edge, grassland) | -0.29 | 0.22 | 0.206 |
| | | | | Semi-open | 0.12 | 0.21 | 0.571 |
| | | | | Forest edge | 0.73 | 0.21 | 0.003 |
| | | | | Crop | 0.31 | 0.28 | 0.293 |
| Flower availability | 15 | 0.558 | 0.440 | Grassland | -0.04 | 0.27 | 0.890 |
| | | | | Semi-open | 0.16 | 0.18 | 0.394 |
| | | | | Forest edge | 0.62 | 0.17 | 0.003 |
| | | | | Crop | 0.31 | 0.18 | 0.108 |
| Flower diversity | 15 | 0.590 | 0.479 | Grassland | -0.30 | 0.20 | 0.133 |
| | | | | Semi-open | -0.06 | 0.17 | 0.716 |
| | | | | Forest edge | 0.49 | 0.17 | 0.011 |
| | | | | Crop | 0.12 | 0.17 | 0.512 |
| | | | | Grassland | 0.06 | 0.17 | 0.001 |

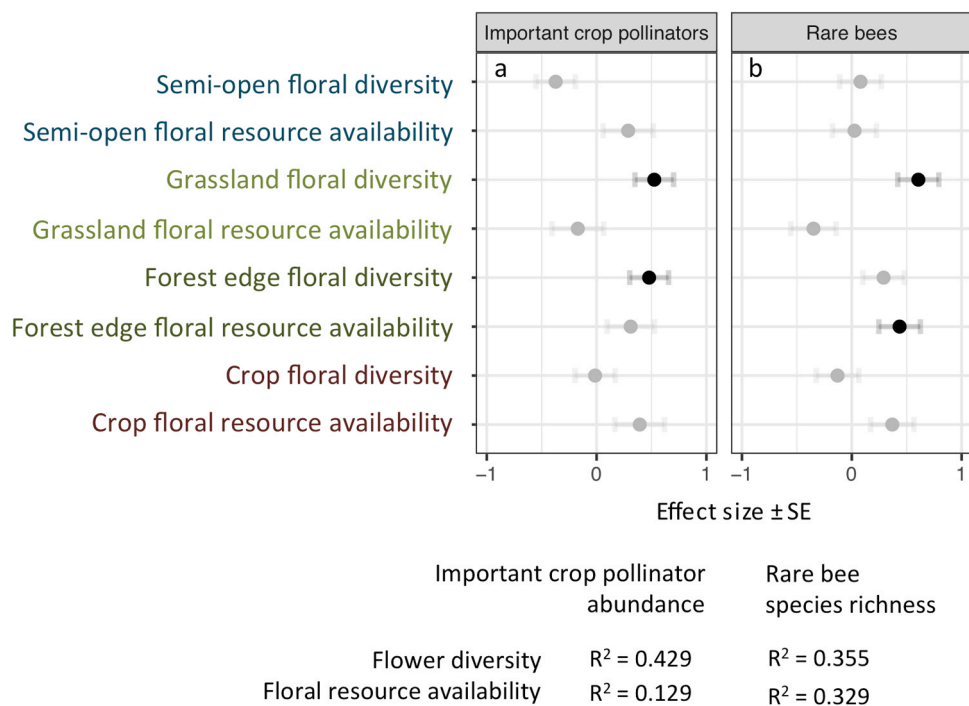


Fig. 3. Relationships between (a) abundance of important crop pollinating bees and (b) species richness of rare bees and flower abundance or floral diversity of major habitat types. Estimated slopes (± 1 standard error) of significant linear relationships are shown in black and those of non-significant relationships in light grey. Additionally, adjusted- R^2 values (“ R^{2*} ”) of all models are provided. Summary statistics of models are provided in Table S5.

Fig. S5) of herbaceous semi-natural habitat types, mainly grasslands, did not strongly increase during the season, but rather their relative contribution to landscape-level flower availability increased as a result of the pronounced decline in floral resources from woody plants. Interestingly, landscape-level floral diversity showed much less pronounced temporal dynamics than floral resource abundance, although it was still clearly higher in spring (April/May) than in summer. Semi-natural habitats, and in particular grasslands and forest edges, contributed most to landscape-level floral diversity (Baude et al., 2016;

Dicks et al., 2015; Lonsdorf et al., 2009; Hellwig et al., 2022). Our findings show that in particular meadows managed extensively according to the prescriptions of the Swiss agri-environment scheme (e.g., no fertilizer input; postponed first cut (no mowing allowed before mid-June)) contributed to this high flower diversity of grasslands in the study region. Thus, appropriate management of grasslands, but also of woody semi-natural habitats (Staley et al., 2012), is key to achieve high ecological quality in terms of floral diversity (Albrecht et al., 2007b; Cole et al., 2020; Kennedy et al., 2013).

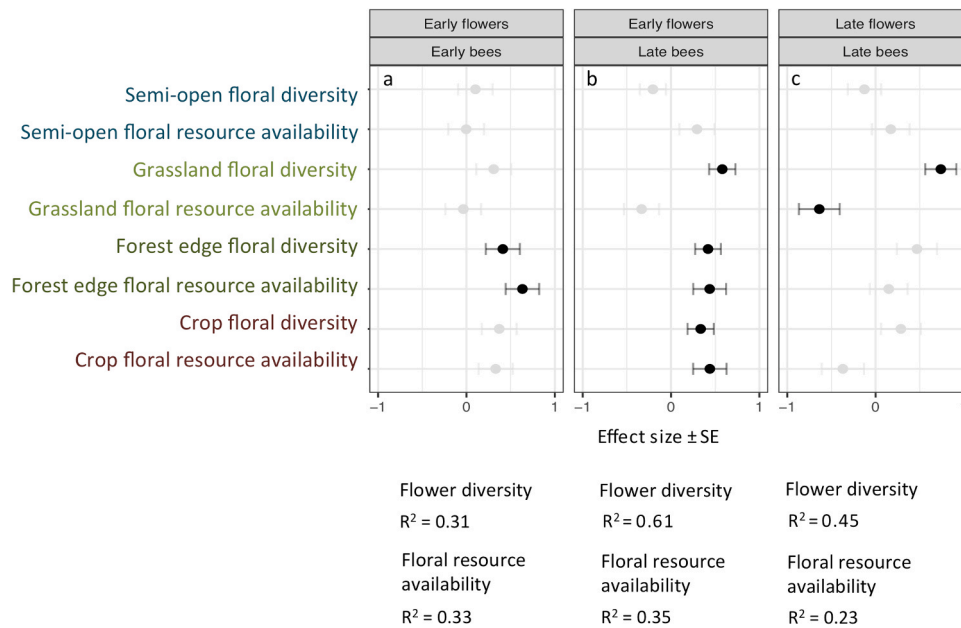


Fig. 4. Relationships between species richness of wild bees and floral resource availability or floral diversity of major habitat types early in the season (beginning of April to mid-May) (a), early floral resources and bees active later in the season (mid-May to end of June) and late floral resources and late active bees (c). Estimated slopes (± 1 standard error) of significant ($P \leq 0.05$) linear relationships are shown in black, those of non-significant relationships are illustrated in light grey. Additionally, adjusted- R^2 values (“ R^2 ”) for results of all models depicted in the panels. Summary statistics of models are provided in Table S6.

4.2. Floral resources driving wild bees in agricultural landscapes

Despite the high amounts of floral resources mainly provided by mass-flowering fruit trees such as apple and cherry in traditional orchards in semi-open habitat in spring, we could not detect strong relationships with the studied focal bee groups. It is conceivable that the relatively short availability of floral resources by a very limited number of species (mainly a few Rosaceae species) are reasons for this lack of clear positive relationships. Moreover, the short availability of these floral resources coincides also with the time period in which floral resource limitation is generally lowest in the studied agricultural landscapes, with many woody and herbaceous wild plant species, as well as mass-flowering crops such as oilseed rape, typically flowering simultaneously during this time of the year. In contrast, floral resources, especially floral diversity provided by forest edges and grasslands, had the most consistent positive effects on both rare bees and important crop pollinators, while floral resources provided by crops were positively associated only with rare bees. A key finding of our study is that in particular floral-rich grasslands appear to play a key role in supporting rare bee species. This positive relationship between floral diversity of grasslands and rare bee richness was observed even without considering the rarest flowering plant species (species occurring in less than 1% of the sampled plots). A further interesting finding is the identified important role of floral resources provided by forest edges, not only for rare species, but for important crop pollinators, despite the considerably smaller area covered by this habit type compared to others in the studied agricultural landscapes. This suggests that forest edges harbour plant species offering floral resources that are particularly valuable for rare bee species and important crop pollinators. Further, it is conceivable that preferred foraging of bees along linear habitat features, suitable micro-climatic conditions or the availability of suitable nesting sites offered by forest edges contributed to these findings (e.g. Bertrand et al., 2019; Eckerter et al., 2022; Mallinger et al., 2016). Targeting management to conserve and restore flower-rich forest edges and grasslands should therefore offer great potential to simultaneously promote rare bee species of high conservation concern as well as wild bees important for crop pollination, and thus create win-win situations for biodiversity conservation and ecological intensification (Ekroos et al., 2014, 2020;

Senapathi et al., 2015; Sutter et al., 2017). High floral diversity ensures a high level of spatio-temporal heterogeneity and complementarity of available resources for a range of bee taxa and may be associated with disproportionately high availability of key plant species offering floral resources of particular importance for different target groups of pollinators (e.g., Mallinger et al., 2016; Sutter et al., 2017). Also spatio-temporal complementarity (*sensu* Mandelik et al., 2012) through the combined contribution of forest edges early in the season and grasslands later in the season may have contributed to the observed positive effects on wild bees, in particular bees with long activity periods (Hellwig et al., 2022; Jachula et al., 2021; Mallinger et al., 2016; Ogilvie and Forrest, 2017; Schellhorn et al., 2015; Timberlake et al., 2019). Such generalist bee pollinators with long activity periods, such as bumblebees, can track floral resources from different vegetation and habitat types across the agricultural landscape and during the season (Bertrand et al., 2019; Timberlake et al., 2021). Thus, as highlighted by our findings, floral resources early in the season are not only important for early active bees, but also for such bees with long activity periods still active later in the season, such as social bumblebees (e.g., Westphal et al., 2003; but see Guezen and Forrest, 2021; Rundlöf et al., 2014). Availability of early floral resources can be key for colony growth in the critical early phase of colony development (Westphal et al., 2003, 2009; Williams et al., 2012), and potentially enhance reproductive success and population growth), although late-season nectar availability can also play an important role (Timberlake et al., 2021). Hence, our results highlight the importance of continuous floral resource availability throughout the season and the important role of diversity and seasonal complementarity across habitats at the landscape scale to sustain wild bees (Guezen and Forrest, 2021; Mandelik et al., 2012; Timberlake et al., 2019; Williams et al., 2012).

Landscape-scale assessments on the role of spatio-temporal floral resources driving bee communities across a high number of landscapes almost inevitably come with some limitations. For example, we are aware that the maximal foraging range of the most mobile bees included in this study, such as bumblebees, is considered larger than the studied 500 m radius landscapes. However, the maximum foraging range of most bees studied here is considered much smaller (Greenleaf et al., 2007; Zurbuchen et al., 2010), and even for bumblebees the average

realized foraging range is generally only few hundred meters (Osborne et al., 2008). Although we acknowledge that further assessments on even larger scales could have provided additional insights, the studied scale is appropriate for our assessments, especially when considering the small-scaled mosaic type mixed farming system typical for Swiss and many other Central European agricultural landscapes. Over- or under-representation of certain taxa cannot be ruled out also in the present study, despite combi traps including window intersections in addition to their very large pans being considered to be less prone to such bias compared to traditional pan trapping (Duelli et al., 1999). While temporally highly resolved records in a very high number of observation plots allowed us to accurately estimate flowering periods of herbaceous plant species and in grasslands, crops and semi-open habitats, flowering period estimations for trees and shrubs could not be estimated with equal precision. Despite accurate estimations of peak flowering times of trees and shrubs, their flowering periods had to be approximated due to logistical constraints, which needs to be considered accordingly in the interpretation of these results. Finally, it was not possible to adequately quantify floral resource availability in the more interior parts of forest, and therefore their role for floral resource availability for bees could not be assessed. Notably, forest edges typically provide higher amounts and diversity of floral resources per area than forest interiors, reflected in higher wild bee abundance and species richness found along forest edges compared to forest interiors (Bartual et al., 2019; Maurer et al., 2022); indeed, explorative analyses confirmed that forest edges also better explained bee response variables in the present study than total forest area.

4.3. Can functional floral resource maps predict bees better than land-cover maps?

Our results highlight not only pronounced spatial heterogeneity of floral resource availability across major habitat and vegetation types in agricultural landscapes, but further indicate strong variation of floral resource abundance and diversity within these habitat types, as illustrated by the significant variation in floral diversity of grasslands influenced by their management, as well as strong temporal variation within and across habitat types. Consequently, considering the positive relationships of floral resources and bees, functional floral resource maps accounting for such marked spatio-temporal variation of resources across habitats predicted wild bees generally much better than land-cover maps. In fact, simple categorisation of the landscape by the amount of semi-natural habitat entirely failed to predict wild bee richness. Similarly, semi-natural habitat cover was a poor predictor of colony density of the bumblebee species *Bombus terrestris* in agricultural landscapes in the UK, which was better predicted by late-season nectar resource availability of the preceding year (Timberlake et al., 2021). The relatively small-scaled mosaic type landscapes typical for Swiss agroecosystems lacking the very simple and cleared landscapes typically part of semi-natural habitat gradients of studies in other agricultural regions might at least partly explain this lack of a clear positive relationship between semi-natural habitat proportion and wild bees observed in other studies (e.g. Kennedy et al., 2013; Le Féon et al., 2010). This strongly supports propositions to utilize functional resource maps as a tool to refine predictions of biodiversity and associated ecosystem services at the landscape scale (Lonsdorf et al., 2009). Moreover, our findings highlight that functional resource maps can be useful tools for conservation and the management of ecosystem services at the landscape scale. For example, they can help to prioritize management options to achieve improved spatio-temporal availability of the basic resource needs of the target groups in agricultural landscapes, e.g. particularly important floral resources provided by certain habitats for rare pollinators of conservation concern and/or important crop pollinators (e.g., Dennis et al., 2006; Schellhorn et al., 2015).

4.4. Conclusions and implications for management and policy

The findings of our study imply the need of a landscape perspective for the conservation and restoration of bee pollinators and their pollination services through enhancements of floral resources in agroecosystems. The pronounced seasonal shift of floral resource contribution from different woody vegetation including single trees, forest edges or hedgerows, as well as arable crops, towards grasslands and other herbaceous vegetation later in the season highlights the crucial role of habitat type and habitat diversity at the landscape scale. These results also reveal the particularly high potential of flowering trees in addition to mass-flowering crops to transiently boost floral resource quantities, while flowering species rich forest edges and grasslands play a key role for ensuring a high and continuous floral diversity in agricultural landscapes. Our results show that management intensification in grasslands can strongly enhance the provisioning of floral resource diversity and thus the potential of grasslands to sustain bee pollinators. Indeed, floral resource diversity offered by forest edges and grasslands could be identified as key drivers for different conservation target groups of bee pollinators, including rare bee species of particular conservation concern, as well as the important crop pollinators. Hence, targeting management on these habitats has a high potential for win-win situations and synergies between landscape management for rare bee species conservation and for crop pollinators and their pollination services. Finally, we conclude that functional floral resource maps at the landscape scale, especially when temporally and spatially sufficiently resolved, can more adequately predict bee pollinator diversity in agricultural landscapes compared to land-cover maps. They can represent a valuable tool contributing to more targeted and effective pollinator conservation and restoration in agricultural landscapes.

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.

Data Availability

Data will be made available on request.

Acknowledgements

This study was funded by the Swiss National Science Foundation (SNSF, grant number 310030L_160253) and the German Research Foundation (DFG, grant number EN 979/3-1). We would like to thank Lucca Andreoli, Timo Bütikofer, Nadine Sandau, Matteo Lehmann and Stephan Bosshart for their assistance during field work, Thomas Walter, Sarina Kivelitz, Jovanka Studerus and Pasha Naeem for sorting and pinning the bees. We thank Mike Herrmann and Sabine Oertli for the identification of bees. Furthermore, we would like to thank Jonas Winizki, Erich Szerencsits, Beatrice Schüpbach, Alessandro Lechmann, Luc Hächler, Roman Coray and Sebastian Kopp for their support with data digitisation and GIS management, Anina Knauer and Louis Sutter for statistical advice and Tom Timberlake and an anonymous reviewer for very valuable suggestions that significantly improved the manuscript. Finally, we thank all landowners for permission to collect data on their property.

Authors' contributions

L.A., M.A., A.B., F.H., and M.E. designed the study; L.A. and A.B. collected the data and lead the field work; D.F. collected and compiled the flower trait data; L.A. and M.A. performed the analysis; L.A. wrote a first draft of the manuscript. All authors contributed substantially to the

writing of the manuscript and gave their approval for submission.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108754.

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