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# Floral resource distribution and fitness consequences for two solitary bee species in agricultural landscapes



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## Abstract

Floral resources are crucial for wild pollinators. Identifying the spatio-temporal floral resource use of wild pollinators and effects of resource distribution on their development might help to promote them and their pollination services to crops in agricultural landscapes.

We established populations of *Osmia cornuta* and *Osmia bicornis*, two solitary wild bees, in 24 agricultural landscapes with varying floral resource availability. Based on their pollen use, we mapped the landscape-scale distribution of the visited plants, estimated pooled specific floral resource availabilities and measured its effects on reproductive output.

Woody semi-natural habitats such as hedgerows provided the majority of pollen sources for both *Osmia* species. Pollen use differed strongly between the two species. The offspring of both *Osmia* increased with availability of pooled specific pollen resources. In accordance with their preferred pollen types, offspring of *O. cornuta* increased with increasing cover of trees and shrubs of the Rosaceae family, and that of *O. bicornis* with increasing cover of *Papaver rhoeas*, *Ranunculus acris* and *Quercus* spp. as well as with the proximity to oilseed rape. In spite of their specific responses to pollen resources, the offspring of both species decreased with the distance to forest. The floral resource availability did not significantly affect the proportion of adult females and the weight of the offspring. As forest does not appear to be a main foraging habitat for both species, the benefit of forest proximity indicates an additional role of forest in addition to food availability.

Specific flowering plants and forests should thus be conserved and enhanced to maintain and support *O. cornuta*, *O. bicornis* and likely other wild bee populations in agricultural landscapes. The combined information of land cover and detailed floral resource availability gives a deeper understanding into population processes in agricultural landscapes.

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## Introduction

Around 88% of flowering plants and roughly 75% of crops at least partly rely on insect pollination (Klein et al.,

2007; Ollerton et al., 2011). During the last decades, however, agricultural intensification has led to declines in the abundance and diversity of wild insect pollinators. This could create a negative feedback on the productivity of agriculture, especially as the dependence on crop pollination is

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increasing (Aizen et al., 2019; IPBES, 2016; Potts et al., 2010).

The availability of floral resources can be a driver of bee populations (Roulston & Goodell, 2011). Information on it can be used to enhance the abundance and diversity of insect pollinators through ecological modifications of agricultural landscapes (e.g. planting flower strips and hedgerows as foraging and nesting habitats; Sutter et al., 2018; Venturini et al., 2017). Still, for effective conservation of wild bee species and their pollination in agricultural landscapes, further research is needed to better understand the relationships between landscape-scale availability of floral resources, their use by pollinators and the consequences on pollinator abundance and reproductive output as major drivers of population growth and persistence in agricultural landscapes (Bertrand et al., 2019; Eckerter et al., 2022; Ganser et al., 2020; Gathmann & Tschardt, 2002; Lawson et al., 2021; Schellhorn et al., 2015; Venturini et al., 2017; Woodard, 2017).

The mason bees *Osmia cornuta* Latreille and *Osmia bicornis* L. (former: *Osmia rufa* L., both Apoidea: Megachilidae) are solitary and polylectic wild bee species with a univoltine life cycle (Westrich, 2018). As with all bees, they require floral resources, nesting resources and nesting habitat for reproduction (Westrich, 2018). The nesting phenology and foraging of *O. cornuta* is in synchrony with the flowering of rosaceous trees and shrubs, including fruit trees such as apple and cherry (Bosch, 1994b; Márquez et al., 1994; Tasei & Picart, 1973). Consequently, *Prunus* type (i.e. the pollen offered by these plants; Appendix A: Table A.1) is usually the dominant pollen type in its diet (Márquez et al., 1994; Tasei & Picart, 1973) and *O. cornuta* is managed as an effective fruit tree pollinator in Southern and Central Europe (Bosch, 1994b, 1994a; Bosch et al., 2021; Vicens & Bosch, 2000). In contrast to *O. cornuta*, *O. bicornis* uses mainly pollen from non-agricultural tree species as well as from herbaceous plants. Its pollen provisions are often dominated by the pollen types *Quercus* and *Ranunculus acris*, in smaller amounts also by *Acer*, *Papaver rhoeas* type, and *Rubus* (Bertrand et al., 2019; Coudrain et al., 2016; Free & Williams, 1970; Hansted et al., 2014; Persson et al., 2018; Radmacher & Strohm, 2010; Ruddle et al., 2018; Tasei & Picart, 1973; Yourstone et al., 2021; see Appendix A: Table A.1 for a list of plants that offer the above-mentioned pollen types in our study region). We used *O. cornuta* and *O. bicornis* as species with similar lifestyles but with different pollen use preferences to explore the relationships between species-specific and landscape-scale floral resource availability and their reproductive output in agricultural landscapes.

The different use of pollen plant species suggests that both solitary bees, although they are generalists, have clear preferences in their foraging behavior in agricultural landscapes and prefer a certain set of plants if they are available (Bertrand et al., 2019; Sutter et al., 2017; Tasei & Picart, 1973). In temperate agricultural landscapes, pollen from

woody plants are highly used by both *Osmia* species and, due to their higher volume, entomophilous trees and shrubs can offer a higher amount of pollen than herbaceous plants (Ammann et al., 2022; Bertrand et al., 2019; Coudrain et al., 2016; Eckerter et al., 2020; Márquez et al., 1994; Yourstone et al., 2021). We therefore expect that a certain set of woody plants contributes most to pollen resource availability in these agricultural landscapes, and that the reproduction of both solitary bee species will increase with the availability of these pollen plants in the surrounding landscape. In addition, as the majority of floral resources for wild bees is offered by non-agricultural plants in semi-natural habitats (Bertrand et al., 2019; Eckerter et al., 2020; Williams & Kremen, 2007), we expect a high contribution of land-use types other than crop fields to floral resource availability for those bees. Pollen contains proteins, lipids, vitamins and minerals that are crucial for the larval development (Nicolson, 2011; Westrich, 2018). A nutritionally balanced diet may be crucial for the development of bee populations (M. Filipiak, 2019; Z. M. Filipiak et al., 2022). A higher availability and proximity to the preferred floral resources should facilitate foraging trips and thus offspring provision and thereby increase the number of offspring (Ganser et al., 2020; Pitts-Singer & Bosch, 2010; Zurbuchen et al., 2010). Increased pollen provision of larvae by higher availability of and proximity to key floral resources might also result in heavier (i.e. larger) offspring (Bosch & Vicens, 2002, 2006; Ganser et al., 2020; Kim, 1999; Peterson et al., 2006; Radmacher & Strohm, 2010, 2010). As the females of both *Osmia* species studied are larger than the males and their development requires a higher availability of food, we also expect increasing proportions of females with increasing availability of floral resources (Bosch, 2008, 2008; Bosch & Vicens, 2002, 2006; Westrich, 2018). Within sexes, a larger body size was shown to enhance e.g. the foraging efficiency, fecundity and survival in megachilid bees (Bosch & Kemp, 2004; Bosch & Vicens, 2006; Kim, 1997; Torchio & Tepedino, 1980) and may thus increase the pollination efficiency of populations in the long run. The cocoon weight and the proportion of adult females can therefore indicate a high productivity of *Osmia* populations (e.g. Bosch & Kemp, 2004; Bosch & Vicens, 2006; Torchio & Tepedino, 1980).

Different mapping approaches are used to assess landscape characteristics to predict wild bee abundances in agricultural landscapes. Most studies indirectly infer flower availability from the cover of land-use types with different vegetation composition (Roulston & Goodell, 2011). The commonly used land cover maps do typically not account for species-specific floral resource occurrences or their temporal availability (Coudrain et al., 2016; Crone & Williams, 2016; Fahrig, 2013; Forman, 1995; Roulston & Goodell, 2011). However, different efforts have been undertaken to map and describe floral resources used by specific pollinators at the landscape scale (Osborne et al., 2008; Persson & Smith, 2013; Yourstone et al., 2021). We created detailed floral resource maps that are based on the pollen use of

specific organisms and the landscape-scale availability of the used floral resources (Ammann et al., 2022; Eckerter et al., 2020). For comparison, we also created land cover maps distinguishing the major classes of land-use found in our landscapes. We expect that detailed floral resource maps better predict wild bee reproductive output than land cover maps. In addition to (bottom-up) resource availability, bee reproduction is modulated by (top-down) natural enemies. By feeding on pollen provisions and/or the brood itself, natural enemies can harm *Osmia* populations (Goodell, 2003; Kronic et al., 2005; Seidelmann, 2006). Attack rates by natural enemies can increase with bee population density (Kronic et al., 2005), and can change with the amount of and proximity of woody habitats around nesting sites (Coudrain et al., 2014; Schüepp et al., 2011). To account for the role of enemies in bee reproduction, we measured attack rates and analyzed them with respect to landscape factors.

In this study, we established populations of *O. cornuta* and *O. bicornis* in 24 agricultural landscapes in southwest Germany. We quantified the species-specific pollen use throughout their foraging periods and mapped the most used plant species across the landscapes. Combining the data on the bees' pollen use and the availability of plants at the landscape scale, we calculated quantitative indices of pollen availability for each species. We tested how well floral resource maps explain the reproductive output of the *Osmia* species in comparison to land cover maps. We additionally quantified the natural enemies (i.e. parasitoids, predators, and brood parasites) in the nests of the *Osmia* species and tested for relationships between parasitism and landscape properties. We tested the following hypotheses:

- (I) *Osmia bicornis* and *Osmia cornuta* use different sets of key pollen resources
- (II) The reproductive output of the two *Osmia* species increases with the landscape-scale availability of specific pollen resources
- (III) Floral resource maps explain the reproductive output of the *Osmia* species better than land cover maps
- (IV) The weight of the offspring and the proportion of female cocoons of both *Osmia* species increase with the availability of specific pollen resources
- (V) The abundances of natural enemies in the *Osmia* nests increase with the proximity to woody habitats

## Materials and methods

### Study landscapes

We selected 24 agricultural landscapes of 500 m radius in the surroundings of Landau, Rhineland-Palatinate, Germany (Appendix A: Fig. A.1). The mean nearest neighbor distance between landscapes was  $1993 \pm 183$  m (average  $\pm$  standard error). The landscapes represented a gradient of pollen resource availability. As the landscapes were located in the

same region and had similar elevation, there were no major differences in the flowering phenology and weather conditions between them.

### Mapping of floral resources

We mapped the cover (in m<sup>2</sup>) of all woody plants and those herbaceous plants that are main pollen providers to either *O. bicornis*, *O. cornuta* or both species in the study region (Bertrand et al., 2019, own data, not published; Coudrain et al., 2016). We mapped the woody plants between June and November 2017, the annual herbaceous plants and the land use between April and July 2019. A more detailed description of the floral resource mapping methodology is provided in Appendix A: A.1. For orientation during the mapping process and ground truthing of each landscape element, we used optical satellite imagery (Copernicus: Sentinel-2, L2A-L2C, 2018, 10 m resolution) processed by the Federal Agency for Cartography and Geodesy (BKG). We ensured the creation of up-to-date floral resource and land cover maps by noting every difference between the satellite imagery and a landscape element during our field inspection in 2019 (Eckerter et al., 2020, 2022).

### Establishment, monitoring of the *Osmia* populations and pollen use

We placed one nesting block providing 100 routed nest cavities inside grassy field margins in each landscape center in mid-February 2019 and released standardized starter populations of *O. cornuta* and *O. bicornis* consisting of 30 cocoons of each species next to them at the end of February (Appendix A: A.2, and A.3, Figs. A.2 and A.3).

We monitored the nesting of the bees weekly across the activity period of both species. This resulted in eleven sampling dates between mid-February and early July 2019. To follow brood cell construction, we controlled every nesting board and marked either the closing position of the last brood cell (containing either stored pollen, or pollen with egg or a larva) or the position of the last collected pollen in a not yet completed brood cell (Appendix A: Fig. A.2C). We studied the pollen use of the established *Osmia* populations throughout their foraging periods. For this, we collected pollen over 10 days during the foraging period of each species. We ensured that multiple pollen samples out of the same nest were collected at different days.

### Creation of floral resource maps

#### Specific pollen availability

With the data obtained on their pollen diet and the landscape-scale availability of flowering plants, we created

specific floral resource maps for each *Osmia* species. With these maps, we describe the pooled specific pollen resource availability in each landscape for each of the two *Osmia* species studied using floral resource availability indices (“fai”, Eckerter et al., 2020, 2022). The indices are calculated as the relative cover of the plants offering the collected pollen types multiplied by their percentage in the total collected volume of each *Osmia* species across the foraging season (Eckerter et al., 2020, 2022, Equation 1).

$$fai_{l,t} = n \cdot \sum_{p=1}^P cr_{p,l} \cdot vr_{p,t} \quad (1)$$

To calculate the specific pollen availability to one of the *Osmia* species, we use  $n$  as the number of our study landscapes,  $P$  as the number of used pollen types that are used during the sampling period  $t$ . We use the variable  $cr$  as the relative area covered by plants that offer the respective pollen type. We calculate it by dividing the cover of plants that provide pollen type  $p$  in the respective landscape  $l$  by their total cover across all landscapes. We calculate the relative volume  $vr$  of a pollen type  $p$  in the food of the species during the sampling period  $t$  by dividing the volume of a single pollen type  $p$  in the food of the species during the sampling period  $t$  by the volume of all pollen recorded in its diet during the same sampling period. In this way, we obtain a positive and dimensionless decimal value that stands for the pollen availability to a species within each landscape and across the sampling period. The average index value is “1”. Values below or above that value indicate below or above average pollen availability, respectively. For more details on the index calculation see (Eckerter et al., 2022, Online Resource, A.2).

We calculated one index value that accounts for the pollen availability in each landscape and for each bee species (i.e. 24 values per species). For the calculations, we included the pollen types that contributed more than 1% to the pollen diet of each species. We excluded *Muscari* (accounting for 1.2% of the diet of *O. cornuta*) from the calculations of specific pollen availability because we did not detect it in our landscapes during the mapping. In total, the pollen types making up around 95% of the pollen grains found in samples of bee provision are represented in the specific pollen availabilities calculated for the floral resource maps (Appendix A: Table A.1). For a complete list of the plant taxa that were excluded from the floral resource maps see Appendix A: Table A.2. Whenever we use the term “specific pollen availability” in the remainder of this paper, we are referring to the usage-weighted pollen availability calculated with the above-described indices.

### Important single pollen resources

In addition to specific pollen availability, we analyzed the effects of single pollen types on bee reproduction for pollen contributing more than 3% to the diets. These were *Acer*,

*Prunus* and *Salix* for *O. cornuta* and *Juglans*, *Papaver*, *Quercus*, *Ranunculus* and *Rubus* for *O. bicornis* (Appendix A: Table A.1). For *O. bicornis*, we also included oilseed rape because it is one of the most important mass-flowering crops for wild pollinators in European agroecosystems and *O. bicornis* benefits from it, most likely through its nectar provision (Holzschuh et al., 2013; Jauker et al., 2012; Raw, 1972; Westphal et al., 2003, 2009; Yourstone et al., 2021).

### Land cover

Additionally, for comparison with floral resource maps, we created land cover maps accounting for habitats providing both pollen, nectar, and other functions using polygon and point layers in QGIS 3.6.2 (QGIS Development Team, 2019). We distinguished the following non-overlapping habitat types: arable land, permanent crops (i.e. fruit and nut orchards and vineyards), forest edges (i.e. the first ten meters into forest), remaining woody semi-natural habitats excluding forest interiors (i.e. hedgerows and single standing trees including those of semi-natural orchards), herbaceous semi-natural habitats (i.e. intensively and extensively managed meadows and pastures) and built-up areas (i.e. rural settlements; Appendix A: Fig. A.2A). We additionally included the distances to forests into our analysis and divided the forest edges from semi-natural habitats because forests can be important predictors of pollinator richness and visitation rates (Ricketts et al., 2008) and colony development of *Bombus terrestris* (Eckerter et al., 2020), and may serve as an indicator for habitat connectivity (Tschamtko et al., 2012).

### Assessment of reproductive output and parasitism

In early July, when nesting activity was over (i.e. no newly constructed brood cells were detected), we collected the nesting blocks and stored them with closed entrances at room temperature. We used the number of cocoons as a measure of reproductive output of each species. We harvested and weighted the cocoons using a precision scale (“Ohaus Pioneer PA 214”) from late September until mid-October in the lab and hibernated them at 3°C. We transferred the hibernated cocoons to room temperature in late February (cocoons preliminary assigned to *O. cornuta*, Appendix A: Fig. A.4) or mid-March, respectively (cocoons preliminary assigned to *O. bicornis*, Appendix A: Fig. A.4), and visually identified the species and the sex of the emerging adults. We manually opened the cocoons of non-emerged individuals by mid-May. Detected natural enemies were determined to the highest possible taxonomic level (Kronic et al., 2005). For statistical analysis, we used the number of cocoons per landscape as reproductive output. The numbers of cocoons were highly correlated to the numbers of brood cells and the numbers of emerging bees after hibernation (Pearson correlation tests:  $n = 24$ ,  $r = 0.99$ ,  $p < 0.001$  and  $n = 24$ ,  $r = 0.88$ ,  $p < 0.001$ , respectively). In

addition to the number of cocoons, we calculated the mean cocoon weight per species and sex and the proportion of emerging female offspring for each landscape. We used the proportion of parasitized brood cells (i.e. the number of parasitized brood cells/total number of brood cells) to account for natural enemies (Coudrain et al., 2013). In each sampling round, up to three pollen samples per landscape and species were taken. We stored the samples in water and froze them at  $-18^{\circ}\text{C}$  until acetolysis (Jones 2012). We mounted the acetolysed pollen in glycerin and counted and identified 100 pollen grains per sample to the highest possible taxonomic level using a light microscope (400 x magnification), a palynological key (Beug 2007) and our own reference slides with pollen collected in the same region (Eckerter et al., 2020).

## Statistical analysis

### Divergence in the use of pollen resources

To describe the degree of divergence of pollen use between the two *Osmia* species, we calculated  $H_2'$  (Blüthgen et al., 2006). This index ranges from 0 to 1 with larger values indicating higher niche divergence of two species within a food web (Blüthgen et al., 2006).

### Contribution of different habitat types to floral resource availability

We calculated the proportional contribution of different habitat types to floral resource availability. For this, we divided the cover of all plant taxa that offered a used pollen type per habitat type per landscape by the total cover of those plants across all habitats and landscapes. We then multiplied these values with the proportion of each pollen type in the diet of the respective *Osmia* species. We used the sum of these values across all plant species per habitat type to estimate its contribution to specific pollen availability (Eckerter et al., 2020).

### Description of variables and used distributions

We tested the relations between the response variables “reproductive output” (i.e. number of cocoons) of each *Osmia* species and the “mean cocoon weight per species” and the floral resources and the landscape using the specific pollen availability and all land cover types as response variables via generalized linear models (GLMs) using a negative binomial error structure, to account for overdispersion present in the data. Explanatory variables were the proportions of land cover types as well as the distances to forests and built-up areas. Response variables on a percent scale (“proportions of emerged females” and “parasitized brood cells”) were analyzed using GLMs with binomial error distributions. In the case of overdispersion (dispersion parameter  $> 1.5$ ), we used quasi-distributions. We pooled response

variables over time to obtain one value for each species and landscape and z-transformed explanatory variables (Field, 2017). We transformed variables prior to analysis as far as necessary to remove skewness (log-transformation: reproductive output, proportions of preferred pollen resources, distances to forest and built-up area; sqrt-transformation: pollen availability indices).

### Model construction and model selection

In a first set of models, the floral resource availability index was the sole explanatory variable. In a second set, we constructed models based on the proportion of and the minimum distances to the important single pollen resources. In a third set of models, we used the proportions of each land cover class as well as the distances to forests and built-up areas as explanatory variables. For the models out of the second and third set (i.e. single pollen type resource plants and land cover classes), we started with full models containing all explanatory variables and simplified them through model selection via an information criterion approach using AICc (QAICc in the case of overdispersion) using the dredge function of the ‘MuMin’ package (Bartón, 2020) and a cut-off rule ( $\Delta(Q)AICc < 2$ ; Burnham et al. 2011; Symonds & Moussalli 2011). To avoid multicollinearity, we excluded models with highly correlated variables ( $r > 0.6$ ) out of the selection of the most parsimonious models. We additionally tested the relation between the proportion of natural enemies in the brood cells of each species and land cover using GLMs. We validated the correct specification of each model using qq-plots and plots of the residuals against the predicted value using the ‘DHARMA’ package (Hartig, 2020). All models fulfilled the model assumptions (i.e. normality of residuals, no outliers, flat simulated residuals according to the DHARMA-Vignettes).

We tested the absence of spatial autocorrelation between our landscapes and specific floral resources, responses of the *Osmia* populations (i.e. reproductive output, weight, proportion of developed females) and parasitism with Mantel tests using Pearson’s correlation and 9999 permutations (Mantel, 1967). We detected no significant spatial autocorrelation.

For the calculation of  $H_2'$  and the creation of a pollen network graph, we used the package ‘bipartite’ (Dormann et al., 2009). We used the package ‘ggplot2’ for bar plots and scatter plots (Wickham, 2016). For the Mantel test, we used the package ‘vegan’ (Oksanen et al., 2019). All analyses were done in R 4.0 (R Core Team, 2020). In the text, figures and tables, means  $\pm$  standard errors are given.

## Results

### Pollen use

In *O. cornuta*, we found 25 pollen types among 16,500 analyzed pollen grains out of 165 cells from 101 nests. As

expected, *O. cornuta* collected mainly *Prunus* type pollen (Fig. 1). Further main contributors to its pollen diet were *Salix* and *Acer*. Each of the remaining pollen types contributed less than 2.5% to their pollen diet. In *O. bicornis*, we found 40 pollen types among 28,100 analyzed pollen grains out of 281 cells from 223 nests. The main pollen types were *Juglans*, *Quercus*, *Rubus*, *Papaver rhoeas* type and *Ranunculus acris* type. Each of the remaining pollen types contributed 1.5% or less to the diet of *O. bicornis*. The pollen use was highly distinct between the two species ( $H_2' = 0.77$ , Fig. 1). Overall, both species mainly used pollen from woody plant species (Fig. 1, Appendix A: Fig. 5A and 5B). However, *O. bicornis* included increasing amounts of pollen from herbaceous plant species during its late foraging season (Appendix A: A.4 and Fig. A.5B).

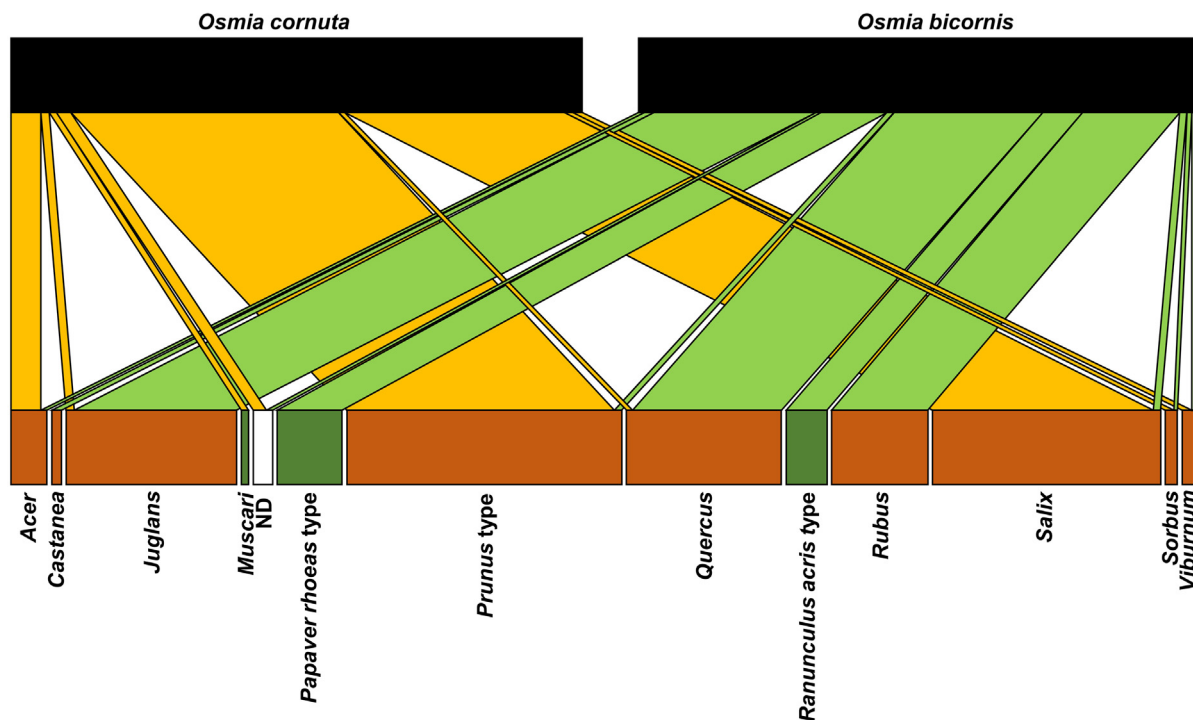
### Specific pollen availability

The landscapes consisted mainly of arable land, followed by herbaceous semi-natural habitats, forest, permanent crops, woody semi-natural habitats, built-up areas, and forest edges (Fig. 2A). The contribution to the pollen availability of each habitat type deviated strongly from their relative cover in the landscape (Fig. 2). Woody semi-natural habitats

accounted for more than half of the pollen use in spite of covering less than 3% of the landscapes (Fig. 2). Moreover, permanent crops and forest edges contributed disproportionately high amounts of pollen to the diet of both bees (Fig. 2). On the other hand, arable land was a minor pollen source to both species, in spite of dominating the landscapes. Similarly, the herbaceous semi-natural habitats provided little pollen relative to their area. This similar contribution of the habitat types to the diet of both bees was, however, based on largely different plant species (see above). See Table A.3 for the proportions of habitat types in each of the studied landscapes and Table A.4 for the contributions of the single pollen types to the pollen availability in each habitat type. See Appendix A: A.5 for the average pollen use of the *Osmia* species versus average resource cover in the landscape.

### Reproductive output

We found 213 nests of *O. cornuta* containing 913 brood cells. *O. bicornis* had 609 nests containing 3,585 brood cells. Female cocoons weighed 68.8% more than male cocoons in *O. cornuta* and 67.2% more than males in *O. bicornis* (see Appendix A: A.6 for mean, SE and range values for each species and sex).



**Fig. 1.** Pollen collection network out of 101 nests of *O. cornuta* (indicated in orange) and 223 nests of *O. bicornis* (light green) in 24 agricultural landscapes in Rhineland-Palatinate (south-west Germany) across the activity period of both species in 2019. Lower bar width indicates the proportional number of pollen grains collected per pollen type across both species. The pollen types collected from woody plants are indicated in brown, pollen from herbaceous plants in dark green. Only the pollen types that constituted > 1% of the pollen diet of at least one species are shown, accounting for 98.6 and 96.1% of the diet of *O. cornuta* and *O. bicornis*, respectively. We indicate the pollen grains that could not be identified with “ND”. See Table A.1 and Table A.2 for a complete list with all the pollen types collected.



**Table 2.** Comparison of models to test for variation in the reproductive output and proportion of female offspring of *Osmia bicornis* explained by landscape-level specific pollen availability (calculated with indices), cover of and distance to plant taxa that offer the important pollen types and proportion of land cover classes and distance. We use the Akaike second-order Information Criterion (AICc) for count data and its quasi-version (QAICc) for proportional data and the *dredge* function from the *MuMin* package to select the best models ( $\Delta_i < 2$ ). Delta weight ( $\Delta_i$ ) is the difference between the AICc of a particular model compared with that of the best model. We z-transformed the explanatory variables. We highlight significant effects (i.e.,  $p \leq 0.05$ ) in bold. “SNH” stands for “Semi-natural habitat”.

Model type	Response	Full model	df	(Q)AICc	$\Delta_i$	Predictor	Estimate	SE	z-value	p value
Specific pollen availability	Reproductive output	Specific pollen availability	22	281.13	0.00	<b>Specific pollen availability</b>	<b>0.46</b>	<b>0.19</b>	<b>2.35</b>	<b>0.019</b>
	Proportion females	Specific pollen availability	22	140.16	0.00	Specific pollen availability	-0.04	0.04	-0.87	0.385
Important single pollen resources cover and distance	Reproductive output	Cover	19	258.72	0.00	<b>Distance Brassicaceae</b>	<b>-0.24</b>	<b>0.10</b>	<b>-2.33</b>	<b>0.020</b>
		Brassicaceae + cover				<b>Cover Papaver</b>	<b>0.29</b>	<b>0.11</b>	<b>2.69</b>	<b>0.007</b>
		<i>Juglans</i> + cover				<b>Cover Quercus</b>	<b>0.54</b>	<b>0.11</b>	<b>4.77</b>	<b>&lt; 0.001</b>
		<i>Papaver</i> + cover				<b>Cover Ranunculus</b>	<b>0.71</b>	<b>0.11</b>	<b>6.26</b>	<b>&lt; 0.001</b>
		<i>Quercus</i> + cover	20	259.72	1.00	<b>Cover Papaver</b>	<b>0.33</b>	<b>0.12</b>	<b>2.79</b>	<b>0.005</b>
		<i>Ranunculus</i> + cover				<b>Cover Quercus</b>	<b>0.45</b>	<b>0.12</b>	<b>3.70</b>	<b>&lt; 0.001</b>
		<i>Rubus</i> + distance				<b>Cover Ranunculus</b>	<b>0.79</b>	<b>0.12</b>	<b>6.36</b>	<b>&lt; 0.001</b>
		Brassicaceae + distance	19	260.32	1.60	Distance <i>Juglans</i>	0.21	0.11	1.85	0.065
		<i>Juglans</i> + distance				<b>Cover Papaver</b>	<b>0.32</b>	<b>0.11</b>	<b>2.88</b>	<b>0.004</b>
		<i>Papaver</i> + distance				<b>Cover Quercus</b>	<b>0.43</b>	<b>0.12</b>	<b>3.73</b>	<b>&lt; 0.001</b>
		<i>Quercus</i> + distance				<b>Cover Ranunculus</b>	<b>0.77</b>	<b>0.12</b>	<b>6.56</b>	<b>&lt; 0.001</b>
		<i>Ranunculus</i> + distance								
Land cover classes proportion and distance	Reproductive output	Proportion arable land + proportion permanent	21	277.50	0.00	<b>Distance forest</b>	<b>-0.49</b>	<b>0.18</b>	<b>-2.70</b>	<b>0.007</b>
		crops + proportion herbaceous SNH + proportion forest + proportion woody SNH + proportion built up + distance to forest + distance to built-up				Proportion herbaceous SNH	0.32	0.18	1.77	0.077
			22	278.19	0.69	<b>Distance forest</b>	<b>-0.61</b>	<b>0.18</b>	<b>-3.30</b>	<b>&lt; 0.001</b>
			20	278.69	1.19	<b>Distance forest</b>	<b>-0.54</b>	<b>0.17</b>	<b>-3.09</b>	<b>0.002</b>
						Distance built-up	0.25	0.19	1.34	0.182
			22	279.24	1.74	<b>Proportion herbaceous SNH</b>	<b>0.45</b>	<b>0.19</b>	<b>2.31</b>	<b>0.021</b>
						<b>Proportion arable land</b>	<b>-0.55</b>	<b>0.19</b>	<b>-2.92</b>	<b>0.004</b>

### Land cover maps

The reproductive output of *O. cornuta* decreased with distances to forest (Appendix A: Fig. A.6A) and the proportions of built-up areas in the landscapes (Table 1). For *O. bicornis*, it decreased with increasing distances to forest (Table 2, Appendix A: Fig. A.6A). In addition, it increased with the proportion of herbaceous semi-natural habitats and decreased with the proportion of arable land in the surrounding landscape.

### Comparison of mapping approaches

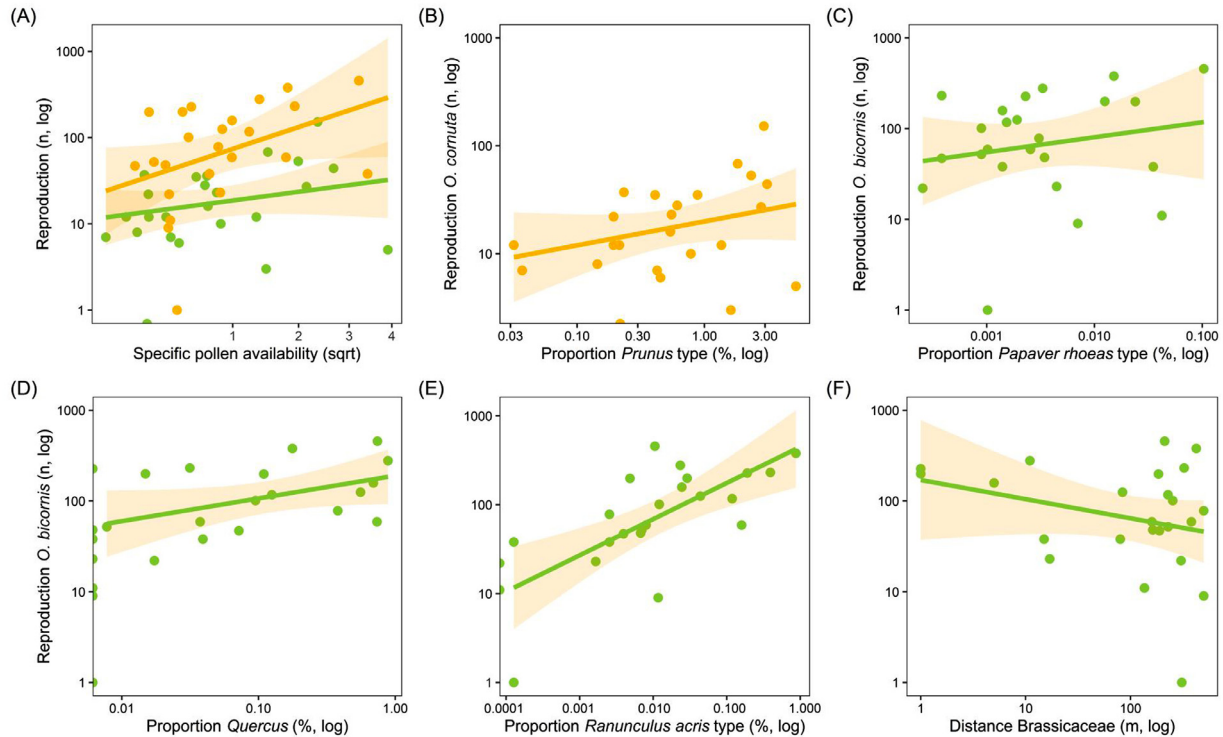
For *O. cornuta*, the land cover variables explained the reproductive output with similar reliability as the specific pollen availability or the important single pollen resources ( $\Delta_i = 0.73$  and  $0.55$ , respectively; Table 1). In contrast, important single pollen resources explained the reproductive output of *O. bicornis* better than the specific pollen availability and the land cover variables ( $\Delta_i = 22.40$  and  $\Delta_i = 18.77$ , respectively, Table 2).

Neither the mean weight of male or female cocoons nor the proportion of developed females showed a significant relation to the specific pollen availability in the surrounding landscapes (Tables 1-3, Appendix A: Fig. A.6B).

### Natural enemies

The average proportion of natural enemies among brood cells per landscape was  $10.4 \pm 2.6\%$  for *O. cornuta* and  $11.3 \pm 1.9\%$  for *O. bicornis*. For an overview of the detected natural enemies in the brood cells of the *Osmia* species see Table A.5. The proportional infestation of brood cells of both species by natural enemies decreased with increasing distance from forests, built-up areas and the proportion of permanent crops (Table 3, Appendix A: Fig. A.6C). The proportional infestation increased with the proportion of woody semi-natural habitats (Table 3). Overall, the proportion of natural enemies had no significant influence on the reproductive output of the *Osmia* populations





**Fig. 3.** The reproductive output (i.e. number of cocoons) of the two *Osmia* species studied (orange: *O. cornuta*, green: *O. bicornis*) in relation to (A) the specific pollen availability (calculated with indices) present in the surrounding landscapes and to (B-F) the proportional cover of and minimum distance to the plant taxa that provided important pollen types for each species. Predicted significant linear relationships and 95% confidence intervals are shown.

(i.e. it did not significantly reduce their population size; Table 3).

## Discussion

As predicted, the reproductive output of both *Osmia* species significantly increased with the specific pollen availability and with the cover or proximity of important key pollen plants present in the surrounding landscapes. Floral resource availability for both species was highest in woody semi-natural habitats. However, later in the season, *Osmia bicornis* also used pollen from herbaceous semi-natural habitats. Our findings highlight the importance of preserving diverse non-agricultural woody and herbaceous key pollen plants to sustain and enhance populations of these solitary bee crop pollinators in agricultural landscapes.

In *O. bicornis*, the important single pollen resources explained reproductive output distinctly better than the specific pollen availability (Table 2), although the indices that account for the specific pollen availability captured 94% of its pollen diet across the foraging period (Appendix A: Table A.1). We speculate that the predictive power of the index is limited by the inclusion of sub-optimal resources in the diet of *O. bicornis*. For example, *Juglans* and *Rubus* were highly used by *O. bicornis* and *Juglans* made up a large share of the mapped floral resources (Fig. 1, Appendix A: Table

A.1). However, the important single pollen resources revealed that the reproductive output of *O. bicornis* was neither significantly related to the cover nor to the distance of *Juglans* and *Rubus* (Table 2). Thus, the predictive power of total floral resources in predicting the reproductive output of *O. bicornis* decreases by including plants offering these two pollen types. Comparably high amounts of *Juglans* pollen in the diet of *O. bicornis* were found by Splitt et al. (2021) in suburban areas and by Biliński and Teper (2004) in nests located inside fruit orchards, after bloom was over. The reason for preferring *Quercus* pollen remains, to our knowledge, not fully understood (Yourstone et al., 2021). *Quercus* pollen is known to increase the speed of nest construction in the early season (Persson et al., 2018) and the reproductive output (Yourstone et al., 2021) of *O. bicornis*. Remarkably, the reproductive output of *O. bicornis* did not increase to a comparable extent with *Juglans* as with *Quercus*, although both pollen types are used to a similar extent. This could be explained by the higher protein content of *Quercus* (>30%) than *Juglans* (25%) (Roulston et al., 2000). In addition, next to the availability and distance to preferred pollen sources in the landscapes, the provisioning of the cells with pollen depends on the availability of nectar. Foraging females are dependent on close-by nectar as energy source during their foraging trips and for managing to carry the poorly cohering pollen of anemophilous plants like *Juglans* and *Quercus* (Chambers, 1945; Nicolson, 2011). In our landscapes,

**Table 3.** Comparison of models to test for variation in the cocoon weight explained by landscape-level specific pollen availability (indices, see Materials and Methods section), as well as parasitism rate with proportion of land cover classes and distance (see Materials and Methods section) and the effects of parasitism on the reproductive output of the *Osmia* species. We use the Akaike second-order Information Criterion (AICc) for count data and its quasi-version (QAICc) for proportional data and the *dredge* function from the *MuMin* package to select the best models ( $\Delta_i < 2$ ). Delta weight ( $\Delta_i$ ) is the difference between the AICc of a particular model compared with that of the best model. We z-transformed the explanatory variables. We highlight significant effects (i.e.,  $p \leq 0.05$ ) in bold. “Sex” is the average cocoon weight that were preliminary assigned to either “male” or “female” individuals (see Appendix A: Fig. A.4). Species “*Cornuta*” stands for the number of cocoons of *Osmia cornuta*. “SNH” stands for “Semi-natural habitat”.

Model type	Response	Full model	df	(Q)AICc	$\Delta_i$	Predictor(s)	Estimate	SE	z-value	p value
Specific pollen availability	Weight	Specific pollen availability + sex	88	672.31	0.00	Specific pollen availability	-0.01	0.02	-0.51	0.613
						<b>Male</b>	<b>-0.52</b>	<b>0.04</b>	<b>-12.62</b>	<b>&lt; 0.001</b>
Land cover classes and distance	Parasitism rate	Proportion arable land + proportion permanent crops + proportion herbaceous SNH + proportion forest + proportion woody SNH + proportion built-up + distance to forest + distance to built-up	42	100.96	0.00	Proportion permanent crops	-0.25	0.13	-1.84	0.072
						<b>Distance forest</b>	<b>-0.42</b>	<b>0.11</b>	<b>-3.87</b>	<b>&lt; 0.001</b>
						Distance built-up	-0.20	0.12	-1.65	0.108
						Proportion woody SNH	0.27	0.15	1.80	0.078
			43	102.04	1.08	<b>Proportion permanent crops</b>	<b>-0.32</b>	<b>0.13</b>	<b>-2.49</b>	<b>0.017</b>
						<b>Distance forest</b>	<b>-0.43</b>	<b>0.11</b>	<b>-3.85</b>	<b>&lt; 0.001</b>
						<b>Proportion woody SNH</b>	<b>0.33</b>	<b>0.15</b>	<b>2.27</b>	<b>0.029</b>
			42	102.63	1.67	Proportion permanent crops	-0.26	0.14	-1.91	0.063
						<b>Distance forest</b>	<b>-0.46</b>	<b>0.12</b>	<b>-3.95</b>	<b>&lt; 0.001</b>
						Proportion woody SNH	0.28	0.16	1.76	0.085
43	102.73	1.76	Proportion built-up	0.16	0.13	1.22	0.228			
			Proportion permanent crops	-0.20	0.14	-1.47	0.148			
			<b>Distance forest</b>	<b>-0.44</b>	<b>0.11</b>	<b>-3.98</b>	<b>&lt; 0.001</b>			
						<b>Distance built-up</b>	<b>-0.27</b>	<b>0.12</b>	<b>-2.18</b>	<b>0.035</b>
						Reproductive output	-0.16	0.14	-1.14	0.256
						<b>Cornuta</b>	<b>-1.53</b>	<b>0.27</b>	<b>-5.60</b>	<b>&lt; 0.001</b>

*Juglans* occurs mainly as isolated individual high-stem trees in the open farmland, where nectar offering plants are sparse compared to the hedgerows and the forest edges, where the majority of *Quercus* trees were located close-by nectar-rich rosaceous trees and shrubs. Foraging flights to *Juglans regia* may thus be less profitable due to the nectar scarcity of this plant and its direct surroundings. This might also be reflected by the significantly lower use of *Quercus* pollen of *O. bicornis* with increasing distance from plants offering *Prunus* type pollen (personal observations, data not shown), which are highly attractive in terms of pollen as well as nectar (McGregor, 1976). Observing fluctuations in the pollen diets of *Osmia* (especially for *O. bicornis*, related to the high use of *Juglans* in this study) across several years could better account for the varying pollen use of this species related to varying weather conditions and phenologies of plants. The similar performance of the pollen availability index and the important single pollen resources on predicting *O. cornuta* reproductive output is unsurprising, since a single pollen type (*Prunus* type) contributed to around 80% of the potential specific pollen availability for *O. cornuta*.

The weight of the *Osmia* cocoons and the proportion of emerged adult females could not be explained by the floral resources present in the surrounding landscapes. We base

the specific indices that represent the floral resources available to the *Osmia* species on the pollen quantity and pollen use during the foraging periods. For their development, bee larvae need a balance in nutritional composition rich in body-building nutrients (Bukovinszky et al., 2017; M. Filipiak, 2018, 2019; Z. M. Filipiak et al., 2022; Z. M. Filipiak & Filipiak, 2020; Lawson et al., 2021). *Osmia* females are able to adapt the pollen foraging to the specific nutritional demands of their larvae (M. Filipiak, 2019). Thus, by using only pollen quantity and pollen use within landscapes as the basis for floral resource indices, we only indirectly account for the nutrient composition and quality of pollen foods in the landscapes studied. This could partly explain why we did not identify significant effects of floral resources on the weight and sex of the offspring in our study.

The high use of pollen types offered by different key woody and herbaceous plant taxa and the increasing use of herbaceous pollen plants by *O. bicornis* later in the season is in accordance with other studies (Bertrand et al., 2019; Coudrain et al., 2016; Free & Williams, 1970; Radmacher & Strohm, 2010; Tasei & Picart, 1973). In addition, both species used a different set of key pollen plants during their foraging seasons. The fact that the identified key pollen plants also lead to a higher reproductive output of both species,

highlights the importance of preserving non-agricultural woody and herbaceous semi-natural habitats with a diverse availability of floral resources across the season to foster bee crop pollinators and their pollination in agricultural landscapes (e.g. Bertrand et al., 2019; Kämper et al., 2016; Requier et al., 2015). Oilseed rape was cultivated in eight of the landscapes studied and we found Brassicaceae pollen (i.e. the pollen type it provides) in the nests of *O. bicornis* in all of these landscapes, albeit in quantities of <1%. In addition, the number of offspring and the reproductive output of *O. bicornis* decrease with increasing distances to oilseed rape. This could be due to the fact that the bees benefit from the nectar supply of oilseed rape (Coudrain et al., 2016; Holzschuh et al., 2013; Jauker et al., 2012; Yourstone et al., 2021). The same applies to *Aesculus hippocastanum*, which was collected in amounts below <1% in each of the landscapes where it was present. Both plants may therefore be important nectar sources for this species. Identifying important nectar resources (i.e. especially those plants that are mainly or solely visited for nectar) and taking into account their contribution to total floral resources when calculating the index might further increase the predictive power of the total floral resource maps.

In this study, we mapped floral resources at a high level of detail and spatial and temporal resolution. The variables created by land cover maps yielded useful information for explaining the development of the two bee taxa, with much less mapping effort. In fact, distance to forest was the most important factor for explaining the reproductive output of both *Osmia* species in our landscapes. It also had been the most important predictor for the development of colonies of the buff-tailed bumblebee (*Bombus terrestris* L.) in the same landscapes and this effect was stronger than the availability of floral resources (Eckerter et al., 2020). As woody habitats outside forest accounted for most of the pollen availability in this study, we suspect that bees have benefited from factors provided in proximity to forests other than floral resources. For example, microclimatic conditions such as decreased wind speed or air temperature near forest could have been beneficial for the bees during dry and hot weather periods (e.g. Bentrup et al., 2019; Chen et al., 1999). Although our study species are not known to forage in closed forest, we cannot fully exclude that they have benefited from the non-mapped resources present in the forest interiors. For example, *Prunus avium*, *Acer* spec., *Quercus* and *Rubus* are commonly found in the interiors of forests in our region and may have served as additional pollen sources for the *Osmia* species. The decrease in the reproductive output of *O. bicornis* with the proportion of arable land is likely related to scarcity of floral resources. Our findings using the variables created by land cover maps underline the important role that forest as one kind of semi-natural habitat can have for adjacent agricultural areas to support wild bee pollinators (Bartual et al., 2019; Eckerter et al., 2020; Holland et al., 2017; Mitchell et al., 2014; Ricketts et al., 2008; Schirmel et al., 2018).

The decrease in parasitism with increasing distance to forests and its increase with proportions of open woody semi-natural habitats is in accordance with earlier studies (Schüepp et al. 2011, Coudrain et al. 2014) and could be related to the higher host abundances in these situations. Stronger negative effects of habitat fragmentation on parasitoids than on hosts also support the trophic rank and the specialist consumer hypothesis, with species of higher trophic levels being more vulnerable to landscape changes than species of lower trophic levels, like, for example, their hosts (Albrecht et al., 2007; Davies et al., 2000; Tschardt et al., 2012). Although also natural enemies benefited from forest proximity and woody semi-natural habitats, these land-use characteristics had an overall positive effect on the *Osmia* populations, either by, for example, increasing their reproductive output and/or offering a high abundance of key pollen types.

## Conclusions

The detailed analysis of resource use by two bee species and landscape-scale mapping of these resources revealed strong benefits of specific resources to the bees' reproductive output. For both bee species and their natural enemies, forests are beneficial not only for reasons of providing floral resources, but for other reasons as well. Both the preferred flowering plants and forests should thus be conserved and enhanced to maintain and support *O. cornuta*, *O. bicornis* and likely other wild bee populations in agricultural landscapes. Our findings highlight the potential of combining different mapping approaches to complement each other in predicting and understanding population processes in agricultural landscapes.

## Data availability statement

The data that support the findings of this study are openly available in figshare at (<https://figshare.com>), at DOI: 10.6084/m9.figshare.16635187.

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## Declaration of Competing Interest

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

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baae.2022.09.005](https://doi.org/10.1016/j.baae.2022.09.005).

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