agronomy

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Using Temporally Resolved Floral Resource Maps to Explain Bumblebee Colony Performance in Agricultural Landscapes

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Received: 13 November 2020; Accepted: 15 December 2020; Published: 18 December 2020

Abstract: Wild bumblebees are key pollinators of crops and wild plants that rely on the continuous availability of floral resources. A better understanding of the spatio-temporal availability and use of floral food resources may help to promote bumblebees and their pollination services in agricultural landscapes. We placed colonies of *Bombus terrestris* L. in 24 agricultural landscapes with various degrees of floral resource availability and assessed different parameters of colony growth and fitness. We estimated pollen availability during different periods of colony development based on detailed information of the bumblebee pollen diet and the spatial distribution of the visited plant species. Total pollen availability did not significantly explain colony growth or fitness. However, when using habitat maps, the weight gain of colonies, the number of queen cells, and colony survival decreased with increasing distance from the forest. The better explanation of bumblebee performance by forest proximity than by (plant-inferred) pollen availability indicates that other functions of forests than pollen provision were important. The conservation of forests next to agricultural land might help to sustain high populations of these important wild pollinators and enhance their crop pollination services. Combining different mapping approaches might help to further disentangle complex relationships between *B. terrestris* and their environment in agricultural landscapes.

Keywords: agricultural landscapes; *Bombus terrestris*; colony development; landscape composition; wild bees

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1. Introduction

Animal pollination is crucial for around one third of worldwide food production, with 85% of leading global crop types relying to varying degrees on pollination [1]. In addition to domestic honeybees (*Apis mellifera* L.), wild bees greatly enhance and stabilize crop pollination, and they are often the most effective pollinators [2–6]. However, habitat loss and intensive agricultural practices contribute to pollinator declines in different regions of the world [7], while the dependency of global agriculture on pollinators is increasing [8]. Hence, supporting wild bees in agricultural landscapes is crucial to future economic and environmental stability [9,10].

Bumblebees are important wild pollinators that increase the yield of many crops, e.g., fruit trees, pepper, pumpkin, strawberries, and tomatoes [11,12]. The buff-tailed bumblebee (*Bombus terrestris* L.) is one of the dominant crop pollinators in Europe [13]. Like all wild bees, wild bumblebees rely on foraging and nesting resources provided by the surrounding landscape [14,15]. Thus, favorable foraging habitats can enhance pollinator populations and crop pollination at the landscape scale [10,16–18]. As habitat types differ in resource availability, habitat maps using broad land use categories are commonly used to predict wild bee development and the service they provide [5]. For example, habitat maps explained faster growing and heavier colonies of *B. terrestris* in suburban gardens than elsewhere [19]. In different studies, the pollen deposition of *B. terrestris* was higher with a decreasing proportion of cropland in the surrounding landscape [20], and *B. terrestris* colonies had higher reproductive success and survived longer in urban areas than agricultural areas [21]. In intensively managed agricultural landscapes, floral resources are mainly offered by small fragments of semi-natural habitats [4,22,23] or single mass flowering crops. Consequently, in addition to habitat maps, maps of single mass flowering species, e.g., apple, oilseed rape, and strawberry, have been found to explain colony development of *B. terrestris* [24–26]. *Bombus terrestris* mainly collects pollen on woody plants [27,28]. No single plant accounts for >15% of the total pollen diet of *B. terrestris* [28]. Furthermore, the flowering of single plant species is temporally restricted, and most pollinators use a sequence of specific plant species during their flight season [28]. Resources may be limited, especially during early stages of colony development [24,29–31]. Hence, comprehensive floral resource maps at the landscape scale that give information on temporal resource availability may further improve our ability to predict the growth and reproductive success of bumblebee colonies [32].

Here, we placed colonies of *B. terrestris* in 24 agricultural landscapes in southwest Germany, quantified their pollen use, mapped the most commonly used plants (71 species derived from 30 pollen types, offering 95% of the total pollen diet), and calculated a weighed pollen availability index for the early and late flight period of the species in each landscape. We tested the effects of detailed plant-inferred pollen availability versus classical land use maps (i.e., distances from and proportions of land use categories in the landscapes) on colony development (i.e., colony growth and longevity). We tested the following hypotheses: (1) pollen resources for bumblebees are mostly provided by woody semi-natural habitats; (2) a high availability of pollen resources in the landscape enhances colony development; (3) early pollen resources have stronger effects on the weight gain of colonies than late pollen resources; and (4) floral resource maps predict colony development better than habitat maps.

2. Materials and Methods

2.1. Study Landscapes and Creation of Floral Resource Maps

The study was conducted in the surroundings of Landau in the Upper Rhine Valley, Rhineland-Palatinate, Germany (Electronic Supplementary Materials, Figure S1). A total of 24 agricultural landscapes of 500 m radius were selected to represent gradients of the amounts of early and late pollen resources for *B. terrestris* [33]. Landscape centers were at least 800 m away from each other and were placed in grassy field margins. The cover of plants offering selected pollen types and the major land use types were mapped according to field inspections between June and November 2017 (woody plants) and between April and June 2018 (land use and annual herbaceous plants; for further details see Supplement S1). We used Copernicus (Sentinel-2; L2A–L2C) optical satellite imagery (2016; 10 m resolution), processed by the Federal Agency for Cartography and Geodesy (BKG), as orientation in the field during mapping. We ground-truthed each landscape element via field inspection during our mapping process in 2018 and noted every change if necessary. Obtained data were later digitized as polygon (land use classes) and point layers (single resources), and they were analyzed with QGIS 3.6.2 [34] using the above-mentioned satellite imagery as a base map. To create land use/land cover (LULC) maps (hereafter: "habitat maps"), the following habitat types were distinguished: arable land, permanent crops, forest edges (i.e., the first ten meter into forests), forest (i.e., forest interiors without its edges), open woody semi-natural habitat (i.e., hedgerows and single standing trees including those of semi-natural orchards), herbaceous semi-natural habitat (i.e., intensively and extensively managed meadows and pastures), and built-up area (i.e., rural settlements). The proportions of habitat types across the landscapes are shown in Table S2. We also measured the Euclidean distances of colonies to forests because these were important predictors of wild bee development or performance in previous studies [23,35–37]. To analyze single resources, the cover of and distance to dominant pollen types were used: *Brassica napus* L. (hereafter: oilseed rape), because it has been an important predictor of bumblebee densities and colony development in earlier studies [24,38,39], and *Cornus*, *Lonicera*, *Prunus*, *Rubus*, and *Tilia* because each of these plant taxa contributed more than 10% of pollen availability to *B. terrestris* in at least one season during our study (Electronic Supplementary Materials, Table S1). To create floral resource maps, the area covered by plant species offering pollen types that constitute at least 5% of the pollen diet of *B. terrestris* in our study region in at least one season, and all remaining woody plant species were mapped [28]. These maps accounted for the area covered by 71 plant species derived from 30 pollen types. Plants in forest interiors (i.e., deeper than ten meters into a forest) were not mapped because most bees [40], and *B. terrestris* in particular, prefer open habitat for foraging [41–43]. Floral resource indices were used as described in [33]. Indices considered the relative cover of plants offering pollen types multiplied by their utilization (i.e., percentage of the total collected pollen volume) by *B. terrestris* during a specific period, summed up over all pollen types. An index value of 1 denotes the average pollen availability of all studied landscapes, while larger or smaller values describe the proportional difference of resource availability in a given landscape relative to the average. Pollen availability was calculated over the whole duration of *B. terrestris* colony field placement (from mid-April to mid-June) and separately for the early and late phase of colony development. The early season started with the placement of colonies in the field (mid-April) and ended when they reached their maximum weight (end of May). The late season was from when the colonies had their maximum weight until colony termination (i.e., when no evidence of living bumblebees could be detected at the nest boxes during measurements; mid-June). Floral resource maps accounted for 96.3% of early, 83.2% of late, and 94.9% of the total pollen diet of *B. terrestris* according to the analysis of pollen diets from the 48 colonies when considering 45,900 pollen grains out of 306 samples (Table S1). The composition of pollen diet excluded from index calculations is given in Table S3.

2.2. Placement of *B. terrestris* Colonies

Two commercially bred *B. terrestris* colonies (STB Control, Aarbergen, Germany) were established in the center of each of the 24 landscapes (48 colonies in total) on a grassy field margin in mid-April 2018. Colonies were even-aged, consisted of one queen and approximately 50–60 workers, and were embedded in a nest box. For acclimatization, a tank filled with sugar water was provided for each colony. Nesting box and tank were enclosed by a cardboard box to protect colonies against unfavorable weather conditions. To protect colonies from soil moisture, boxes were placed on wooden plates that were 10 cm above ground level. Colony entrances were facing south-east. The day after placement, colonies were weighted and colony entrances were opened. After one week of acclimatization, sugar tanks were closed. The weight of nest boxes containing colonies was measured every second week until colony termination. After that, colonies were harvested and frozen at −18 °C for later dissection in the laboratory. Weight gain was obtained by subtracting the maximum colony weight by its initial weight. After colony dissection, cells were counted and assigned to two classes: queen cells (diameter ≥ 11 mm or length ≥ 19 mm if diameter was not measurable because cells were fragmented) and other cells (i.e., male/worker cells with diameter < 11 mm and length < 19 mm; [44]). Male and worker cells could not be consistently differentiated and were therefore grouped together [19,29,31]. Days of survival were measured from the day of colony placement until colony termination. Weight gain, the number of cells, and the survival of the two colonies in each landscape were averaged.

2.3. Pollen Collection, Preparation and Determination

The pollen diet of *B. terrestris* was recorded at up to four sampling dates between 24 April and 16 June 2018. At each nest, pollen loads were collected from up to four workers returning from foraging trips per sampling date. The start of the sampling period coincided with the peak flowering of oilseed rape and *Crataegus* spec., while at the end, *Rubus fruticosus* L. and *Tilia* spec. were flowering, which are dominant flowering resources of *B. terrestris* in the respective seasons [28]. Pollen was stored in water, frozen at −18 °C, and then acetolyzed [45]. Acetolyzed pollen was mounted on permanent slides in glycerin, and 150 pollen grains per sample were counted starting at a random position of the slide and identified to the highest possible taxonomic resolution using a light microscope (400× magnification), a palynological key [46], a photo atlas [47], and the reference pollen collection of the Institute of Plant Sciences of the University of Bern. Pollen types that contributed more than 3% of the diet of *B. terrestris* colonies in any period (i.e., before colonies reached their maximum weight or from this moment until colony termination) were classified as key pollen types. Deformed pollen grains that could not be assigned to pollen types (2.2% of detected pollen) and pollen fragments were excluded from the analysis. The pollen type Brassicaceae could not be identified to the species level. However, oilseed rape accounted for 98.3% of the cover of Brassicaceae in the landscapes.

2.4. Statistical Analysis

Correlations between colony response (i.e., weight gain, queen cells, and survival) and explanatory variables (i.e., variables used to describe floral resource maps, habitat maps, or single resources) were tested with linear regression. To visualize the interaction among variables, a correlation matrix among all variables was drawn (Figure S3). All variables were standardized before the analysis using the standardize function of the arm package [48] in order to allow for a comparison between effect sizes between models. To compare the predictive power of the mapping approaches, three different sets of linear candidate models were set up for each colony response variable. The explanatory variables of the candidate models were either the pollen availability indices, the parameters derived from habitat maps, or the single pollen resources. The correlations of variables in models were below $|r| \leq 0.7$ (Figure S3). Models were compared via the Akaike second-order Information Criterion (AICc) [49–52] using the dredge function from the MuMin package [53]. We compared the overall best model(s) using $\Delta_i < 2$ as a cutoff rule [50,52]. In addition to this statistically based model comparison, models with single explanatory variables that contain either one of the focal predictors of this study (resource availability and dominant single pollen resources) or key variables reported in the literature (distance to forests, cover of arable land and built-up area, see introduction) are displayed. To compare the predictive power of the different mapping approaches, the best models of each approach were compared to each other. Data analyses were conducted in R 4.0 [54]. Model diagnostic plots were visually checked (residuals vs. fitted values and normal Quantile–Quantile plots). A pollen network graph was created using the package bipartite [55]. The plotting of bar plots and linear models was done using the package ggplot2 [56], and the correlation matrix was drawn using the corrplot package [57].

3. Results

3.1. Pollen Diet

We identified 45,900 pollen grains collected from 306 returning foragers of *B. terrestris*. The key pollen types collected in the early season were *Prunus* (16.2%), *Rubus* (15.5%), and *Rosaceae* other than *Prunus* (12.3%); these were followed by *Cornus sanguinea* (8.5%), Brassicaceae (8.4%), *Acer* (7.3%), *Papaver rhoeas* type (5.5%), *Lonicera xylosteum* type (4.8%), *Sorbus* (4.0%), and *Lamium album* type (3.5%; Table S1). Key pollen types in the late season were *Rubus* (28.6%), *Tilia* (26.8%), *Phacelia tanacetifolia* (10.3%), *Vitis* (3.6%), and *Rosaceae* (3.5%; Table S1). During both periods, the majority of pollen was collected on woody plants (74.1% in the early season and 67.4% in the late season; Figure S2).

3.2. Landscape and Pollen Availability

The studied landscapes were dominated by arable land (69.0% ± 0.047—average ± standard error), followed by the herbaceous semi-natural habitat (10.7% ± 0.024), forest (5.7% ± 0.024), permanent crops (4.0% ± 0.012), woody semi-natural habitat (3.2% ± 0.006), built-up area (2.1% ± 0.010), and forest edges (0.8% ± 0.003).

After giving each pollen type a weight proportional to its use by bumblebees, open woody semi-natural habitats (woody semi-natural habitat excluding forests and forest edges) provided 75.2% of the total pollen availability (expressed with indices) in the 24 studied landscapes (Figure 1). In open, woody semi-natural habitats, plants offering *Cornus sanguinea*, *Lonicera xylosteum* type, and *Prunus* type pollen were the most important contributors to pollen availability in the early season (39.8%, 15.4%, and 6.8%, respectively). In the late season, *Tilia*, *L. xylosteum* type and *Rubus* were the most important contributors (25.2%, 23.2%, and 17.4%, respectively). Forest edges contributed to 11.3% of total pollen availability. Additionally in the early season, *C. sanguinea* and *L. xylosteum* type were most important contributors (5.0% and 1.6%, respectively); and in the late season *Rubus*, *Tilia*, and *L. xylosteum* type (9.7%, 4.2%, and 2.4%, respectively). The herbaceous semi-natural habitat contributed 3.5% to early pollen availability and 8.5% to late pollen availability. Here, the main contributors in the early season were *Papaver rhoeas* type, *Lamium album* type, and *Trifolium pratense* type (1.4%, 1.3%, and 0.6%, respectively), and the main contributors in the late season were *T. pratense* type and *Phacelia tanacetifolia* (5.3% and 2.8%, respectively). In permanent crops (average cover: 4.0%), the most important contributors were fruit trees in the early season (5.2%) and *Vitis* in the late season (1.8%). Though arable land covered the major part of the landscapes, its contribution to pollen availability over the seasons did not exceed 3.2%. The most important crop pollen resources were oilseed rape in the early season (2.5%) and *Asparagus officinalis* type in the late season (1.1%). The contributions of built-up area to pollen availability were low (<2.1% in any season). Figure 1 shows the average area of habitat categories in the studied landscapes, as well as their average contributions to pollen availability (indices) during different periods. For a list of the plants detected in the landscapes offering collected pollen types and their contributions to pollen availability during different time periods, see Table S1.

3.3. Colony Development and Survival

On average, each colony contained 675 ± 218 male/worker cells (minimum: 177; maximum: 1206), contained 88 ± 64 queen cells (min: 2; max: 245), gained 648 ± 202 g of weight (min: 146; max: 1076), and survived for 68 ± 9 days (min: 50; max: 84). The maximum weight gain increased with the number of total cells (i.e., male/worker and queen cells; $t_{1,22} = 3.15$, $R^2_{mult} = 0.311$, and $p < 0.01$) and with the number of queen cells ($t_{1,22} = 4.54$, $R^2_{mult} = 0.484$, and $p < 0.001$). Colony survival and the number of queen cells were positively correlated ($t_{1,22} = 4.07$, $R^2_{mult} = 0.430$, and $p < 0.001$). Correlations between other colony variables were non-significant (i.e., $p \geq 0.05$; Figure S3).

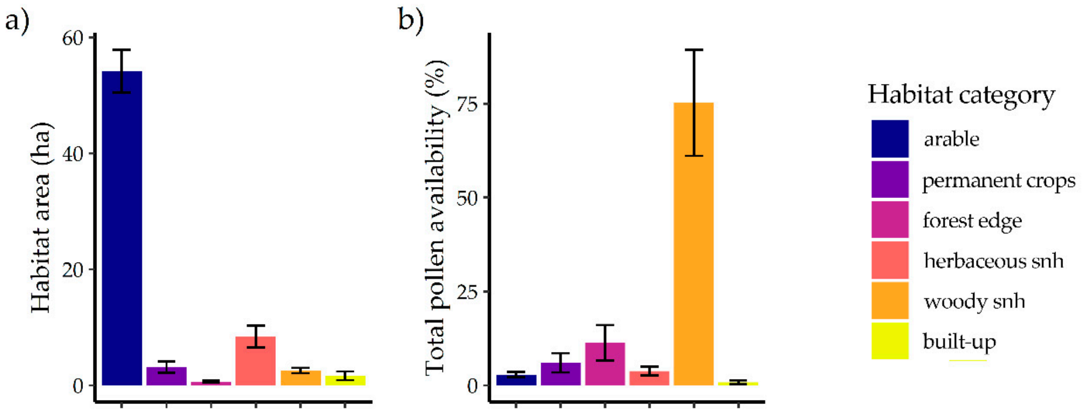

Figure 1. *Cont.*

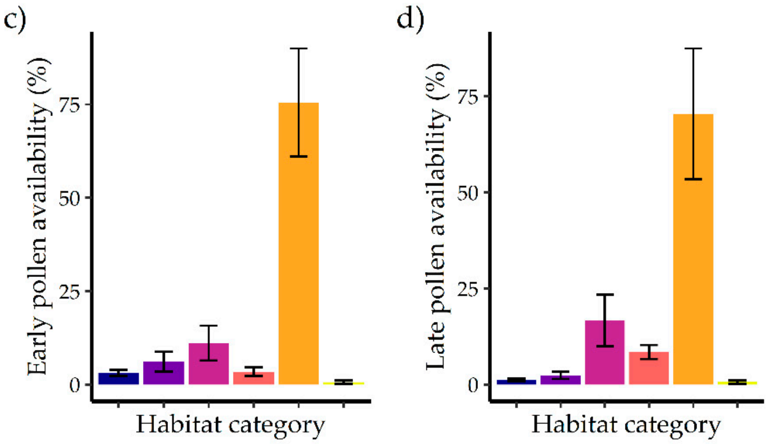

Figure 1. Average (±1 standard error) area of habitat categories (arable, permanent crops, forest edges, herbaceous semi-natural habitats, and woody semi-natural habitats but excluding forests and built-up area) in the studied landscapes (**a**), their average contribution to pollen availability per landscape (**b**), in the early season (**c**), and in the late season (**d**). Pollen availability is based on the relative area covered by plant species offering a pollen type in the respective habitat type across all landscapes multiplied by the relative collected pollen volume of each type over the whole season.

3.4. Pollen Availability and Colonies

The total pollen availability in the landscapes during any time did not significantly affect colony weight gain, survival, or the number of queen cells ($p > 0.35$; Table 1 and Figure S3). Using habitat maps, we found that the weight gain of colonies, queen cells, and survival decreased with distance to forests (Figure 2). In addition to the distance from forests, the best models contained either increases of survival with distance to built-up area or decreased survival with an increasing proportion of it in the landscapes (Table 1). Using important predictors from previous studies, we found that the number of queen cells tended to decrease with the proportion of arable land (Table 1). However, this model was distinctly worse than models containing distance to forests ($\Delta_i \geq 2$; Table 1).

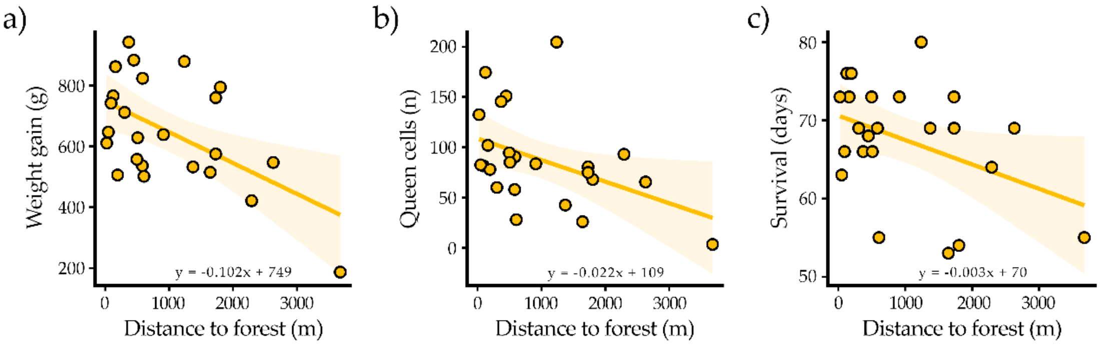

Figure 2. Relations of (**a**) weight gain ($t_{1,22} = -2.28$, $R^2_{mult} = 0.191$, and $p = 0.033$), (**b**) number of queen cells ($t_{1,22} = -3.09$, $R^2_{mult} = 0.302$, and $p < 0.01$), and (**c**) survival and distance to forests ($t_{2,21} = -2.67$, $R^2_{adj} = 0.286$, and $p = 0.015$). Predicted linear relations (regression lines) and 95% confidence intervals (shaded area) are drawn for significant relations.

Regarding single pollen resources, weight gain decreased with increasing distance to oilseed rape, and no significant relationship was found with any other variable (Table 1). The number of queen cells showed no significant relationship with any of the single pollen resources. Colony survival decreased with increasing distance to *Cornus sanguinea* in all of the best-ranking models (Table 1). Alternatively, a negative correlation also existed between colony survival and the distance to *Rubus* ($\Delta_i = 2.11$). For correlations among all observed variables, see Figure S3.

Table 1. Comparison of models explaining bumblebee colony response variables with pollen availability indices, classical habitat maps, and single resources (see main text for description of mapping approaches). The abbreviation "SNH" is used for "Semi-natural habitat". The Akaike second-order Information Criterion (AICc) and the dredge function from the MuMin package [53] were used to select the best models ($\Delta_i < 2$). Delta weight (Δ_i) is the difference between the AICc of the model and the best model. Best models containing pollen availability and important predictors using habitat maps or single pollen resources are displayed regardless of AICc values (see main text). Models listed below a dashed line are not included in the best model set ($\Delta_i < 2$). Variables were standardized [48].

Explanation	Response	Model Description	df	R^2_{mult}	AICc	Δ_i	Predictor	Estimate	SE	*t*-Value	*p* Value
Pollen availability indices	Weight gain	(Empty)	23		319.7	0.00	(Intercept)	648.90	35.85	18.10	<0.001
		Early pollen availability	22	0.001	322.3	2.60	Early	12.55	74.84	0.17	0.868
		Total pollen availability	22	0.000	322.4	2.62	Total	7.29	74.87	0.10	0.923
		Late pollen availability	22	0.000	322.4	2.63	Late	0.72	74.89	0.01	0.992
	Queen cells	(Empty)	23		256.2	0.00	(Intercept)	87.73	9.54	9.20	<0.001
		Late pollen availability	22	0.007	258.7	2.46	Late	7.85	19.86	0.40	0.697
		Total pollen availability	22	0.006	258.7	2.47	Total	−7.49	19.87	−0.38	0.710
		Early pollen availability	22	0.005	258.7	2.51	Early	−6.64	19.88	−0.33	0.741
	Colony survival	(Empty)	23		166.8	0.00	(Intercept)	67.54	1.48	45.62	<0.001
		Early pollen availability	22	0.040	168.4	1.66	Early	2.89	3.03	0.95	0.350
		Total pollen availability	22	0.033	168.6	1.82	Total	2.63	3.04	0.87	0.396
		Late pollen availability	22	0.027	168.7	1.97	Late	2.39	3.05	0.78	0.442
Habitat distance and cover	Weight gain	Distance forest	22	0.302	313.7	0.00	Distance forest	−193.12	62.55	−3.09	0.005
		Distance forest and built-up	21	0.342	315.2	1.51	Distance forest	−208.73	63.74	−3.28	0.004
							Built-up	−71.38	63.74	−1.12	0.275
		Distance forest and woody SNH	21	0.339	315.3	1.59	Distance forest	−210.35	64.29	−3.27	0.004
							Woody SNH	−69.82	64.29	−1.09	0.290
		Distance forest and distance built-up	21	0.333	315.6	1.83	Distance forest	−202.71	63.37	−3.20	0.004
							Distance built-up	62.11	63.37	0.98	0.338
		Arable	22	0.060	320.9	7.20	Built-up	85.85	72.61	1.18	0.250
		Built-up	22	0.035	321.5	7.80	Arable	−65.42	73.58	−0.89	0.384

Table 1. *Cont.*

Explanation	Response	Model Description	df	R^2_{mult}	AICc	Δ_i	Predictor	Estimate	SE	*t*-Value	*p* Value
	Queen cells	Distance forest	22	0.191	253.8	0.00	Distance forest	−40.82	17.93	−2.28	0.033
		Distance forest, herbaceous SNH, and built-up	20	0.344	254.9	1.10	Distance forest	−45.71	18.16	−2.52	0.020
							Herbaceous SNH	−22.37	18.16	−1.23	0.232
							Built-up	−34.66	18.74	−1.85	0.079
		Distance forest and built-up	21	0.245	255.0	1.23	Distance forest	−45.71	18.16	−2.52	0.020
							Built-up	−22.37	18.16	−1.23	0.232
		Arable	22	0.142	255.2	1.41	Arable	−35.20	18.46	−1.91	0.070
		Forest edge	22	0.135	255.4	1.60	Forest edge	34.31	18.54	1.85	0.078
		Distance forest and herbaceous SNH	21	0.232	255.4	1.66	Distance forest	−33.46	19.19	−1.74	0.096
							Herbaceous SNH	20.31	19.19	1.06	0.302
		Permanent crops and distance forest	21	0.227	255.5	1.84	Permanent crops	17.97	18.02	1.00	0.330
							Distance forest	−42.59	18.02	−2.36	0.028
		Arable and distance forest	21	0.225	255.6	1.87	Arable	−19.86	20.67	−0.96	0.348
							Distance forest	−30.98	20.67	−1.50	0.149
		Built-up	22	0.018	258.41	4.61	Built-up	−12.38	19.75	−0.63	0.537
	Colony survival	Distance forest and distance built-up	21	0.348	162.0	0.00	Distance forest	−6.90	2.59	−2.67	0.015
							Distance built-up	6.23	2.59	2.41	0.025
		Distance forest and built-up	21	0.337	162.4	0.40	Distance forest	−7.27	2.64	−2.75	0.012
							Built-up	−6.12	2.64	−2.32	0.031
		Distance forest, distance built-up, and permanent crops	20	0.401	163.2	1.20	Distance forest	−7.23	2.55	−2.83	0.010
							Distance built-up	6.25	2.54	2.46	0.023
							Permanent crops	3.35	2.52	1.33	0.199
		Distance forest, distance built-up, and built-up	20	0.396	163.4	1.38	Distance forest	−7.43	2.59	−2.87	0.009
							Distance built-up	4.22	3.01	1.40	0.177
							Built-up	−3.85	3.05	−1.26	0.221
		Built-up	22	0.026	168.8	6.75	Built-up	2.36	3.05	0.77	0.448
		Arable	22	0.016	169.0	7.02	Arable	−1.81	3.07	−0.59	0.561

Table 1. *Cont.*

Explanation	Response	Model Description	df	R^2_{mult}	AICc	Δ_i	Predictor	Estimate	SE	*t*-Value	*p* Value
Single resource distance and cover	Weight gain	Distance Brassicaceae	22	0.209	316.7	0.00	Distance Brassicaceae	−160.60	66.60	−2.41	0.025
		Distance Brassicaceae and distance *Lonicera*	21	0.258	318.1	1.37	Distance Brassicaceae	−193.91	71.82	−2.70	0.013
							Distance *Lonicera*	−84.62	71.82	−1.18	0.252
		Distance Brassicaceae and cover *Prunus*	21	0.243	318.6	1.86	Distance Brassicaceae	−181.46	70.08	−2.59	0.017
					318.6	1.86	*Prunus*	−67.92	70.08	−0.97	0.344
		Distance Brassicaceae and cover *Lonicera*	21	0.243	318.6	1.86	Distance Brassicaceae	−184.22	71.04	−2.59	0.017
							Lonicera	68.63	71.04	0.97	0.345
		Cover Brassicaceae	22	0.136	318.7	2.16	Brassicaceae	129.50	69.61	1.86	0.076
		Distance *Prunus*	22	0.016	322.0	5.28	Distance *Prunus*	44.26	74.29	0.60	0.557
		Cover *Rubus*	22	0.007	322.2	5.51	*Rubus*	28.43	74.64	0.38	0.707
		Distance *Cornus*	22	0.003	322.3	5.59	Distance *Cornus*	20.06	74.76	0.27	0.791
		Cover *Tilia*	22	0.002	322.3	5.63	*Tilia*	−14.02	74.83	−0.19	0.853
		Cover *Prunus*	22	0.001	322.3	5.64	*Prunus*	−12.17	74.84	−0.16	0.872
		Cover *Cornus*	22	0.001	322.3	5.65	*Cornus*	10.06	74.85	0.13	0.894
		Distance *Lonicera*	22	0.001	322.3	5.65	Distance *Lonicera*	−8.28	74.87	−0.11	0.913
		Distance *Rubus*	22	0.001	322.4	5.66	Distance *Rubus*	−8.07	74.87	−0.11	0.915
		Distance *Tilia*	22	0.000	322.4	5.66	Distance *Tilia*	−7.50	74.87	−0.10	0.921
		Cover *Lonicera*	22	0.000	322.4	5.66	*Lonicera*	5.23	74.88	0.07	0.945
	Queen cells	(Empty)	23		256.2	0.00	(Intercept)	87.73	9.54	9.20	<0.001
		Distance *Prunus*	22	0.066	257.2	1.00	Distance *Prunus*	23.95	19.27	1.24	0.227
		Distance *Rubus*	22	0.026	258.2	1.99	Distance *Rubus*	−15.19	19.67	−0.77	0.448
		Distance *Tilia*	22	0.015	258.5	2.28	Distance *Tilia*	11.28	19.79	0.57	0.574
		Cover *Prunus*	22	0.013	258.5	2.32	Cover *Prunus*	−10.58	19.80	−0.53	0.598
		Cover *Rubus*	22	0.011	258.6	2.37	Cover *Rubus*	9.72	19.82	0.49	0.629
		Distance *Cornus*	22	0.007	258.7	2.46	Distance *Cornus*	−7.87	19.86	−0.40	0.696
		Cover *Tilia*	22	0.005	258.7	2.51	Cover *Tilia*	6.56	19.88	0.33	0.744
		Distance *Lonicera*	22	0.004	258.7	2.52	Distance *Lonicera*	−6.27	19.89	−0.32	0.756

Table 1. *Cont.*

Explanation	Response	Model Description	df	R^2_{mult}	AICc	Δ_i	Predictor	Estimate	SE	*t*-Value	*p* Value
		Cover *Cornus*	22	0.003	258.7	2.55	Cover *Cornus*	−5.44	19.90	−0.27	0.787
		Distance Brassicaceae	22	0.001	258.8	2.59	Distance Brassicaceae	3.60	19.92	0.18	0.858
		Cover *Lonicera*	22	0.000	258.8	2.63	Cover *Lonicera*	0.55	19.93	0.03	0.978
		Cover Brassicaceae	22	0.000	258.8	2.63	Cover Brassicaceae	0.22	19.93	0.01	0.991
	Colony survival	Distance *Cornus*	22	0.253	162.4	0.00	Distance *Cornus*	−7.29	2.67	−2.73	0.012
		Distance *Cornus* and cover *Tilia*	21	0.301	163.7	1.29	Distance *Cornus*	−7.40	2.65	−2.80	0.011
							Cover *Tilia*	3.21	2.65	1.21	0.239
		Distance *Cornus* and distance *Lonicera*	21	0.294	164.0	1.55	Distance *Cornus*	−9.15	3.15	−2.91	0.008
							Distance *Lonicera*	3.48	3.15	1.10	0.282
		Distance Brassicaceae and distance *Cornus*	21	0.289	164.1	1.71	Distance Brassicaceae	−2.80	2.70	−1.04	0.311
							Distance *Cornus*	−7.69	2.70	−2.85	0.010
		Distance *Cornus*, distance *Lonicera*, and cover *Tilia*	20	0.376	164.2	1.81	Distance *Cornus*	−10.04	3.08	−3.26	0.004
							Distance *Lonicera*	4.87	3.15	1.55	0.138
							Cover *Tilia*	4.33	2.67	1.62	0.120
		Distance *Cornus* and distance *Prunus*	21	0.281	164.4	1.97	Distance *Cornus*	−8.10	2.83	−2.87	0.009
							Distance *Prunus*	2.58	2.83	0.91	0.373
		Distance *Rubus*	22	0.184	164.5	2.11	Distance *Rubus*	−6.23	2.79	−2.23	0.036
		Distance *Tilia*	22	0.102	166.8	4.42	Distance *Tilia*	4.63	2.93	1.58	0.129
		Cover *Cornus*	22	0.047	168.2	5.84	Cover *Cornus*	3.15	3.02	1.04	0.308
		Cover *Tilia*	22	0.041	168.4	5.98	Cover *Tilia*	2.95	3.03	0.98	0.340
		Cover *Prunus*	22	0.030	168.7	6.27	Cover *Prunus*	2.50	3.05	0.82	0.421
		Distance Brassicaceae	22	0.014	169.1	6.66	Distance Brassicaceae	−1.70	3.07	−0.55	0.585
		Distance *Lonicera*	22	0.010	169.2	6.77	Distance *Lonicera*	−1.42	3.08	−0.46	0.650
		Cover Brassicaceae	22	0.010	169.2	6.77	Cover Brassicaceae	1.42	3.08	0.46	0.650
		Cover *Rubus*	22	0.002	169.3	6.94	Cover *Rubus*	0.67	3.09	0.22	0.830
		Cover *Lonicera*	22	0.000	169.4	6.99	Cover *Lonicera*	0.31	3.09	0.10	0.922
		Distance *Prunus*	22	0.000	169.4	7.00	Distance *Prunus*	0.02	3.09	0.01	0.994

4. Discussion

As expected, *B. terrestris* mostly used pollen from woody semi-natural habitats. Surprisingly, however, species-specific floral resource maps at the landscape level did not explain the colony development of *B. terrestris*, although they accounted for the vast part of their pollen diet. Instead, all three parameters of colony performance declined with the distance to forests. This suggests that forest edges had other important functions for bumblebees than pollen provision, such as protection from adverse weather or nectar provision. Alternatively, our results could indicate that the proximity to floral resources is more important than their amount in the landscape, which was expressed by the pollen availability index. In line with a high importance of proximity rather than amount, colony survival decreased with increasing distance to major pollen sources like *Cornus sanguinea* and *Rubus*. In turn, the cover of *Rubus* and *Tilia* declined with distance from the forest (see Supplementary Materials, Figure S3). Our findings therefore suggest that, in addition to pollination [37], pollinator species richness and flower visitation rate of pollinators [23], bumble bee colony growth and fitness might be positively affected by proximity to forests. Positive effects of forests on *B. terrestris* may be surprising, because the species is considered an inhabitant of open landscapes [41–43]. Following the literature on *B. terrestris* habitat use, we only mapped pollen resources in open habitats and in the first 10 m of forests ("forest edge"). Still, we cannot fully exclude that bumblebees were exploiting floral resources, e.g., *Acer* spec., *Castanea sativa* Mill., *Tilia* spec., and *Rubus fruticosus*, within forests and that our floral resource index is thus incomplete. Flower use by pollinators in the forest canopy is difficult to quantify, and we are unaware of studies that have comprehensively described pollinator communities of trees growing in European forest interiors. Furthermore, other pollen resource plants commonly used by *B. terrestris* such as *Asparagus officinalis* L., *Brassica napus*, *Cornus sanguinea* L., *Papaver rhoeas* L., *Phacelia tanacetifolia* Benth., and *Trifolium pratense* L. are absent or rare in forest interiors. Of the most important pollen resource plants collected by bumblebees in our study, only *Lonicera xylosteum* L. and *Rubus fruticosus* can be commonly found in forest interiors, but they are equally found along forest edges, in hedgerows, and in gardens. Typically, forests are semi-natural habitats that often have positive effects on pollinator richness, visitation rate, or pollination service [5,23,58,59]. Apart from food availability, possible benefits of forests for pollinators were summarized in [60]: already established bumblebee colonies may benefit from the reduced daytime temperature in forest interiors in comparison to open habitats during summers (e.g., [61]), and *B. terrestris* might have benefited from microclimatic conditions along and inside forests during its foraging flights. Other benefits of forests include the reduction of air movement, which leads to reduced energetic costs of foraging flights compared to open habitats (e.g., [60,61]). In addition, in the same study year, *B. terrestris* was found collecting honeydew from a colony of the giant willow aphid in England, probably due to an increase of nectar sugar concentration while floral nectar resources were simultaneously restricted, followed by exceptional hot and dry weather [62]. Our study year was extremely hot, with the highest average temperature ever recorded in Germany along with drought due to low summer rainfall in combination with a high sunshine duration [63]. These extreme weather conditions could have caused a shift in limitations from pollen towards nectar resources and potentially enhanced the collection of honeydew in forest interiors. Weather conditions that exceed the thermal tolerance limits of species are likely to increase with climate change [64,65].

Bombus terrestris tend to forage on close-by patches with high resource densities [27,42,66], and their average flight distances lie below or close to 500 m if rewarding resources are available [67,68]. However, they were also found foraging up to several kilometers from their nests [42,69]. Hence, although bumblebees prefer patches of abundant floral resources close to their colonies, the unexpected low effect of local floral resource availability on colony development might partly be explained by the potentially long foraging distances of *B. terrestris*. On the other hand, during early phases of colony development, the number of workers is still low and every lack of resources is detrimental to colony development [30,70]. In addition, long distance flights are more energy-consuming than short distance flights, making close resources more valuable than resources further away from the nest [70].

Further, a mean foraging range of 275.3 ± 18.5 m with a range of 70–631 m was observed for *B. terrestris*, indicating that the major part of their foraging may occur at that scale [71]. Thus, we believe that our landscape radius of 500 m is still appropriate.

The negative effect of built-up area on colony termination contrasts with findings of increased weight gain, higher numbers of males and queens, higher queen survival, and more food stores in colonies of *B. terrestris* in suburban areas and sites with varying degrees of urbanization [19,21]. Bumblebees can profit from large proportions of beneficial habitats at the outskirts of urban areas related to urban sprawl [72]. In our landscapes, built-up areas had a minor role in providing pollen resources compared to some previous studies [73], probably because landscapes were selected to be dominated by agricultural land use.

The increasing amount of arable land in the landscape provides an alternative explanation for the decreased colony performance with increasing distance to forests. The negative effects of arable land on pollinators have commonly been observed (e.g., [20]) and can be explained by, e.g., the negative effects of pesticides or the scarcity of floral resources in intensive agriculture. Pollen availability in our study was lowest in arable land. In addition, longer foraging trips and foraging on scarce, widely distributed, and distant pollen resources (thus less efficient foraging flights) might have had a negative influence on colony development. Large fields in arable land largely lack the beneficial microclimate offered by rural settlements or woody semi-natural habitats [61,72]. The decreasing number of queen cells with arable land was in accordance with the decrease of seed set in *Vicia faba* L. with arable land observed in [33]. When we excluded forest distance from our models, weight gain increased with the proximity to oilseed rape fields in the landscape. This resembled the results of [24,38], the authors of which found increasing abundance and weight gain in colonies of *B. terrestris* with larger amounts of oilseed rape in the landscape. The less strong effect on weight gain on *B. terrestris* observed in our study may be explained by the lower amounts of oilseed rape in our study (the mean proportion of oilseed rape was 1.8%, compared to 7.0% in [24]). In addition, weight gain during the early season does not account for differences in colony growth during the different phases of early colony development. In our study, pollen from *Cornus sanguinea* and from oilseed rape were collected in similar amounts, despite oilseed rape, as a mass flowering crop, theoretically being highly attractive for *B. terrestris*. In addition, Brassicaceae pollen has a lower mean pollen grain volume than *Cornus sanguinea* pollen. Thus, despite its benefits for colony development, oilseed rape has a rather low contribution to early pollen availability indices. The high effect of oilseed rape on colony growth despite low pollen use indicates that *B. terrestris* might visit oilseed rape mostly for nectar rather than for its pollen [27]. Thus, the true effect of oilseed rape and of plants visited for nectar rather than for pollen might also be underestimated when using the pollen diet as base for floral resource indices.

The high importance of pollen from woody plants in the diet of *B. terrestris*, especially in the early season (mid-March to end of May) is in line with other studies [27,28]. A positive effect of woody floral resources on the development on wild pollinators might be stronger in the beginning of the early season, with the full flowering of *Salix*, *Acer*, and *Prunus* (especially *Prunus spinosa*, *Prunus domestica*, and *Prunus avium*), which are important floral resource plants of *B. terrestris* in the early season [28].

5. Conclusions

Classical habitat maps predicted the colony development of *B. terrestris* better than detailed landscape-scale floral resource maps based on pollen use. This indicates that high amounts of attractive pollen food resources in the landscape alone are not sufficient to ensure a high fitness of bumblebee colonies. Still, the floral resource maps and diet analyses provided information that was not accessible only through classical habitat maps, e.g., that hedgerows play an overriding role in pollen availability to bumblebees in our study region despite their very small cover. More knowledge of floral resource use by *B. terrestris* inside forest areas is needed to better understand its effects on colony development. Microclimatic conditions in or along forests may help bumblebees to better survive hot and dry weather periods and counteract possible stressors like pesticide exposure in arable land. Overall, our study demonstrates how predictors created by different mapping approaches are needed to complement each other and help to explain their complex relationships between *B. terrestris* colonies and their development in agricultural landscapes. Using a combination of predictors created by different mapping approaches might help to clearly identify dominant drivers of wild pollinator development and their service in crop pollination in agricultural landscapes.

Supplementary Materials: The following materials are openly available in figshare (https://figshare.com/) at DOI:10.6084/m9.figshare.13233893, Figure S1: Location of landscapes, Supplement S1: Floral resource mapping, Figure S2: Pollen collection network, Figure S3: Pearson correlation matrix between colony parameter and predictors using different mapping approaches, Table S1: Use and availability of key pollen types included in the study and used for calculating the resource availability index for *B. terrestris*, Table S2: Proportions of habitat types across landscapes, Table S3: Composition of remaining pollen diet of returning foragers of *B. terrestris* excluded from index calculation, data presented in this study, and R script used for the analysis.

Author Contributions: Conceptualization, M.H.E., M.A., and F.H.; methodology, M.H.E., F.H., M.A., and P.W.E.; software, P.W.E.; validation, P.W.E., L.A. (Lars Albus), and S.N.; formal analysis, P.W.E.; investigation, P.W.E., L.A. (Lars Albus), S.N., and E.G.; resources, M.H.E. and W.T.; data curation, P.W.E.; writing—original draft preparation, P.W.E.; writing—review and editing, P.W.E., M.H.E., L.A. (Lars Albus), S.N., M.A., L.A. (Lolita Ammann), E.G., F.H., and W.T.; visualization, P.W.E.; supervision, M.H.E., M.A., and F.H.; project administration, M.H.E. and F.H.; funding acquisition, M.H.E., F.H. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the German Research Foundation (DFG), grant number EN 979/3-1 and the Swiss National Science Foundation (SNSF), grant number 6571210.

Acknowledgments: We thank Farnaz Faramarzi and Johanna Kaiser for their support during field work and mapping as well as Anna Mikulowska, who assisted in the lab. We especially thank the farmers and municipalities for their permission to conduct the fieldwork on their land.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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