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A multitude of bee pollinators in a phenotypic specialist - pollinator diversity from the plant's perspective

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ABSTRACT

Bilabiate flowers are phenotypically specialized and primarily pollinated by bees. However, this phenotypic specialization does not necessarily result in functional and/or ecological specialization. We use the bee-pollinated *Salvia pratensis* L. (Lamiaceae) as a model species to elucidate the number of pollinators, their fitting to the flower and their behavior in order to identify the best fitting pollinators and most capable foragers. Field observations at 12 localities between 2018 and 2023 revealed in total 37 bee species as pollinators. Based on morphometric and behavioral data, handling time per flower, number of flowers visited per minute and an index of the proportion of bee contacts with reproductive surfaces per flower visit, big and long-tongued bee species were identified as the best fitting pollinators and most capable foragers. We conclude that *S. pratensis* is a functional specialist and ecological generalist at the same time. This combination is advantageous in species assemblages with moderately specialized partners as it combines the advantages of generalization (high number of pollinator species) with those of specialization (economic pollen transfer).

1. Introduction

Plant-pollinator interactions are characterized by a conflict of interest as both partners search for the greatest benefits against the lowest costs (Howe, 1984; Waser and Price, 1983; Westerkamp, 1997). Plants need a vector to transfer pollen to other conspecific individuals and produce rewards to attract animals. Animals visit flowers to satisfy their demands, usually intake of food for their own support or their offspring and passively act as pollinators in the process (Fenster et al., 2004; Ollerton, 2021).

Given a species assemblage with several co-flowering plants and potential pollinators, different pairs of interacting partners are likely to occur. Partners range from specialists to generalists and their interaction from well-balanced mutualism to parasitism (Vogel, 1978, 1975). Specialist plants tend to have a limited number of pollinators and precise pollen transfer with low to moderate pollen loss (Cruden, 2000), whereas generalists usually do not suffer from pollinator limitation, but from imprecise pollination (Rademaker et al., 1997; Johnson and Steiner, 2000; Aigner, 2001; Waser and Ollerton, 2005; Sahli and Conner, 2006; Johnson and Harder, 2023).

Generalists and specialists are not distinct categories, but extremes of a natural continuum (Waser et al., 1996; Johnson and Steiner, 2000). To characterize the degree of floral specialization, it is, thus, helpful to define the latter in more detail. Ollerton et al. (2007) distinguished three types of specialization: 1) phenotypic specialization is the adaptation exhibited by a flower, e. g. specific floral shape, complex scents, specialist rewards, 2) functional specialization means the diversity of pollinators, i.e., different functional pollinator groups like bees, birds or butterflies, and 3) ecological specialization is the total number of pollinator species with which the respective plant species interacts.. This distinction allows to differentiate between the number of pollinator groups and the number of pollinator species that can pollinate plants with a given flower construction. Consequently, the same flower can be a specialist and a generalist depending on the perspective that is being considered. Bilabiate flowers, for instance, are phenotypic specialists excluding some of the potential local flower visitors as pollinators (Westerkamp and Claßen-Bockhoff, 2007). However, their phenotypic specialization does not necessarily lead to ecological specialization. Phenotypic specialists can be ecological generalists by combining the advantages of generalization (high number of pollinator species) with those of specialization (economic pollen transfer; Herrera, 1987, 1989; Potts et al., 2001; Kuppler et al., 2023).

Bees are the most effective pollinators of many bilabiate flowers (Westerkamp and Claßen-Bockhoff, 2007; Willmer et al., 2017). Many

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species evolved a long tongue to suck nectar from the flower base and specific structures like pinnate hairs, bristles and pollen baskets to collect pollen (Michener, 2007; Müller, 1996; Müller and Westrich, 2023). Almost all bees collect pollen and nectar for their offspring. Polylectic bees use various food plants, whereas oligolectic bees are specialized on pollen of few closely related plant families, genera or even species (Michener, 2007). The selection of food plants by bees strongly depends on the ratio of costs vs. benefits, including the distance between individual flowers, their accessibility and the amount of energy that can be gained (Dreisig, 1995; Pyke, 1980). Economy is particularly important for big bees like bumblebees that loose high amounts of energy due to thermoregulation and flying (Heinrich, 1975). For them, sucking nectar and collecting pollen at the same time might be favorable, since this saves energy (Brian, 1957; Liu et al., 1975). For an economic intake of nectar, the length of the proboscis is important, because it determines the speed and efficiency with which nectar can be ingested (Harder, 1982, 1983a). In particular, flowers with long corolla tubes can be more easily exploited by long-tongued bees compared to short-tongued bees (Benedek 1973; Benedek et al., 1973; Inouye, 1980; Balfour et al., 2013). The degree of fitting is reflected by the bee's handling time at the respective flower (Harder, 1983a), although handling-time might vary depending on the amount of reward that is present inside the flower at a given time.

Phenotypic specialization in *S. pratensis* flowers goes along with the staminal lever mechanism formed by two modified stamens. The lever is triggered by bees which insert their proboscis into the flower tube. Thereby, the fertile thecae move lower down and load pollen onto the bees' back (Claßen-Bockhoff et al., 2003; Reith et al., 2007). Although flower morphology and ecology of *Salvia pratensis* have repeatedly been investigated (e.g., Müller, 1873; Correns, 1891; Ouborg and van Treuren, 1995; Reith et al., 2007; Zhang and Claßen-Bockhoff, 2019) a comprehensive analysis considering the full range of pollinators and their implication for the pollination biology of the species is still missing. Previous studies indicate that *S. pratensis* attracts a high number of bee species (Claßen-Bockhoff et al., 2004; Reith et al., 2006). This renders the species into an interesting model to study the degree of ecological generalization in a phenotypically specialized plant species.

In the present study, we investigate the partnership among the bee-pollinated *Salvia pratensis* L. (Lamiaceae) and its pollinators. We focus on the plant's perspective of pollinator diversity (Herrera 2005), i.e., we not only count the number of pollinator species, but also consider their different body proportions, flower handling and ability to transfer pollen. We assume that the better a bee morphologically fits to the flower, the more effective it may be as a pollinator (Galen, 1989; Joly et al., 2016). However, as the relative abundance of bee species and individuals varies with season and locality, and as the competition among bees for food plants severely influences flower-bee-interactions, the best fitting pollinator may not always be present (Ott et al., 2016; Prendergast et al., 2021; Prendergast and Ollerton, 2022; Rasmussen et al., 2021). Therefore, we conducted detailed field studies in several populations to identify all pollinators, including those which were able to transfer pollen but were less abundant or less effective than the most frequent ones (Ohashi et al., 2021; Ott et al., 2016; Xiao et al., 2022). We recorded the number of pollinator species vs. visitors and characterized the pollinators as to their body proportions, foraging behavior, abundance, visitation frequency and handling time. Following the visit-centered approach (Herrera 2005), we aim to understand the interaction of the phenotypically specialized flower of *Salvia pratensis* with its diverse pollinators in an ecological context.

2. Material and methods

2.1. Study species

In the present study, we use available data of flower dimensions to compare them with the pollinators' body dimensions. Flowers are of medium size (16.81 mm ± 2.26 SD, $n = 90$, Fig. 1a, Thimm, 2008). The distance between pollen-sacs and barrier in the flower entrance, indicating the minimal length of a regular pollinator, is 10.34 mm ± 0.1 SD (Fig. 1a, Thimm 2008). Tube length is on average 9.15 mm ± 0.12 SD ($n = 42$, Fig. 1a, Zhang and Claßen-Bockhoff, 2019) and the tube contains 2.5 μl nectar (min. 0.35 to max. 4.66 μl, $n = 20$, Kradolfer and Erhardt, 1995). The width of the flower entrance ranges from 1.91 to 2.25 mm ($n = 32$) and the height of it is 1.65 mm ± 0.30 SD ($n = 40$, Fig. 1a, b, Claßen-Bockhoff, unpubl. data).

2.2. Study sites

In 2018, six populations from localities around Mainz, Germany, were investigated in detail (Table A.1). Between 2019 and 2023, additional observations were performed at the same six localities and five further localities in South-West Germany and one in North Hungary (Table A.1). Detailed pollinator observations were only conducted in 2018.

2.3. Characterization of flower visitors and pollinators

Flower visitors were observed daily from 07/05/2018 to 08/06/2018, between 9:00 am and 7:00 pm, alternating among the six localities. Total observation time was 128 h.

For the identification of bees, we used Schmid-Egger and Scheuchl (1997), Scheuchl (2000), Amiet et al. (2001, 2004, 2007, 2017) and Gokcezade et al. (2017). If necessary, bees were killed with ethyl acetate for identification in the lab using a Leica MZ8 stereo microscope. Females of *Bombus hortorum* (Linnaeus) and *B. ruderatus* (Fabricius) are extremely difficult to distinguish (Burger, 2021). We confirmed the presence of both species in the lab, but treated all individuals in the field as *Bombus hortorum* agg.. Likewise, we treated all female individuals of *Bombus terrestris* (Linnaeus) and the closely related, cryptic species of the *B. lucorum* complex as *B. terrestris* (which was confirmed by the presence of males). The identification of difficult bee species was confirmed by experts. Insect specimens are deposited in the Botanical Collections of the Johannes Gutenberg-University Mainz, Germany (www.ub.uni-mainz.de/de/sammlungen/botanische-sammlungen/4380).

We treated visitors as pollinators if they made contact with the pollen sacs or stigma of the flower (reproductive surfaces). To count the number of times a pollinator made contact with the pollen sacs (ps), stigma (s) and stigma and pollen sacs (sps), we used the smartphone app "Thing Counter" (Karuma). For each category, a button was created in the app and tapped while observing single flower visits of bee individuals.

We characterized pollinator species by quantifying abundance, visitation rate, handling time and body dimensions.

To assess the visitor abundance of the bee species, a video camera (Panasonic HC-VX989 4 K) was placed in front of a defined number of plants and open flowers. Flower visits were recorded for a total of 203 min; in addition, 95 min of video material taken with hand-held smartphones. Flower visitation was documented on 745 open flowers from 100 inflorescences and 26 plants.

In order to determine the frequency of bee visits and the handling time of bee individuals on flowers, we recorded the time of each visit and then calculated the number of flower visits per minute (FV). Handling-time (HT), defined as the time between landing on the flower and departure, was taken from video material. During the additional observations (2019–2023) visiting bees were only observed by eye; behavior was not quantified and no videos were taken.

To quantify the structural diversity of the pollinators, we measured the bees' body dimensions (Fig. 1c, d). Data were taken from at least ten individuals per species (except *Bombus pratorum* (Linnaeus): 7 individuals). The body length was measured from the tip of the abdomen to the tip of the mandibles; the body width was measured as the maximum width of the thorax (Fig. 1d). To measure the length of the

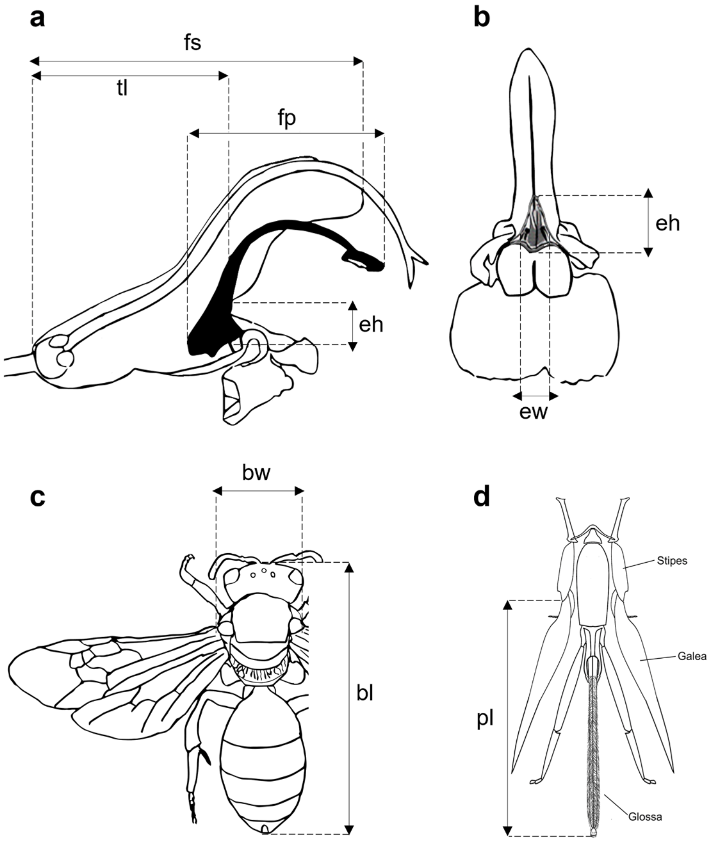

Fig. 1. Schematic drawing of measured parts of *Salvia pratensis* flowers and bee bodies. For the flowers, flower size (fs), tube length (tl), distance from flower entrance to pollen sacs (fp), flower entrance height (eh) and flower entrance width (ew) were considered and for the bees, body width (bw), body length (bl) and proboscis length (pl). a, b modified from Celep et al., 2014; d, by courtesy of Johann Neumayer (unpubl.).

proboscis, bees were cooled to 4 °C until they were unable to move. The functional unit of labial palp, galea and glossa was carefully extended with a needle which stimulated the bees to stretch out their glossa as if they would ingest nectar. The proboscis was measured from the tip of the glossa to the base of the galea (Fig. 1c).

2.4. Evaluation of pollinator fitting and foraging capability

To evaluate functional differences between pollinator species, visitation rate and effectiveness as a pollen vector need to be considered for each bee species (Johnson and Steiner, 2000).

In the present study, visitation rate was based on handling-time (HT) and number of visited flowers per minute (FV). The ease of handling is an important factor for flower choice (Harder, 1983b) and can be taken as a tentative indicator for foraging efficiency. The number of flower visits and the recorded visitor abundance reflect the abundance of a respective pollinator species at the flowers, and the FV additionally includes the movement between flowers and the speed of the movement.

Pollinator effectiveness can be measured in terms of pollen deposition on the stigma and/or seed production after a single flower visit of an individual bee (Ne'eman et al., 2010; Wilson and Thomson, 1991). This method was, however, too time-consuming in the present study for identifying and ranking the full range of pollinators. Instead, a quicker measurement that could directly quantify the observations in the field was used. We introduced a contact-index (CI) as an approximate value for the bees' ability to deposit pollen and defined it as the proportion of pollen sac (ps) and stigma (s) contacts per flower visit (f), i.e., $\mathrm{CI} = \sum (ps + s)/\sum f$. If an insect touched pollen sacs and stigma during a single visit (sps), the contact was counted one half each as ps and s, respectively. Since *S. pratensis* is protandrous and the stigma takes the position of the faded anthers in the receptive phase, sps does not negatively affect the pollination success by autogamy or stigma clogging.

Handling time and contact index are closely linked with the structural fitting of the bee's body dimensions and the flower dimensions (Harder, 1983b; Celep et al., 2014). We compared the three data sets to test for the best fitting bees. The morphologically best fitting bee is defined as a bee with the measured body dimensions closely corresponding to flower dimensions. For instance, bees with large bodies and proboscises equally long to the flower tube length trigger the lever, reach nectar and get in contact with reproductive surfaces much easier than short bodied and tongued bees. Based on all collected data, i.e., morphological fitting, handling time and contact index, we characterized the pollinator species and ranked them as potentially main or less important pollinators of *Salvia pratensis*.

2.5. Statistical analyses

To test the interdependence between the bee body dimensions, pollinator fitting and foraging behavior, the FV-, CI- and HT values were correlated with the bees' morphometric data. Normality of residuals was tested via Shapiro-Wilk tests. Depending on whether residuals were normally or non-normally distributed, Spearman rank correlation and Pearson correlation analyses were applied, respectively. We aimed to test whether a significant relationship between (1) proboscis length and speed of flower visits, (2) body width and pollen deposition, and (3) body length and pollen deposition exist. Since the bees measured and the bees observed on flowers were different individuals, we calculated the means of all variables for each bee species and subsequently correlated them against each other. We also tested for differences in HT, CI and FV among the pollinators to detect heterogeneity between species by implementing Kruskal-Wallis tests. Both analyses were performed in RStudio (Version 3.4.3). Additionally, we used Past (Version 3.20) to test for differences of the bee species' HT, CI and FV using paired Mann-Whitney-U tests incorporating the Bonferroni correction. We only included bee species with a sample size of $n \geq 10$ in the statistical analyses. Based on the differences of the HT-, CI- and FV-values from the Mann-Whitney-U tests, we searched for species groups that were not significantly different within, but to each other, regarding the values in the different categories. For each statistically different species group, ranks were established for the CI, FV and HT of each species.

To identify the best fitting pollinators and most capable foragers, the means of the combined FV and CI group ranks or FV and HT group ranks, respectively, were calculated for each species. Finally, these mean-values were rounded up and used as ranks for pollinator fitting and foraging capability.

3. Results

In total, 50 visiting insect taxa were observed foraging on *Salvia pratensis* (Table 1). Of these, 44 (88%) were polylectic bee species (or were only recorded in the male sex) falling into four families (Andrenidae (1), Apidae (19), Halictidae (9), Megachilidae (8)) and 13 genera; six taxa were ants, flies or butterflies (Table 1).

Among the visitors, 37 bee species were identified as potential pollinators, regularly touching the pollen sacs and stigma (Table 1). Four species were only observed once and not further considered and three *Hylaeus* species (Colletidae) were observed to rob pollen and nectar. This means that at least 84% of the bee species and 74% of all flower visitors were confirmed as potential pollen vectors.

Of the 22 recorded bee pollinator species in 2018, six species (27.27%), i.e., four bumble bee species, *Apis mellifera* Linnaeus and *Xylocopa violacea,* were present at all localities; four species (18.18%) appeared at four localities and only three species (13,64%) at a single locality (Table 1).

By far the most abundant visitor species was *Apis mellifera*, which showed the highest individual number at the flowers at each locality (1.82 individuals/10 min). Bumblebees were the second most abundant visitor group (1.18 individuals/10 min.) followed by small *Lasioglossum*

Table 1

Flower visitors and pollinators of *Salvia pratensis*. Bees were collected and observed from 2018 to 2023 at twelve different localities (Tab. A.1). Observations of species or sexes that were added after the sampling period in 2018 are marked in bold. Numbers for the localities refer to Table A.1.

Pollinator fitting	Species	Sex	Family	Attracting rewards	Locality	Observation Year
High	*Anthidium manicatum*	M+F	Megachilidae	Pollen and nectar	3	2018
	Anthophora aestivalis	M + F	Apidae	Pollen and nectar	5	2018–2021
	Anthophora plumipes	M+F	Apidae	Pollen and nectar	1, 5	2018, 2021
	Anthophora quadrimaculata	M+F	Apidae	Pollen and nectar	1	2018, 2021
	Bombus lapidarius	F	Apidae	Pollen and nectar	1–6, 9	2018–2020
	Bombus hortorum	F	Apidae	Pollen and nectar	1–11	2018–2020
	Bombus hypnorum	**F**	Apidae	Pollen and nectar	7	2021
	Bombus pascuorum	F	Apidae	Pollen and nectar	1–11	2018–2022
	Bombus pratorum	M+F	Apidae	Pollen and nectar	3	2018
	Bombus ruderatus	F	Apidae	Pollen and nectar	4–6, 10, 11	2018–2021
	Bombus sylvarum	F	Apidae	Pollen and nectar	1, 2, 4, 5, 9–11	2018–2021
	Bombus terrestris	F	Apidae	Pollen and nectar	1–7, 9, 10	2018–2021
	Megachile parietina	M+F	Megachilidae	Pollen and nectar	12	2022
	Xylocopa violacea	M+F	Apidae	Pollen and nectar	1–6	2018, 2021
Medium	***Andrena lathyri***	**F**	Andrenidae	Nectar	4	2023
	Apis mellifera	F	Apidae	± nectar	1–10	2018–2022
	Eucera interrupta	M	Apidae	Nectar	1, 2, 5	2018–2021
	Eucera longicornis	**M**	Apidae	Nectar	1	2021
	Eucera nigrescens	**M**	Apidae	Nectar	1	2020
	Hoplitis adunca	M	Megachilidae	Nectar	1	2018–2021
	Lasioglossum xanthopus	F	Halictidae	Pollen and nectar	1, 4–6	2018, 2021
	Megachile ericetorum	M	Megachilidae	Nectar	1	2018, 2021
	Megachile willughbiella	M+F	Megachilidae	Pollen and nectar	1	2018, 2021
	Melecta albifrons	**F**	Apidae	Nectar	7	2021
	Osmia aurulenta	M+F	Megachilidae	Pollen and nectar	1, 9, 11,12	2019–2022
	Osmia bicornis	M+F	Megachilidae	Pollen and nectar	1, 3, 7, 10	2018–2021
	Osmia caerulescens	M+F	Megachilidae	Pollen and nectar	1, 3, 4, 7	2018, 2021
Low	***Ceratina cucurbitina***	**F**	Apidae	Pollen	9	2020
	Ceratina cyanea	**F**	Apidae	Pollen	11	2021
	Halictus scabiosae	**F**	Halictidae	Nectar	1	2021
	Halictus tumulorum	**F**	Halictidae	Pollen	11	2020
	Lasioglossum interruptum	**F**	Halictidae	Pollen	1	2019
	Lasioglossum laticeps	**F**	Halictidae	Pollen	1	2021
	Lasioglossum morio	**F**	Halictidae	Pollen	2	2019–2021
	Lasioglossum pauxillum	**F**	Halictidae	Pollen	8	2020
	Lasioglossum politum	F	Halictidae	Pollen	1–7, 9, 11	2018–2021
	Lasioglossum malachurum	F	Halictidae	Pollen	5, 6	2018
Data lacking or non-pollinators	*Andrena ovatula* s. l.	M	Andrenidae	N/A	4	2018
	Bombus rupestris	F	Apidae	N/A	4	2018
	Chelostoma rapunculi	M	Megachilidae	N/A	1	2018
	Hemaris fuciformis	N/A	Sphingidae	Nectar	2	2018
	Hylaeus angustatus	**F**	Colletidae	Pollen	11	2021
	Hylaeus communis	**F**	Colletidae	Pollen	11	2021
	Hylaeus difformis	**M**	Colletidae	Nectar	11	2021
	Macroglossum stellatarum	N/A	Sphingidae	Nectar	1, 4, 5	2018
	Melitta haemorrhoidalis	M	Melittidae	N/A	1	2018
	Pieris brassicae	N/A	Pieridae	Nectar	1, 2, 4–6	2018–2020
	N/A	N/A	Bombyliidae	Nectar	1, 2, 4–6	2018
	N/A	N/A	Syrphidae	N/A	5, 6	2018
	N/A	N/A	Formicidae	Nectar	1, 2, 4, 5	2018

species (0.74 individuals/10 min). The visitor abundance of the remaining species was moderate (0.5 individuals/10 min.) to low (0.05 individuals/10 min.) and varied among localities.

3.1. Foraging behavior

Pollinating bee species differed considerably in their foraging behavior on *S. pratensis* (Fig. 2). All bumblebee species, *Anthophora* spp., *Xylocopa violacea* (Linnaeus) and some of the female megachilid bees sucked nectar and collected pollen during the same visit. Pollen was either wiped off from the back (Fig. 2a) or actively collected by pressing the abdomen against the staminal lever arm and rubbing the legs on the thecae. Occasionally, bumblebees moved to one side of the flowers so that the fertile theca was lowered down onto the scopa on the hindlegs (Fig. 2b). Female megachilid bees triggered the lever mechanism and sucked nectar, while scooping pollen onto their metasomal scopa.

Seven *Lasioglossum* species were recorded as pollinators; however, only *Lasioglossum xanthopus* (Kirby) was able to trigger the lever and reach nectar (Table 1). This species and the smaller *Lasioglossum* species that could not trigger the lever collected pollen by hanging upside down on the fertile thecae, style, or upper lip (Fig. 2j, k, l). They were mostly observed on flowers in the pollen-releasing phase, but also touched the stigma with their scopa in the receptive phase. The same behavior was documented for small *Halictus* and *Ceratina* species.

Stigma contact was achieved in various ways. In general, medium sized and large bees often made contact with the stigma either when entering or leaving the flowers.

3.2. Morphometric fitting between floral traits and pollinator bodies

Bee species differed significantly in their body dimensions (Table 2). The biggest species with a body length of almost 26 mm was *Xylocopa violacea,* followed by the *Bombus* species; the smallest was *Lasioglossum politum* (~ 6 mm; Table 2). Except for the small *Lasioglossum* species, all bees had a body length of at least 13 mm, thus fitting the length of the upper staminal lever arm and allowing pollen deposition on their back.

Body width corresponded to body length (Fig. A.1) and ranged from more than 9 mm to less than 1.6 mm (Table 2). *Bombus hortorum* agg. had the longest tongue, exceeding the flower tube length of *Salvia pratensis* by almost 5 mm. However, since the glossa is movable at the tip of the proboscis, the species was able to handle flowers easily and fast (Fig. 3). The tongues of *Xylocopa violacea* and *Bombus pascuorum* were only slightly shorter (Table 2), thus also fitting the tube length. Apart from *Lasioglossum politum*, which has a very short proboscis, the

Fig. 2. Pollinating bee species visiting *Salvia pratensis* near Mainz, Southwest-Germany in 2018. Pollen collecting behavior was observed for all *Bombus* species (a-c) as well as for the *Anthophora* species (e, d) and the *Lasioglossum* species (j-l). The flowers of *Salvia pratensis* were visited by *Bombus pascuorum* (a), *B. hortorum* (b), *B. sylvarum* (c), *Anthidium manicatum* (d), *Anthophora aestivalis* (e), *A. plumipes* (f), *Xylocopa violacea* (g), *Eucera interrupta* (h), *Osmia bicornis* (i), *Lasioglossum* spec. (j) and L. *xanthopus* (k, l) among others. Photos were kindly provided by Philipp Meyer (d) and Heike Strücker (a-c, e-l).

Table 2
Body proportions of different bee species pollinating *Salvia pratensis*. For each character, sample size (n), mean and standard deviation (SD) are given. Mean values are given in cm. Maximum values are given in bold. Colors represent the best fitting bees in descending order: green (rank 1), yellow (rank 2), blue (rank 3), red (rank 4), orange (rank 5).

	Bee species	Body-length			Body-width			Tongue-length		
		n	Mean	SD	n	Mean	SD	n	Mean	SD
🟩	*Bombus hortorum* agg.	14	19.44	± 1.60	14	6.32	± 0.26	15	**9.52**	± 1.17
🟩	*Bombus pascuorum*	10	16.75	± 1.60	10	6.10	± 0.64	12	6.67	± 0.67
🟨	*Bombus pratorum*	7	15.42	± 1.17	7	5.82	± 0.64	7	5.66	± 0.49
🟨	*Bombus sylvarum*	12	16.64	± 2.96	12	5.74	± 1.02	11	5.90	± 0.49
🟦	*Anthidium manicatum*	20	13.60	± 1.97	20	5.31	± 0.53	25	5.08	± 0.90
🟦	*Bombus lapidarius*	11	16.14	± 1.53	11	6.34	± 0.27	11	4.94	± 0.48
	Bombus terrestris	11	18.83	± 1.28	11	6.80	± 0.79	15	5.50	± 0.56
🟦	*Xylocopa violacea*	9	**25.91**	± 0.80	9	**9.27**	± 0.72	13	7.43	± 0.66
🟥	*Apis mellifera*	10	15.27	± 0.72	10	4.43	± 0.25	10	3.94	± 0.32
🟥	*Lasioglossum xanthopus*	10	13.65	± 0.47	10	3.85	± 0.15	-	-	
🟧	*Lasioglossum malachurum*	10	8.15	± 0.36	10	2.24	± 0.22	-	-	
🟧	*Lasioglossum politum*	15	5.98	± 0.56	15	1.56	± 0.24	10	1.44	± 0.16

remaining bee species were able to reach nectar, but only if they inserted their heads into the flower tubes (Table 2).

Based on the body dimensions, five bee groups with different morphological fittings were distinguished and are assigned different color codings (Table 2). The first group comprised *Bombus hortorum* agg. and *B. pascuorum* with a big body and long tongue (green). Species of the second group (*B. pratorum, B. sylvarum*) had the same body size, but a slightly shorter tongue (yellow). Group 3 consisted of bees with a long tongue (fitting to the tube length of *S. pratensis* flowers) and a very large body (*Xylocopa violacea*) or a big body size (fitting to the flower dimensions) and a shorter tongue (blue). Bee species with moderate body sizes and tongue lengths represented group 4 (red). The last group included species that were too small to regularly forage on the flowers and thus bypassed the flower construction of *S. pratensis* using a different foraging strategy (orange).

3.3. Pollinator fitting and capability of foraging

We quantified foraging behavior in 18 bee species and species aggregates, respectively (Table A.2). There were significant differences among the observed bee pollinators in the flower visits per minute (FV) (Kruskal-Wallis, $\chi^2 = 344.22$, df = 15, $p < 0.001$), contact index (CI) (Kruskal-Wallis, $\chi^2 = 135.16$; df = 15; $p < 0.001$) and handling-time (HT) (Kruskal-Wallis, $\chi^2 = 101.57$, df = 15, $p < 0.001$).

As for the FV, five groups of bees were established based on statistical differences between the bee species in the paired Mann-Whitney-U tests (Fig. 3a, Table A.2, A.3). *Bombus pascuorum* and *B. hortorum* agg. had the highest FV (Fig 2a, green) and the *Lasioglossum* species the lowest values (Fig 2a, orange).

The CI-values resulted in three significantly different groups (Fig. 3b, Table A.2, A.4). Except for *Bombus sylvarum,* the CIs of all *Bombus* species and *Anthidium manicatum* differed significantly from all other pollinators (Fig. 3b, green). The CIs of *Anthophora* spp. and *Xylocopa violacea* were the highest (Fig. 3b, Table A. 2), but their sample sizes did not suffice to include them in the analyses. The lowest CI belonged to the *Lasioglossum* species (Fig. 3b, blue).

As for the HT, six groups were distinguished based on statistical differences (Fig. 3c, Table A.2, A.5). The fastest HT belonged to *Bombus pascuorum* and *B. hortorum* agg. (Fig. 3c, green) followed by *B. sylvarum* and *Anthidium manicatum* (Fig. 3c, yellow), *Bombus lapidarius, B. terrestris, Anthophora plumipes* and *Xylocopa violacea* (Fig. 3c, blue) and *Apis mellifera, Osmia bicornis* and *O. caerulescens* (Fig. 3c, red). The last two groups included the *Lasioglossum* species (Table A.2, Fig. 3c, orange, gray).

Based on these results, *Bombus pascuorum* and *B. hortorum* agg. were considered to be the best fitting pollinators and the most capable foragers whereas the *Lasioglossum* species were the least fitting pollinators and the least capable foragers (Table 3).

3.4. Relationships between morphology and pollination

There was a significant correlation between the HT and the proboscis-length of the bee species (Fig. 4a). The relationships between the proboscis length and the FV and CI, respectively, were not significant, but the p-value of the correlation between tongue length and the FV was below 0.1 (Fig. 4d, g). Body-length and body-width were each significantly correlated to the CI (Fig. 4h, i). In contrast, there were no significant correlations between body size and FV or HT, respectively (Fig. 4b, c, e, f).

4. Discussion

The most remarkable results of the present study are (1) the identification of such a high number of potential pollinator species in a phenotypically specialized plant, (2) the diversity of pollinator behavior including active pollen collection while sucking nectar and (3) the finding that the best fitting pollinators were also the most capable foragers.

4.1. Diversity of pollinators

Even though the bilabiate flower construction of *S. pratensis* with its force-demanding staminal lever mechanism and hidden nectar clearly defines the species as a phenotypic specialist (*sensu* Ollerton et al., 2007), 37 bee species were identified as potential pollinators in the present study. This diversity is much higher than previously reported for *S. pratensis* (Claßen-Bockhoff et al., 2004; Reith et al., 2006; Westrich, 2018) and most other bee-pollinated *Salvia* species, which usually have (1-)3–8(−12) pollinators (Cairampoma et al., 2020; Celep et al., 2020; Claßen-Bockhoff et al., 2004; Ott et al., 2016; Xiao et al., 2022, 2023; Zhang et al., 2011).

However, as for pollinator diversity from the plant's perspective, the

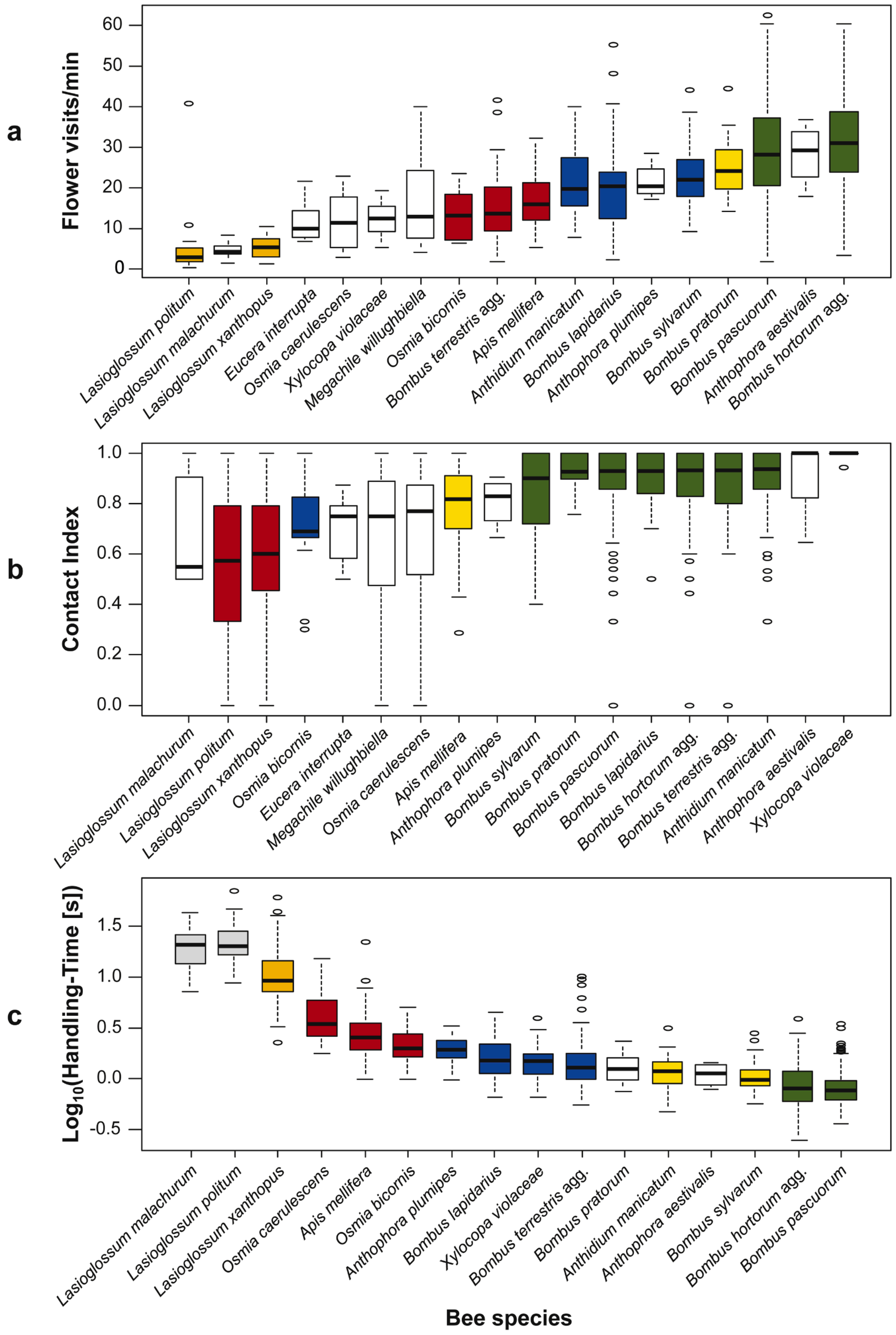

Fig. 3. Flower visits/min (a), Pollination Index (b), and handling-time (c, log-transformed) of different bee species on *Salvia pratensis*. Boxplots of bee species with a minimum sample size of 10 are colored. Colors indicate different groups of pollinators and foragers that were established based on statistical differences in pairwise Mann-Whitney-*U tests* with Bonferroni correction and correspond to best adapted to lowest adapted groups in descending order: green (group 1), yellow (group 2), blue (group 3), red (group 4), orange (group 5), gray (group 6).

number of potential pollinators appears less important than the abundance, visitation rate and specificity of the pollinator species (Herrera, 2005; Sahli and Conner, 2006). In the present study, abundance was based on video material. However, as the number of observed inflorescences and flowers was small and varied among the recordings, the data only gives a rough insight into the relative visitor abundances of the bees on *Salvia pratensis* flowers. Thus, the flower visits per minute (FV) of the observed individuals are a more reliable measure of the visitation rate of the pollinator species. Similarly, we used the contact-index (CI) and the handling time (HT) of the bees to characterize their potential

Table 3
The most capable foragers, best fitting pollinators, and morphometrically best fitting bees on *Salvia pratensis*. The capability of foraging is based on handling-time (HT) and flower visits per minute (FV), the pollinator fit on the contact index (CI), i.e., pollen sac and stigma contacts, and the FV, and the morphometric fitting on body width, body length and proboscis length with respect to the flower's proportions. Some species are not listed for all categories, as only species with a minimum sample size of 10 were included.

Rank	Foraging capability	Pollinator fitting	Morphometric fitting
1	*Bombus pascuorum* *Bombus hortorum* agg.	*Bombus pascuorum* *Bombus hortorum* agg.	*Bombus pascuorum Bombus hortorum* agg
2	*Anthidium manicatum Bombus sylvarum*	*Bombus pratorum*	*Bombus pratorum Bombus sylvarum*
3	*Bombus lapidarius*	*Anthidium manicatum* *Bombus sylvarum* *Bombus lapidarius*	*Anthidium manicatum* *Bombus lapidarius Bombus terrestris Xylocopa violacea*
4	*Bombus terrestris*	*Bombus terrestris*	*Lasioglossum xanthopus Apis mellifera*
5	*Apis mellifera* *Osmia bicornis*	*Apis mellifera Osmia bicornis*	*Lasioglossum politum* *Lasioglossum malachurum*
6	*Lasioglossum xanthopus*	*Lasioglossum xanthopus* *Lasioglossum politum*	
7	*Lasioglossum politum*		

effectiveness as pollinators. This method is not as precise as the quantitative determination of pollen deposition by single visit experiments, but can easily be quantified in the field. Usually, effectiveness is assumed to play a larger role in pollinator importance than visitation rate, but studies of particular plant species have questioned this view (Motten et al., 1981; Olsen, 1997; Sahli and Conner, 2006).

The bee species identified as potential pollinators of *Salvia pratensis* differed considerably in their abundance and foraging behavior. As for their relative importance as pollinators, four groups can be distinguished, which are discussed below.

The first group includes the *Bombus* and *Anthophora* species, *Anthidium manicatum, Megachile parietina* and *Xylocopa violacea*, which are assumed to be the main pollinators based on fitting, behavior and abundance. Their long and wide bodies perfectly matched the flower dimensions and the hairiness of the bees likely promotes pollen transfer. Within the group, *Bombus hortorum* agg. and *B. pascuorum* were the best fitting bees. They were present at all localities, had the highest flower visitation rate, shortest handling time and longest proboscis. As long-tongued bees can ingest nectar more efficiently than short-tongued bees (Balfour et al., 2013; Benedek, 1973; Harder, 1983a), these two bumble bee species also represent the most capable foragers.

The second group only includes *Apis mellifera*. Though the honey bee was the most abundant pollinator, it fit less well with to the flower dimensions, did not always contact the reproductive surfaces, handled flowers significantly slower than bumblebees, and sometimes failed to contact the lever arm due to its small body width. This finding indicates that honeybees are poor pollinators (Diller et al., 2022; Page et al., 2021; Vicens and Bosch, 2000; Westerkamp, 1991). However, from the plant's perspective, the pollen loss caused by less effective pollinators may be compensated by the high number of honey bee visits assuring some level of pollen transfer. This mechanism was shown in the Californian *Salvia apiana* (Ott et al., 2016). The phenotypically best fitting bee species,

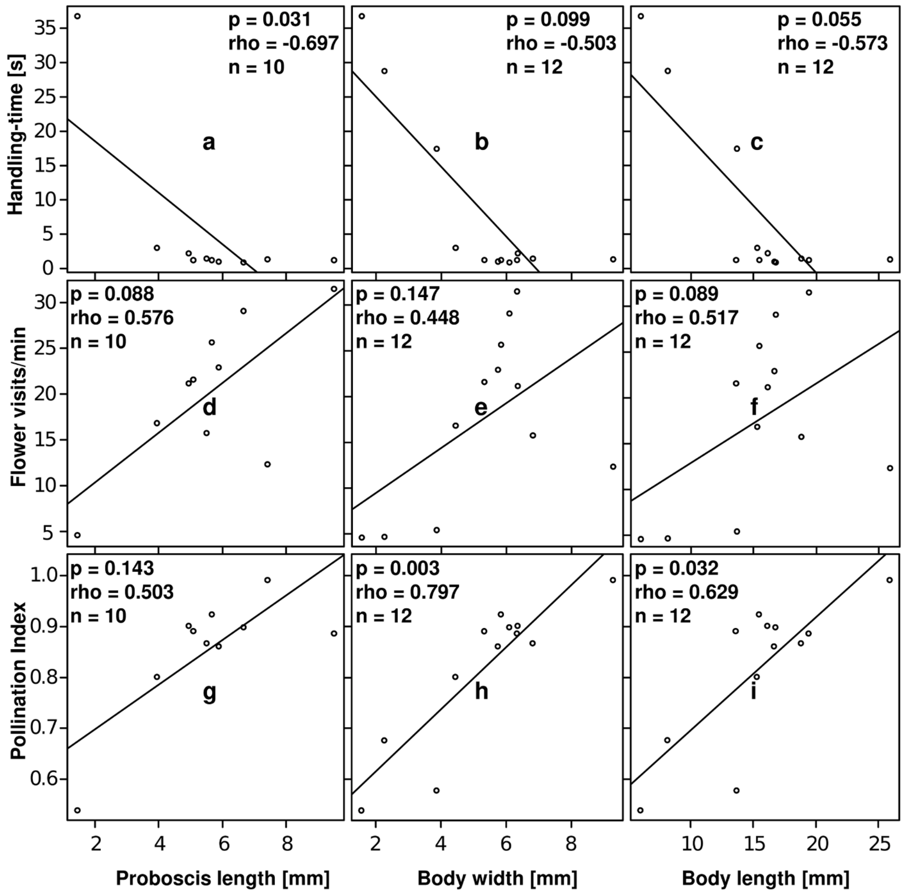

Fig. 4. Spearman correlations between handling-time, flower visits per minute and pollination index, i.e., contacts with pollen sacs and stigma per flower visit, respectively, with proboscis length (a, d, g), body width (b, e, h) and body length (c, f, i), respectively, of pollinating bees on *Salvia pratensis*. Spearman correlation coefficient (rho), *p*-values (p) and sample size (n) are given for each plot.

Xylocopa varipuncta, was very rare and contributed little to the overall pollination success of the plant, whereas the honeybee (*Apis mellifera*), though being more ineffective in pollen transfer, was the most effective pollinator due to the high number of visiting individuals. Honeybees in both California and Germany owe their high abundance to the domestication by beekeepers. Therefore, their dominance in the wild is not representative for the evolutionary history of *S. apiana* and *S. pratensis*. Nevertheless, we considered *Apis mellifera* to be an effective pollinator of *Salvia pratensis* due to its great numbers.

The third group is constituted of medium fitting bees, including most megachilid female bee species and their associated patrolling males that were able to regularly forage on the plants (Table 2). In terms of fitting, these bees turned out to be good potential pollinators, like *Apis mellifera*, but were too rare to play a significant role as pollen vectors in the populations investigated.

The fourth group is characterized by the remaining 10 bee species with lower fitting (Table 2). They bypassed the flower construction due to their small body size and were therefore less adapted to the *Salvia pratensis* flower. These *Halictus, Ceratina* and *Lasioglossum* species exclusively collected pollen, which explains their extremely long handling time. They only occasionally touched the receptive stigma. However, as these bees transfer some pollen to stigmas, they also contribute to the fitness of the plant (Barrionuevo et al., 2021; Rosas-Guerrero et al., 2014; Ohashi et al., 2021).

The present study not only illustrates that the observed bees have a different importance as pollinators based on our inferences in *Salvia pratensis*, but also that even good pollinators do not always behave in the appropriate way from the plants' perspective. In fact, imprecise pollen deposition and, most remarkably, active pollen collection occurs regularly. This highlights the need for detailed field observations to comprehensively understand flower-pollinator interactions (Herrera 2005).

4.2. *Ecological generalization within a phenotypic and functional specialist*

The diversity of bee pollinators in *Salvia pratensis* reveals that differently sized bees with different foraging behaviors can act as pollen vectors. Within the limits of the bilabiate flower construction (phentotypic specialization) and the bee-adapted floral traits (functional specialization), the broad variety of pollinators indicates that *S. pratensis* is a phenotypic and functional specialist and an ecological generalist.

In *S. pratensis,* three-fourths of all visitors were able to transfer pollen. This high number may be due to the specialization of the plant on bees as functional pollinator group, the dominance of opportunistic social bees in Europe limiting the possibilities for floral specialization (Johnson and Steiner, 2000), and the lever mechanism (Claßen-Bockhoff et al., 2003). The lower connective arms close the tube entrance of the flowers and force bees that search for nectar to push back the barrier. The force needed to release the mechanism is low (Reith et al., 2006; Thimm, 2008) and allows various bees access to nectar. As the lowering of the pollen-sacs also allows bees with a low body height to come into contact with the pollen sacs, potential nectar thieves might become pollinators. Dependent on the length of the upper lever arm relative to the bee's body length, pollen is deposited on the head, thorax or abdomen allowing differently sized bees to be loaded with pollen. The flexible response to different bee dimensions characterizes many *Salvia* species, but may be particularly distinct in *S. pratensis* . As shown in the present study, short insects are loaded with pollen on the tip of the abdomen, whereas middle-sized or long insects get pollen on their head and thorax. Thus, the upper connective length of *S. pratensis* fits to a broad range of differently sized bee species.

Pollinator species composition usually varies among populations of the same plant species (e.g., Gómez and Zamora, 1999; Thompson, 2001; Eckert, 2002), raising the question whether generalization is a species-level or population-level trait (Fox and Morrow, 1981; Herrera 2005). In *S. pratensis*, the pollinator assemblage differed among localities and seasons, but in each of the six intensively studied populations (2018) at least 10 bee species were found, seven of them being present at each locality. This points to a similar degree of generalization among populations and leads to the preliminary conclusion that the pollination system of *Salvia pratensis* may be ecologically generalized at the species level.

The only known *Salvia* species comparable to *S. pratensis* with respect to the high number of pollinator species, is *S. virgata* from Central Anatolia. Both species belong to *Salvia* subgen. *Sclarea* (Will and Claßen-Bockhoff, 2017; Kriebel et al., 2019) and closely resemble each other regarding floral traits, proportions and habitat preferences. Among the 23 documented pollinator species of *S. virgata*, three long-tongued fly species matched the flower proportions as good as bees (Celep et al., 2020, 2014). These 'melittoid' flies are functionally equivalent to bees sharing the same character syndrome (Vogel, 2012). *Salvia virgata* is thus likewise a functional specialist and ecological generalist.

Among Lamiaceae, phenotypic specialization is common due to the dominance of bilabiate flowers. However, detailed data on functional and ecological specializations are rare. Potts et al. (2001) found 34 visitors in *Satureja thymbra*, 94% of which were bees. Among these, *Bombus terrestris, Apis mellifera* and a group of 12 solitary bee-species were regarded as main pollinators. Kuppler et al. (2023) conducted a comprehensive study on the interaction of plants and wild bees in Europe and listed *Stachys recta, Ballota nigra, Thymus* spec., *Origanum vulgare, Betonica officinalis* and *Salvia pratensis* as species with a high species richness of visiting bees. An outstanding study was presented by Herrera (1987, 1989) who recorded more than 100 bee, fly and butterfly species as pollinators in a six year study on *Lavandula latifolia.* Though most pollinator species were rare, they all contributed to the plant́s fitness. Thus, it was evident, that *Lavadula latifolia* was a phenotypic specialist and a functional and ecological generalist.

5. Conclusion

Even though *Salvia pratensis* has long been known for its intriguing pollination mechanism, the present study represents the first detailed analysis considering both partners involved in the pollination mutualism. As a result, we found the species to be a phenotypic and functional specialist, but an ecological generalist.

Salvia pratensis is a perennial species, growing in medium sized populations. It has the widest distribution area of all Central European sages ranging from the Mediterranean area to southern Scandinavia and the Caucasus Mountains, and grows as a non-native species in North-America. In these areas, bees are the main pollinators and present in a multitude of species (Michener 2007). Adapted to bees, but not closely adapted to a certain sub-group of them, *S. pratensis* combines the pros and cons of specialization and generalization. The species can find pollinators everywhere. If the main pollinators are lacking, rarer, or less effective, bees may assure pollen transfer. This flexibility is particularly important in widely distributed species as geographical turnover of the pollinator fauna is likely to occur.

Within the limits of phenotypic and functional constraints, some pollinators fit better to a given flower than others. As the best fitting promises the highest net-gain of energy, these partners will likely preferentially interact with each other. This may explain, that the best fitting bees also forage most efficiently as found in the present study.

Interactions such as those reported here should be expected in species communities with only moderately specialized partners. Both *S. pratensis* and its pollinating bees are opportunistic in terms of pollinators and food plants (Westrich, 2018). This is ecologically advantageous because no partner will suffer from an absence of particular partners and, thus, will be able to survive at many localities.

CRediT authorship contribution statement

Noel Silló: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Regine Claßen-Bockhoff:** Conceptualization, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2024.152461.

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