

Deliverable D1.3

Resource quality and forage selection

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Abbreviations, Participant short names

Abbreviations

- P:L Protein:Lipid
- K:Na Potassium:Sodium

Participant short names

AU	Aarhus Universitet				
COA	Co-Actions				
IPB	Instituto Politécnico de Bragança				
IRIAF	Instituto Regional de Investigación y Desarrollo Agroalimentario y Forestal de Castilla-La Mancha				
IZSLT	Istituto Zooprofilattico Sperimentale delle Regioni Lazio e Toscana				
KUL	Katholieke Universiteit Leuven				
MLU	Martin-Luther-Universität Halle-Wittenberg				
NB	Norges Birokterlag Forening [Non-governmental organisation				
SCIPROM	SCIPROM Sàrl				
TNTU	The Nottingham Trent University				
UCOI	Universidade de Coimbra				
UGENT	Universiteit Gent				
UJAG	Uniwersytet Jagiellonski				
UM	Université de Montpellier				
USAMV	Universitatea de Științe Agricole și Medicină Veterinară Cluj-Napoca				
υυ	Uppsala Universitet				
VDSJ	Van Der Steen Joseph				
WR	Stichting Wageningen Research				



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- Figure 2: Image retrieved from Vaudo et al., 2024 (doi.org/10.1073/pnas.2317228120): Conceptual framework for considering bee nutritional niches and pollen foraging behaviour. Plants' positions in space represent their pollen protein and lipid concentrations and lines connecting them to the origin represent their protein:lipid (P:L) ratios. Target symbols represent hypothetical nutritional intake targets for different bee species. Direction and colour of arrows illustrate how bees might use different foraging strategies while sharing similar resources to balance their diet to reach different nutritional intake targets: 1) foraging from a single plant species offering rewards close to the intake target, 2) foraging equally from nutritionally complementary resources close to an intake target, 3) foraging among all plants in the nutritional landscape at varying frequencies to balance their diet to reach a target.
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Table 1: Number of plant-pollinator interactions extracted from databases and literature. The number of individual plant species was obtained by removing all the duplicates in the data. This final dataset (individual species) was compared with the 408 ALMaSS plant species. Most pollinators, except the honey bee, visit less than half of the species coded into ALMaSS.

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Summary

This deliverable describes the data collection strategies and outputs related to the BETTER-B work on 'Pollinator Ecology'. This work has two main goals:

- To develop models to predict landscape-specific pollinator carrying capacities based on pollen and nectar phenology models, taking local context into consideration but creating European-wide coverage;
- To provide a management tool for landscape-level management of honey bee density to foster resilient beekeeping taking into account resource availability that mediates competition with wild pollinators.

To achieve these goals, we needed to deepen our knowledge on the available resources for pollinators and to better understand what drives these pollinators to visit certain flowers. Therefore, in these tasks, we have focused on the resource's quality and forage selection for honey bees, bumble bees and solitary bees. Two literature reviews were performed:

- Literature searches on flowering phenology data, floral density and pollen and nectar production data, conducted in national languages and focusing on existing data gaps identified in B-GOOD;
- Literature searches on plant-pollinator interactions and on pollen composition, as well as the drivers that affect pollinators choices (e.g., honey bees, bumblebees and solitary bees).

The first literature review was coordinated by the Jagiellonian University in Kraków, Poland (UJAG), and carried out by 15 consortium partners: UGENT, WR, MLU, AU, UCOI, UU, USAMV, IRIAF, IZSLT, NB, COA and UM. The second literature review was conducted by the Coimbra University, Portugal (UCOI) with the support of UJAG and AU.

This report first provides a brief overview of the background and framework for modelling of floral resources for different groups of pollinators, followed by presentation of the literature review outputs.

1. Background and framework for modelling of floral resources

The aim of WP1 is to develop models for predicting landscape-specific pollinator carrying capacities based on floral resource models, taking into account the local context, but with European coverage. The first floral resource models were developed within the B-GOOD Horizon 2020 project. The framework integrates data on the amount of pollen, nectar and sugars produced by a single flower/inflorescence of a given plant species with information on flower/inflorescence abundance (i.e. density of flowers/inflorescences per unit area), flowering phenology, plant composition of the flora/habitat and flora/habitat composition and configuration within the ecosystem/landscape. This approach enables the spatio-temporal availability of floral resources to be predicted within different flora/habitat types and across different ecosystems/landscapes. The literature review on floral resource traits (flowering phenology, floral density and floral resource production) was conducted within the B-GOOD project to support the development of floral resource models (Filipiak et al., 2022a).

The floral resource models were implemented in the landscape simulation that is part of the Animal Landscape and Man Simulation System (ALMaSS; Topping, 2022, Topping et al., 2024). ALMaSS is a system of spatially explicit agent-based/subpopulation-based models with a landscape simulation model for use in predicting the effects of human landscape management on a range of key animal species, including pollinators. Currently, ALMaSS includes models for the honey bee (ApisRAM), and solitary bee Osmia bicornis. In addition, it has been proposed to develop models to represent hoverflies and butterflies, given their paramount importance for pollination services as well as for Bombus terrestris. These new models, for Eristalis tenax and Sphaerophoria scripta (hoverflies), and Noctua pronuba and Pieris napi (butterflies), are being developed as part of the ongoing PollinERA Horizon Europe project (Topping et al., 2024).

The model species in ALMaSS utilize the dynamic landscape simulation capturing both spatial and temporal landscape heterogeneity. The spatial component is represented by a detailed land cover / land use map, and the temporal component allows landscape elements properties to change with a temporal resolution of one day. These include daily changes in vegetation height, green and total biomass and floral resources in response to weather conditions and agricultural management. The proper modelling of floral resources is especially crucial for pollinator model species. The floral resource models developed in B-GOOD will be improved and extended in Better-B to provide more realistic predictions of floral resources. This includes the application of advanced models for predicting flowering phenology (Task 1.1), increasing the data inputs (by filling in data gaps identified in B-GOOD), and including the pollen quality and choice assessment (Task 1.2). Specifically, within Task 1.2, we aim to identify the factors that influence pollinator choices for pollen collection and establish a semi-quantitative scale to measure these preferences. This will feed into Task 1.1, which focuses on modelling the floral resources available to different groups of pollinators, and support agent-based models of representative pollinator species within the ALMaSS modelling framework. The data on flowering phenology and pollinator-plant interactions gathered using the citizen science approach in Task 1.3 will be used to validate the models generated in Task 1.1. This will improve the modelling of the interactions between the model pollinators and the dynamic landscape, producing foraging patterns that closely resemble reality.

The results of Task 1.1 and Task 1.2 will be combined to create a simulation-based decision-support model using the ALMaSS framework (Task 1.4), which will be used to identify critical landscape and time-specific points when pollinator forage is limiting, leading to competition both among honey bee colonies and between honey bees and wild bees.



2. Literature survey on flowering phenology, floral density and floral resource production (Lead: UJAG)

The database of floral resource traits (flowering phenology, floral density and floral resource production) developed within the B-GOOD project and published by Filipiak et al. (2022a) pointed out to knowledge gaps related to floral resource traits of plants important for pollinators. It also clearly showed that some European countries were over-represented, while others were under-represented in this respect. One of the possible reasons for this was the authors' limited access to literature published in local European languages. Therefore, within task 1.1 we aimed to overcome these limitations and collect data on floral resource traits from the published and grey literature in national languages to (i) complement existing databases and (ii) to be able to identify the real knowledge gaps and drive further research.

The literature surveys in national languages were carried out by 15 consortium partners: Ugent, WR, MLU, AU, UCOI, UU, USAMV, IRIAF, IZSLT, NB, Co-Actions and UM; in 12 languages: Danish, Dutch, French, German, Greek, Italian, Norwegian Bokmål, Portuguese, Romanian, Spanish and Swedish. In addition, local data published in English and not included in the Filipiak et al. (2022a) database were also included. The following search strategies were used:

- own data and/or knowledge in others' data,
- searching Google, Google Scholar, Scopus, Web of Science, national libraries, government agencies, local websites and repositories, using the translation of keywords used by Filipiak et al. (2022a) into local languages,
- asking local researchers publishing in the field for any published studies or grey literature,
- searching books dedicated to the topic and published in local languages.

The final data collection contains 2382 records for 1132 plant species from 113 families. Most of the data collected is on flowering phenology, with a relatively large amount of data on nectar/sugar production and less on pollen production and floral density (1474, 1141, 325 and 152 records respectively).

The details of methodology and results were described in the manuscript "Reviewing published and grey literature in local European languages to supplement existing databases on floral resource traits" (5.2 Supplementary material), which was accepted for publication in the Ecological Solutions and Evidence journal in May 2025. In addition, each of the partners involved in the literature survey, prepared a work summary document indicating the searching methodology, and workload. These documents were collected by UJAG and are available on request.



3. Literature survey on pollen quality and choice for different pollinators (Lead: UCOI)

An extensive literature review was carried out to support the identification of the factors that influence pollinator choices for pollen collection, and a semi-quantitative scale was created to measure these preferences.

The work was divided into several steps:

- Defining model pollinator species and a list of plant species for which interactions will be studied.
- Defining a strategy to determine which factors influence pollinator pollen choice.
- Conducting a literature review according to the strategy.
- Creating a database of plant species and the level of preference for each pollinator species.

3.1 Defining model pollinator and plant species

The pollen quality and preference data will be used in ALMaSS to improve the prediction of plant-pollinator interactions. Therefore, the list of pollinators (Figure 1) explored for this deliverable includes those already present in the system (Apis mellifera and Osmia bicornis) as well as those for which models are under development (Bombus terrestris, Eristalis tenax, Sphaerophoria scripta, Noctua pronuba and Pieris napi). Similarly, priority was given to plant species that are already modelled in the system (5.1 Supplementary material). These include 408 plant species, belonging to 221 genera and 67 families.



Figure 1: Pollinator species already modelled in ALMaSS, (A) *Apis mellifera* and (B) *Osmia bicornis* as well as the ones under development, (C) *Bombus terrestris*, (D) Eristalis tenax, (E) *Sphaerophoria scripta*, (F) *Noctua pronuba* and (G) *Pieris napi*.

3.2 Strategy to set pollen preferences

Insect pollinators have co-evolved with plant species (i.e., angiosperm flowers) in a dynamic process in which plants and their pollinators mutually influence each other's evolution (Leonhardt et al., 2024). This complex relationship has led to the evolution of specialised traits and behaviours in both plants and pollinators that enhance their mutual survival and reproductive success: plants benefit from pollen transfer (leading to fertilisation and seed production), and pollinators benefit from food sources such as nectar and pollen. These interactions are therefore strongly driven by their characteristics and nutritional needs, resulting in a heterogeneous geographical distribution of plants and pollinators.

Pollinator choice is influenced by climatic factors, flowering periods, and floral diversity and abundance. To address this complexity, it is therefore necessary to move beyond system-specific studies (Mitchell et al., 2009) by implementing modelling approaches. One of the most complex challenges in modelling insect



pollinators is modelling their interaction with the landscape and with each other. To study this complexity, researchers create pollination networks, which take into account the level of interaction between a pollinator and a plant species. However, extrapolation of these networks to different ecological scenarios is not encouraged because networks are usually context-dependent. To use context-dependent data for modelling purposes, it is necessary to understand the mechanisms behind these interactions.

The most common approaches to explain plant-pollinator interactions are the plant-pollinator phenological, morphological, and physiological traits relatedness (e.g., corolla tube and tongue size; Naghiloo et al., 2021, Cappellari et al., 2022, Adedoja & Mallinger, 2024) or the amount of the reward (e.g., nectar and/or pollen amount; Prasifka et al., 2018). More recently, the nutritional role of the reward (mainly for pollen) has also been used to understand these interactions (Vaudo et al., 2016, Vaudo et al., 2020a, Lan et al., 2021; Leonhardt et al., 2024) by exploring two concepts from nutritional ecology: the nutritional geometric framework and ecological stoichiometry. Therefore, the strategy to set pollen preferences will be based on the plant-pollinator interactions and nutritional ecology.

A plant-pollinator interaction refers to the relationship between flowering plants and pollinators over time and space and reveals patterns of interactions from the individual to the community level, and how these patterns change at different spatial and temporal scales. To remove the influence of context from several interaction studies, interactions can be classified on a presence/absence scale. If a pollinator has ever been seen visiting a plant, it is assumed that the pollinator has some preference (use) for that particular plant species. If there is no evidence of plant-pollinator interaction, it is assumed that the pollinator does not interact with that plant species.

The nutritional geometric framework is a conceptual and analytical approach used to explore how the nutritional role of the reward is correlated with the species preferences. The framework analyses how species balance intake of multiple nutrients to optimize fitness (intake target). This means mapping the intake of different nutrients, such as proteins and lipids, onto a multidimensional space. Within this space, the dietary requirements and limitations of an organism are represented, and various combinations of nutrient intakes can be plotted to study their effects on the organism's health, behaviour, and survival. Essentially, the 'intake targets' can be reached if the species has appropriate foods available. Foods are presented as radials, in the nutrient space, extending outwards from the origin at an angle defined by the ratio of nutrients found in each food (Figure 2). A nutritionally balanced food is one where the radial intersects the intake target, allowing the animal to move directly to its target, thus meeting its multiple nutritional requirements simultaneously (Figure 2, bee number 1). Nutritionally imbalanced foods do not intersect the target and force the animal to trade-off eating too little of some nutrients for too much of others relative to the intake target, with physiological consequences and potential health costs. Nutritionally complementary foods are those that, although individually nutritionally imbalanced, can be mixed to reach the intake target by virtue of their rails jointly subtending an angle in nutrient space that contains the target (Figure 2, bees 2 and 3; Simpson et al. 2017, Vaudo et al., 2024).



Figure 2: Image retrieved from Vaudo et al., 2024 (doi.org/10.1073/pnas.2317228120): Conceptual framework for considering bee nutritional niches and pollen foraging behaviour. Plants' positions in space represent their pollen protein and lipid concentrations and lines connecting them to the origin represent their protein:lipid (P:L) ratios. Target symbols represent hypothetical nutritional intake targets for different bee species. Direction and colour of arrows illustrate how bees might use different foraging strategies while sharing similar resources to balance their diet to reach different nutritional intake targets: 1) foraging from a single plant species offering rewards close to the intake target, 2) foraging equally from nutritionally complementary resources close to an intake target, 3) foraging among all plants in the nutritional landscape at varying frequencies to balance their diet to reach a target.

Ecological stoichiometry is the study of the balance of energy and multiple chemical elements in ecological interactions with trophic relations (Persson et al., 2010). This research framework considers how nutritional requirements for basic body-building blocks shape the ecology of organisms and ecosystems (Filipiak et al., 2023). Thus, as in the nutritional geometric framework, an organism has specific nutritional needs to obtain the necessary building blocks for a healthy development. By feeding on certain types of pollen, a pollinator can guarantee the exact elements (proportions of all the atoms that make up the organism's body) that it needs for its development, or, in the case of unbalanced diets, there are physiological trade-offs that affect the distribution of the required elements. Therefore, each species has its own stoichiometric balanced diet and when feeding on unbalanced pollen diets there will be energetic trade-offs to acquire stoichiometrically limited molecules. "Discrepancies between the stoichiometry of food and that of the consumer's body result in high physiological effort of the consumer to absorb nutrients in the necessary proportions, leading to costs such as prolonged development time or decreased body size" (Filipiak & Filipiak, 2022).

For both above mentioned concepts, several macro and micro nutrients can be considered in bee pollen: protein, amino-acids, lipids, sterols, minerals, or even their ratios. These are described below.



Protein

The amount of protein in angiosperm pollen ranges from 2.5 to 60%, but insects do not use a fixed percentage of protein. The percentage of protein ingested changes with the season and, therefore, with the frequency of the flowering of pollen-bearing plants. Insects' protein intake can change not only because of their metabolic needs and genetic background, but also because of their need to adapt to environmental conditions. In honey bees, for example, a higher level of protein abundance has been found in summer bees compared to winter bees (Ward et al., 2022). At the same time, spring pollen has a higher protein level than autumn pollen (DeGrandi-Hoffman et al., 2018), and bees feeding on spring pollen will have higher hypopharyngeal gland development as well as higher gene expression levels. However, as indicated by DeGrandi-Hoffman, et al. (2021), these can differ between colonies, showing that the genetic factors (different queen lines) can influence the use and effects of protein levels in pollen. On the other hand, protein level alone as an indicator of pollen quality can be misleading, as higher protein content does not always mean higher amino acid content. For example, pollen mixtures with the same amount of protein (421 and $425 \,\mu g/mg$ of proteins in spring and autumn samples, respectively) tested by DeGrandi-Hoffman et al. (2018), contained different amino acids. Spring samples had more amino acids such as tryptophan, valine, isoleucine, serine, asparagine and glutamine; while autumn ones were poorer in proline and hydroxyproline (DeGrandi-Hoffman et al., 2018). Therefore, amino acid content could also be valuable to assess the level of pollen quality.

Amino acids

Only 20 amino acids are encoded for the process of translation and integration into proteins. Ten of these proteinogenic amino acids are essential for honey bees (and probably other pollinators) because they cannot be synthesized by the bees themselves: methionine, arginine, tryptophan, lysine, isoleucine, phenylalanine, histidine, valine, leucine, and threonine (DeGroot, 1953). Some of these amino acids are available for direct use by the bees' metabolic system (water-soluble), while others are protein-bound amino acids, which require the organism to expend energy to 'release' the amino acids. Forcing honey bees to feed on a diet deficient in essential amino acids can negatively affect their foraging patterns and colony growth (Bonoan et al., 2019). Furthermore, even the non-essential amino acids can help in their development: by adding non-essential amino acids (proline and glutamic acid) to honey bee syrup, Noor-ul-Ane & Jung (2022) showed a reduction in brood development time and increased larvae survival. Despite the role of amino acids, there are only a few studies showing that insect pollinators can discriminate between different amino acids in pollen (e.g., Cook et al., 2003; Linander et al., 2012). Bees have shown the ability to recognize their presence but correlation between amino acid content and bee preference has not been confirmed (e.g., Ruedenauer et al., 2019, Ruedenauer et al., 2021).

Fatty acids

The nutritional value of pollen also depends on the content of saturated and unsaturated fatty acids. The total lipid content of pollen varies from 3 to 20% of its dry weight. Fatty acids are essential nutrients for the development and cognition of pollinators. For example, omega-3 and omega-6 fatty acids are essential for honey bees and must be ingested (mostly through pollen). The presence of 74 fatty acids has already been discovered in the bee pollen (Ruedenauer et al., 2021). It has been shown that an excess of fatty acids in pollen can lead Bombus terrestris to avoid its consumption (Ruedenauer et al., 2019), but the presence of oleic acid enhances their learning performance and survival (Muth et al., 2018). Nevertheless, there are no studies that only consider the amount and/or diversity of fatty acids to guide pollinator decisions. On the other hand, the presence of fatty acids has been identified as an important macronutrient for bee choice when protein content is also considered (Vaudo et al., 2020a).

Sterols

Sterols are key components in the production of hormones that control development and can also be found in cell membranes. These components cannot be synthesized by insects, so they must be ingested. The most abundant phytosterols in all plant species are 24-methylenecholesterol, $\Delta 5$ - avenasterol (= isofucosterol) and



 β -sitosterol. These sterols are essential for bumble bee development (Vanderplanck et al., 2014) and honey bees increase their longevity when supplemented with 24-methylenecholesterol (Herbert et al., 1980). On the other hand, stingless bees have been shown to prefer other sterols (e.g., Ferreira-Caliman et al., 2012). Zu et al. (2021) examined the sterol profiles of pollen from 122 plant species belonging to 51 families but only tested whether their presence/abundance was associated with pollinator guilds, not within different bee species. Therefore, it is unknown how sterol diversity and abundance may influence pollinator choice.

Protein to Lipid (P:L) ratio

As insect pollinators undoubtedly forage for pollen to meet both their protein and lipid needs, both macronutrients can be considered together as possible drivers of bee foraging preferences. This was the basis for the studies conducted by Vaudo et al. (2016, 2020, 2024) to assess the preferences of different bee species. A major advantage of this approach, in addition to the use of two macronutrients, lies in the methods used to analyse the pollen composition. If different methods are used to measure protein or lipid content (including the collection method), the comparison of results can be misleading. If pollen is dried before the analysis, the macronutrients content will be higher (more concentrated). On the other hand, their P:L ratio will be similar because both protein and lipid levels will increase equally. The same logic can be applied to pollen collected by bees (which also contain some nectar). Interestingly, the P:L ratio of pollen has a low variability within plant families and most of the plant species and families fall within P:L ratios below 3:1 (Vaudo et al., 2020a). The P:L ratio was initially employed to evaluate the preferences of Bombus spp. (Vaudo et al., 2016). Subsequently, the P:L ratio of at least 80 plant species and the foraging preferences of three bee species were evaluated. This demonstrated that different bee species have different P:L ratio requirements (Apis mellifera: 1:1 and 2:1 P:L; Bombus impatiens: 4:1 P:L; Osmia cornifrons: 2.9 P:L; Vaudo et al., 2020a). More recently, Vaudo et al. (2024) published one of the most comprehensive databases on interactions between wild bees, taking into account their P:L ratios, once again demonstrating the usefulness of this ratio in determining pollen preferences. Thus, the P:L ratio has been shown to be a useful measure to evaluate pollen quality and to guide bee choice.

Minerals

The most common elements (minerals) found in bee pollen are Phosphorous (2.3–5.1 g/kg), Potassium (2.3– 4.9 g/kg), Calcium (0.58–2.8 g/kg), Magnesium (0.36–1.3 g/kg), and Sodium (0.082–0.612 g/kg) (Valverde et al., 2023). Several other microelements are present, but in lower concentrations (see Valverde et al., 2023). Sodium (Na) is a key nutrient (building-block) for pollinators, and pollinators have shown a preference for food with higher Na concentrations (VanValkenburg et al., 2024). Insects even regulate their Na intake by drinking animal secreta or by performing cannibalistic behaviour (Kaspari, 2020; Cairns et al., 2021). These behaviours considered to be complementary mechanisms to the Na obtained from pollen. Since plants' Na metabolic function is minor, the concentration of Na in plant tissues is low. Therefore, in order to access the desired Na, pollinators need to ingest other elements, resulting in an unbalanced diet. For example, stingless bees have shown avoidance of nectar solutions with higher K concentrations (Afik et al., 2014), but honey bees show no preference for nectar with high Na, K or other nutrients. The K:Na ratio on the other hand has indeed been shown to drive honey bees' preferences (Cairns et al., 2021). Considering that Na and K are physiologically linked as they are jointly involved in fundamental physiological processes (Kaspari, 2020), the K:Na ratio is therefore a better indicator of pollen quality than the Na or K concentration alone (Filipiak et al., 2023). Furthermore, it appears that the K:Na ratio of pollen does not change even if the soil is fertilized with extra Na (Filipiak et al., 2022b). Recently, this ratio has been explored to understand bee ecology and evolution by considering bee diet, as K and Na concentrations alone do not encompass the complexity of the ecophysiology of organisms (see Filipiak et al., 2023).

Nutritional endpoints selected to set pollen preferences

Considering the strong evidence between the P:L and the K:Na ratios towards pollinators choices, these two endpoints were selected to set the pollinators preferences alongside the plant-pollinator interactions data. For P:L, the preference was set according to the reported values from the literature for each pollinator. As for K:Na ratio, it was considered that a higher ratio is detrimental to the organisms and therefore pollinators



prefer to avoid this pollen. Pollen with a lower K:Na ratio will be considered beneficial to pollinators and therefore these pollen types will be preferred. However, this classification is only applied to the plant species with which these pollinators interact.

A semi-quantitative scale (from 0 to 3) was created based on these premisses. Each pollinator has a set of plants that will interact with, ignoring the other plant species modelled into the system, and will "prefer" to interact with certain plant species in detriment of others (for pollen collection) according to the preference score. Therefore, this approach will ultimately create a dynamic interaction with the landscape, which will change according to the plant species present on it.

The scale will be applied in a stepwise approach:

- 1. Plant-pollinator interactions will set the baseline for the pollen preference. If a pollinator has never interacted with the plant species, a preference score of 0 is set and no further analysis is performed. If a pollinator interacts with a particular plant species, a score of 1 is assigned.
- 2. The P:L ratio is then applied according to the literature data on pollinator preferences. If the P:L ratio is within the range of pollinator preferences, a score of 1 is added and the plant species will have a higher preference value (2). If not, it retains the same score as before (1).
- 3. The minerals content is then used by giving preference to lower K:Na ratios. Taking into account the plant species visited by the pollinator (point 1), and that bees prefer to visit plants with a lower K:Na ratio, plant species with K:Na ratio lower than the mean are given a score of 1. Plant species with higher than the mean K:Na ratio do not receive any score. In the end, each plant species can have a score from 0 to 3, which determines the level of preference of the pollinator: 0 = no interaction, 1 = poorly preferred, 2 = moderately preferred and 3 = Strongly preferred.

When data on pollinator-plant interactions at the plant species level are scarce, data at the plant genus level will be considered. Since interactions can also be driven by palynological studies of pollen samples collected from bee's nests, if the data indicates the pollen type, this will only be considered if it belongs to a particular species or genus. If the pollen type belongs to a family, it will not be considered to obtain a possible interaction. For the nutritional content of pollen (P:L and K:Na ratios), if there is no data at the species level, data at genus or family level will be applied.

This strategy will be applied to the already modelled bee species and for Bombus terrestris. On the other hand, only the interaction data (step 1) will be considered for the other pollinators since these species do not collect pollen to feed their larva. Butterflies do not actively eat pollen as a primary food source, although they may occasionally come into contact with it while feeding on nectar. Hoverfly species, especially females, consume pollen as a protein source necessary for sexual maturation and egg development. Pollen provides essential amino acids that support oogenesis, making floral resources critical for reproductive success (Gilbert, 1981; Haslett, 1989). Selection of flowers for pollen in hoverflies is influenced by a combination of factors, including hoverfly morphological traits (e.g., proboscis length), flower traits (mainly colour) and nutritional content. No studies are, however, available exploring how the nutritional content of pollen can drive hoverfly's preferences. In the future, other metrics (e.g., flower colour, pollen accessibility) will be explored to drive the preferences for these species.

3.3 Literature review and obtained data

The literature review was divided into two categories: plant-pollinator interactions and pollen quality.

3.3.1 Plant-Pollinator Interactions

In order to carry out such an analysis, databases on plant-pollinator interactions were searched: Database of Pollinator Interactions (DoPI) and the Global Bee Interaction Data (GloBI). Additional information was obtained from scientific publications, mainly for species with a low number of records in the database (all the species except Apis mellifera and Bombus terrestris). To conduct that search, a search string was created for each pollinator, following the same rationale:



Search in the "tittle, abstract and keywords" for "Species name" OR "common name" AND "pollen" OR "preference" OR "interaction"

Example: TITLE-ABS-KEY ("Sphaerophoria scripta" OR "S. scripta" OR "long hoverfly" AND pollen* OR preference* OR interaction*)

Considering that the output of this analysis was the presence/absence of interactions, the duplication of information (from scientific publications and databases) was not considered a limitation for the data analysis.

3.3.2 Nutritional content of pollen

For the nutritional approach, considering both the nutritional geometric framework and the stoichiometric balance, an intensive literature search was conducted to develop a database on pollen composition. A systematic review, based on the PICO model (PICO stands for patient/population, intervention, comparison and outcomes) was conducted. First, a search string was created based on the research question (focus on pollen composition of plant species). Three different databases (SCOPUS, WEB OF SCIENCE, and PUBMED) were searched to access most of the available data. All study titles and abstracts were extracted, and duplicates were removed/merged using the Rayyan software (rayyan.ai). This software was also used for abstract and full text screening. All papers were assessed, and the inclusion/exclusion criteria were implemented, first for abstract screening and later for full text screening.

Inclusion criteria for abstract screening: 1. Publication in English; 2. The study is about the pollen composition (fatty acids, proteins, etc.) of plant species.

Inclusion criteria for full-text screening: 1. Full-text is available; 2. It has information about the collection method; 3. It has information about the sample's storage; 4. It has information about the analytical method.

After full-text screening, data was retrieved, giving priority to review studies in which there is already accumulated information on the subject.

Search: SCOPUS; WEB OF SCIENCE; PUBMED (26/03/2024 and repeated on 07/10/2024)

Filters: Pollen* AND protein* OR lipid* OR sodium OR potassium OR nutri* OR mineral* OR vitamin* OR "plant secondary metabolite*" OR element* OR nitrogen OR "total phenolic compound*" OR carbohydrate* OR sterol* OR starch* OR fat OR "fatty acid*" OR "amino acid*" AND "honey bee*" OR honeybee* OR bombus OR bumblebee* OR "bumble bee*" OR dry OR frozen OR dried OR fresh OR osmia OR flower* OR pollinator* OR bee OR "wild bee*" OR anther* AND occurrence OR concentration* OR quanti* OR level* OR presence OR amount OR value OR ratio* OR distribution OR content OR composition

A total number of 15,318 papers were extracted, which were reduced to 230 after abstract screening. From those, 168 papers had relevant data on nutritional content of pollen and were considered after full-text screening. Furthermore, experts in the field of nutritional ecology, who have performed chemical analysis on monofloral pollen samples, were contacted to share additional data. Previously unpublished data on the nutritional content of 336 plant species were shared under a confidentiality agreement. Therefore, this data was used to calculate the pollinator preferences based on the adopted strategy (score attribution), but it is not available until being published by the original authors. Such data sharing has allowed to fill data-gaps and improve the reliability of preference scoring.

The nutritional values were extracted from the papers that were selected after the abstract and full-text screening phases. Nevertheless, to avoid over/under representations of these nutrients due to methodological issues, only the studies that measured lipids and protein, or potassium and sodium, in the same sample were considered. This ruling has diminished the available dataset, but it increases its robustness and reliability. Considering that most of the studies reporting P:L and K:Na ratios are from the last 5 years, and there is a substantial increase in interest in nutritional ecology to study pollinators behaviour, it is expected that more studies will be available in the next few years and this database will be updated.



3.4 Results

3.4.1 Plant-pollinator interactions

The number of recorded interactions varies strongly between pollinators (Table 1). Apis mellifera and B. terrestris have the highest number of registered plant-pollinator interactions, with a total of 798,730 and 48,972 interactions, respectively. From these interactions, Apis mellifera visits almost 4 times more different species than B. terrestris. This is expected considering the ubiquitous distribution of this species, as well as humans' familiarity with it, since many of these interactions are obtained by citizen-science collaborations. High number of records were also found for hoverflies (Table 1), especially for S. scripta. This species has, however, a less generalist behaviour than the other hoverfly, E. tenax, which visits approximately 2.5 times more individual plant species than S. scripta. This was expected, considering the worldwide distribution of E. tenax. On the other hand, O. bicornis distribution is constricted to Europe, Northern Africa and western Asia, leading to less plant-pollinator records than for S. scripta. Interestingly, O. bicornis visits more individual plant species of the same genus, which could lead to an underrepresentation of plant-pollinator records. From the studied Lepidoptera species, a low number of records was found for P. napi, and only 10 records were found for N. pronuba. This low number of records can only be justified by the species nocturnal behaviour.

There are 408 plant species coded in ALMaSS, and while honey bees interact with 230 of these species (approximately 56%), some pollinators only interact with less than 2% (N. pronuba). The level of interactions also varies within the different plant families, demonstrating the plant-pollinator preferences (Figure S1 - https://doi.org/10.6084/m9.figshare.29145377.v1). If focused only on bee species, approximately 19% of these plants are visited only by one of the bee species, while overlap (visiting the same plants) occurs in approximately 44% of ALMaSS plant species (Figure 3). Therefore, the pollen preference score will be determinant to simulate and predict possible interactions in these plant species. Apis mellifera and B. terrestris generalist behaviours makes these species the ones with most possible interactions (share approximately 41% [29% + 12%] of the species). On the other hand, considering only the species visited by O. bicornis (68 species), there are only 5 plant species that are exclusively visited by this pollinator, leaving the other 63 species with possible competition events with other bees (Figure 3).

Table 1: Number of plant-pollinator interactions extracted from databases and literature. The number of individual plant species was obtained by removing all the duplicates in the data. This final dataset (individual species) was compared with the 408 ALMaSS plant species. Most pollinators, except the honey bee, visit less than half of the species coded into ALMaSS.

Species	Apis mellifera	Osmia bicornis	Bombus terrestris	Eristalis tenax	Sphaerophoria scripta	Noctua pronuba	Pieris napi
Number of records	798668	452	48971	6701	11145	10	252
Number of individual plant species	4030	199	1216	301	138	10	73
Number of ALMaSS plant species	230	68	190	98	122	7	31
Percentage of ALMaSS plant species (%)	56.4	16.7	46.6	24	29.9	1.7	76



Figure 3: Interactions to all the plant species coded in ALMaSS only by bee species. A high number of plants is not visited by any of these bees (ap. 37%). 19% of the coded species are visited only by one bee species, while the remaining 44% are shared amongst the tree bee species.

3.4.2 Pollen composition

3.4.2.1 P:L preferences

Considering that bees are the ones that carry pollen to feed their larva, these were the only group from which this strategy was applied. According to previous research, Apis mellifera prefers to forage on pollen with a ratio of 1:1 to 2:1 (Vaudo et al, 2020) while B. terrestris prefers to forage on flowers with a high protein content (P:L ratio of 14:1; Vaudo et al., 2016). On the other hand, information on O. bicornis P:L preferences is scarcer but it has been reported a preference of approximately 3:1 for O. cornifrons (Vaudo et al., 2020a). Based on these data, and the number of species with available data on P:L ratios (Figure 4), the following preferences were set:

Apis mellifera: range from 0.5 to 2.5

Osmia bicornis: range from 2.5 to 3.5

Bombus terrestris: above 10

Considering only the 408 ALMaSS plant species, the exiting data does not cover all the species visited by these bees. For Apis mellifera, there are data for 203 out of the 230 species it visits (88%); For B. terrestris 169 out of 190 (89%); while for O. bicornis, there are data on 61 out of the 68 species it visits (90%).



Deliverable D1.3



Figure 4: Total amount of proteins and lipids (in µg/mg) for each plant species. Each dot represents an individual plant species, belonging to a plant family along a gradient from low to high pollen P:L. Families with a higher P:L mean are shown in the top (dark blue), while the ones with lower P:L mean are shown in the bottom (dark green). The number of species from each family are in brackets after the family name. To help visualize each pollinator preferences on the P:L nutritional scale, the insect pictures were added in the approximate area of preference. Each blue line crossing the graph represents the different P:L ratios.

3.4.2.2 K:Na preferences

The K:Na ratio has stronger variations than the P:L ratio within the same plant family (Figure 5). Bees seek pollen with higher Na to reach the desired K:Na balance in bee larval food, to ensure the building blocks for optimal larvae development. The K:Na preference was further analysed only for the plant species that are visited by either *Apis mellifera*, *O. bicornis* or *B. terrestris*. Thus, a relative scale was created separately for each bee (Figure 6). The mean K:Na ratio for the plant species visited by *Apis mellifera* was 18.8 (SD = 33.6), while *B. terrestris* visits plants with a mean K:Na of 15.8 (SD = 31.4). By contrast, *O. bicornis* seems to prefer plants with rather lower K:Na ratios (mean of 4.9, SD = 16.4), but the number of measurements was much lower than in the case of two other analysed bees.





Figure 5: K:Na ratios for different plant families based on available data. The number of species analysed from each family are in brackets after the family name. Many families are represented by only one or two plant species.



Figure 6: K:Na ratio for the species visited by each one of the represented bees. Exiting data does not cover all the species visited by these bees. For *Apis mellifera*, there are data for 171 out of the 230 species it visits (74%); for *B. terrestris* 141 out of 190 (74%); while for *O. bicornis*, there are data on 45 out of the 58 species it visits (78%).

3.4.3 Pollen preferences across bee species

Apis mellifera

Of the 230 species visited by Apis mellifera, a preference score of 3 was attributed to 32 species, a score of 2 to 118 species, and a score of 1 to the remaining 80 (5.1 Supplementary material; figure 7). Apis mellifera has the highest mean preference score for the species of the Cistaceae (3), Papaveraceae (2.5), and Lamiaceae (2.44) family. The families Araliaceae, Convolvulaceae, Dipsacaceae, Iridaceae, and Myrtaceae, have all a mean score of 2. These families include several Cistus spp., the common poppies (Papaver rhoeas), and several Lamium spp. (Figure 7).



O. bicornis

O. bicornis visits less species than Apis mellifera. From the visited 58 species, 10 received a score of 3, while 17 species had a score of 2, and the remaining 31 a score of 1. This species pollen preference lies in Araliaceae, Papaveraceae, Rannunculaceae families (all families had a mean score above 1.5). It is also noteworthy the high scores (2 and 3) for Glechoma hederacea, Helianthemum nummularium, Lamium spp., Taraxacum officinale, Thymus spp., Rubus fruticosus, Rosmarinus officinalis, Rannunculus spp. and Quercus robur (Figure 7). Food provisions directly collected from O. bicornis nests have found pollen from most of these species (Haider et al. 2014; Coudrain et al., 2016; Bednarska et al. 2022). On the other hand, species like Acer pseudoplatanus, have been also found in high quantities in O. bicornis nests (Tourbez et al., 2025), but have received a poor score. This means that the P:L and K:Na ratio of some pollen types is not considered appropriate for this bee species. This suggests that the P:L ratio preference for O. bicornis can be improved, since it was based on O. cornifrons, and that the K:Na ratio needs to be updated in the future.

B. terrestris

B. terrestris had also only 10 species with a score of 3, 88 species with a score preference of 2 and the remaining 92 with a score of 1. A lot of the high scored species (Vaccinium spp., Rhododendron ponticum, Calluna vulgaris, Arbutus unedo) belong to the Ericaceae family, which have been pointed essential for Bombus spp. survival (Moquet et al., 2017). Judging by the high number of species visited by B. terrestris (190), it was expected a higher number of species with the maximum score, like happened with Apis mellifera. Nevertheless, the search for plants with a higher protein content limited the achievement of high scores. From the visited plant species by B. terrestris, only 21 had a high P:L ratio.



Figure 7: Preference score for each bee species according to the genus considering only the 180 species in which there are interactions between pollinators. For a better detail, all pictures have been updated in figshare (see link at the end).



3.5 Final considerations

From the 408 coded plant species in AlMaSS, approximately 37% are not visited by any of the bee species (Figure 3). If butterflies and overflies are considered (the future model species), then the percentage of plants not visited by any pollinator, drops 3 points to approximately 34%. Meaning that, according to our interaction databases, 34% of ALMaSS plant species are irrelevant for pollinators. On the other hand, there are species that pollinators interact with that are not present in ALMaSS, evidencing the need for an update on the modelled plant species. When considering just bee species, approximately 19% of the ALMaSS plants are visited only by one species. So, possible competition events between bee species can occur on the remaining 44%. Bottom line, these 180 species are the most relevant when evaluating plant-pollinator interactions and possible competition between these pollinators while simulating environmental scenarios (modelling approach).

The pollen preference score was based on two main subjects: interactions and nutritional value. We believe the interactions data produced a strong baseline to set the preference score. The high number of interactions that was extracted from databases and scientific publications offers substantial confidence in these data. On the other hand, the nutritional approach, besides being based on insightful publications in which strong links (nutrients ratios) between pollen nutrition and plant-pollinator interactions were found, still has room for improvement. O. bicornis P:L ratio preference was set based on O. cornifrons preferences, and despite being from the same genus, these species are not native from the same continents. O. cornifrons is from eastern Asia while O. bicornis native to Europe, which affects their interactions and preferences with the plants were these species are introduced (Vaudo et al., 2020b). Also, there were no information on the P:L and K:Na ratios for all the species visited by bees. These may especially bias the scoring applied to K:Na ratios, as it is based on means. Furthermore, most of the available nutritional data was considered at the genus level. To fill this data-gap, new scientific collaborations have been created and pollen is being extracted from several species that are visited by bees. This work is being performed at the European level (COST ACTION 22105 https://www.besafebeehoney.eu/; Varenina et al., 2024) and it is expected to enlarge the pollen nutritional database, allowing for a precise prediction of pollen preferences. Thus, we consider our database more like a "living" document, which will be updated when new data or insights are available.

The full data-set on the preferences score, including the interaction presence/absence, as well as the score for P:L and K:Na ratios, can be found in the Supplementary material. The P:L and K:Na ratios that were extracted from scientific publications will be provided by the authors on request. All pictures from this deliverable are available from https://figshare.com/projects/BETTER-B Deliverable 1 3 - Resource quality and forage selection/250151.



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5. Supplementary material

5.1 Bee pollen preference score

The (.xlsx format) downloaded from supplementary material file can be https://doi.org/10.6084/m9.figshare.29154506. It contains the preference score for A. mellifera, B. terrestris, and O. bicornis, that was calculated according to the rules set in the section 3.2 (Strategy to set pollen preferences) of this deliverable. Furthermore, since it was not possible to use the nutritional approach for the other species that are being modelled (Eristalis tenax, Sphaerophoria scripta, Noctua pronuba and Pieris napi), the excel file only contains the presence/absence data of interactions. This database is a living document, and it will be uploaded as more nutritional data on plant species is collected.

5.2 Reviewing published and grey literature in local European languages to supplement existing databases on floral resource traits

The database of floral resource traits developed within the B-GOOD project (Filipiak et al., 2022a) pointed out to knowledge gaps related to floral resource traits of plants important for pollinators and clearly showed that some European countries were over-represented, while others were under-represented in this respect. One of the possible reasons for this was the authors' limited access to literature published in local European languages. Therefore, within task 1.1 we aimed to overcome these limitations and collect data on floral resource traits from the published and grey literature in national languages to (i) complement existing databases and (ii) to be able to identify the real knowledge gaps and drive further research. From this collaborative work was possible to expand the flower resource traits database and to go forward with a scientific publication. The manuscript described below was accepted for publication in the Ecological Solutions and Evidence journal in May 2025 and will soon be available for download.

The dataset from this manuscript can be downloaded from https://uj.rodbuk.pl/dataset.xhtml?persistentId=doi:10.57903/UJ/LNZGXM.

