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Validation of Floral Resource Models

Deliverable D3.4

31 May 2022

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B-GOOD
Giving Beekeeping Guidance by cOmputatiOnal-assisted Decision making

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Preface

This deliverable (D3.4) focuses on the optimization, accuracy assessment, and validation of the phenology models of floral resources (floral resource models) for bees based on field data from Belgium, Portugal, and the UK, and is an output of subtask 3.3.3. Floral resource models describe pollen, nectar, and sugar production levels and their changes throughout the year, and their development was described in detail in Deliverable D3.3. Floral resource models are incorporated into the ALMaSS landscape model representation of landscape elements and crops important to bees across Europe. The floral resource models are of crucial importance for the ApisRAM (honey-bee colony) model being developed under the ALMaSS modelling platform within WP5.

This deliverable consist of the following components:

1) Report, being the present document, in which the methodology and summary of outputs are described;
2) Appendix A: Results of accuracy assessment for flowering phenology [*Accuracy_assessment_flowering_phenology.xlsx*] – file available in a GitLab Repository (see explanation below);
3) Appendix B: Parameters for final floral phenology models [*Flowering_phenology.xlsx*] – file available in a GitLab Repository (see explanation below)
4) Appendix C: Validation results [*Validation_results.xlsx*] – file available in a GitLab Repository (see explanation below).

In addition, we modified the interactive script in Python for the Jupyter Notebook allowing calculation of floral resources available for bees in different habitat units in different years and locations, and generating outputs for the ApisRAM model [*Resources_calculator.ipynb*] by including results of our optimization procedure. The up-to-date version of the script (and all necessary input files) as well as Appendices A-C are available in a publicly available GitLab repository (https://gitlab.com/ALMaSS/floral_resource_models).

To contextualise the deliverable described here, the integration of subtask 3.3.3 within the entire WP3 strategy and in relation to WP5 is first explained in section 1. The short summary of floral resource models, optimization methods applied, and accuracy assessment results are then presented in section 2. Section 3 focuses on the validation of floral resource models and includes a description of field data collection procedures using previously developed field protocols.

Summary

The main objective of WP3 is to develop a dynamic landscape model across the EU, capturing the major floral resources for bees, considered a key driver of bee health status. Floral resource models developed in task 3.2 allow one to predict the amount of pollen, nectar, and sugar produced by a given bee-friendly species per unit area of a specific landscape element as a function of accumulated growing degree-days. Here, the modified version of the floral resource models described in Deliverable D3.3 is presented. These modifications relate to the modelling of flowering phenology and include adding maximum daily temperature for plant growth and corrections related to altitude and latitude. Furthermore, an optimization procedure for the selection of base and maximum temperatures for growth is applied, together with an accuracy assessment, also for the final models and including corrections related to altitude and latitude. The final models are validated using field data on flowering phenology from Belgium, Portugal, and the UK. The new version of floral resource models is implemented in the *Resources_calculator.ipynb* script producing outputs for the foraging component of the ApisRAM model.

1. Introduction

WP3 “Ecology and environmental drivers” aims to develop a dynamic landscape model, capturing the major floral resources for bees, and to construct landscape suitability maps for honey bees across Europe. To achieve these general aims, this WP is divided into four tasks, with different sub-tasks that have specific aims and links between them, as represented in the WP workflow (Figure 1).

In task 3.1, based on literature information, databases on plant traits and plant-pollinator interactions, beekeeper plant catalogues and bee expert advice (via a questionnaire sent to all B-GOOD members), the most important bee--friendly plant species in different landscape elements across the EU were identified. The list of the bee--friendly species, together with the map and database of the major landscape elements at the EU level (Deliverable D3.1), served as input for task 3.2, and as a platform to construct the landscape suitability maps in sub-task 3.4.2.

The primary aim of task 3.2 was the construction of the phenology models for the most relevant bee-friendly species across Europe. To complete this task, we first generated a database of the floral resources (Deliverable D3.2), including bee-friendly species, considering both crops and wild plants. For each plant species, information on the amount of pollen, nectar and sugar produced, the number of flowers per unit area, single flower lifetime, and flowering start, peak, and end dates were all compiled in sub-task 3.2.1. The databases of major landscape elements with bee-friendly species (Deliverable D3.1) and of flower resources (Deliverable D3.2) were used in sub-task 3.2.2 to develop the floral resource models that were incorporated within the ALMaSS modelling framework to serve the ApisRAM model (WP5; Deliverable D5.1), and other pollinator (mason bee and bumblebee) models being currently under development in other projects.

Task 3.3 focuses on validation of floral resource models based on field data and the generation of spatio-temporal dynamic landscape models for study areas in Belgium, Portugal, and the UK to be able to test the performance of the ApisRAM model. The first-stage integration of floral resource models was applied using spatio-temporal dynamic landscape models for study areas in Belgium and the UK (WP5; Deliverable D5.1). Further tests are planned for study areas in Portugal. The field studies to support validation of floral resource models were performed in Belgium, Portugal, and the UK following specific field protocols developed by the WP3 team (Milestone M15). The field studies included assessment of the composition of plant communities (coverage and abundance of main species within communities), and flowering phenology observations. The field data on plant communities wasere not used as typical validation data. However, they were of crucial importance and serve as: (1) input data to floral resource models for habitat types not described in the EUNIS database, but important from the point of view of pollinators (e.g., urban parks); and (2) a source of verification for major bee-friendly species reported for the habitat types from the EUNIS database. The field data on flowering phenology was used for validation of phenology models, which are described in this deliverable. The validated floral resource models will be updated within the ALMaSS platform to run together with the ApisRAM model (second-stage integration; subtask 3.4.1).

In sub-task 3.4.2, the main goal is to build landscape suitability maps using geospatial data sources at the pan-European scale, namely land cover maps (from task 3.1), plant species distribution, weather data, digital elevation models, topographic data, and remote sensing to construct detailed spatio-temporal dynamic landscape maps at the EU scale. Combining this geospatial information with nutritional values from the database of floral resources (sub-task 3.2.1) and phenology models (sub-task 3.2.2) will provide spatio-temporal information about the main resources available for bees across the EU.

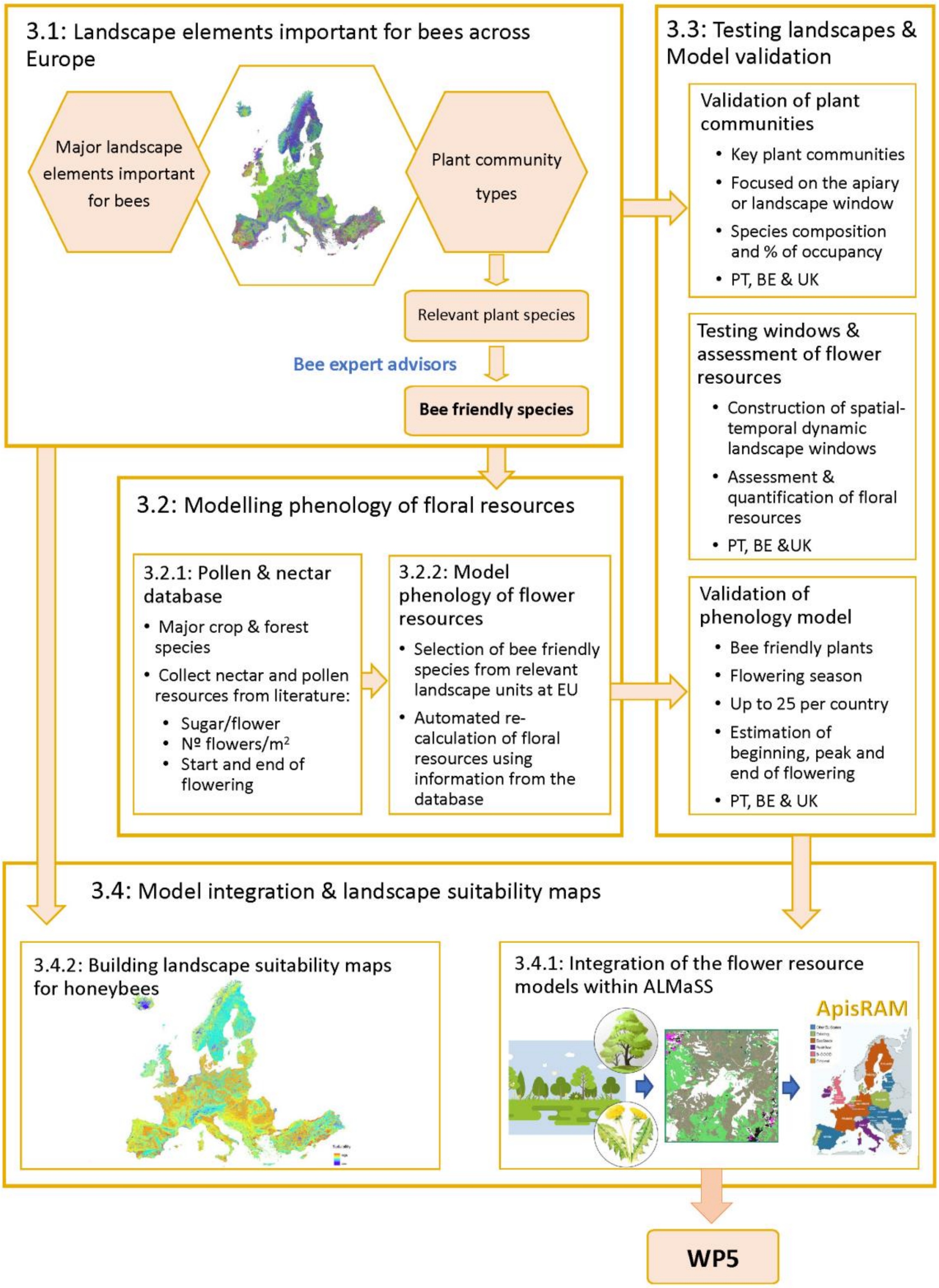


Figure 1: Diagram of the workflow of the work package 3, showing the major links between tasks and sub-tasks.

2. Optimization and accuracy assessment of flowering phenology models

The floral resource models (Deliverable D3.3) describe pollen, nectar, and sugar production levels as a function of growing degree-days (GDD) (i.e., degree days above the base temperature T_b, a temperature threshold below which plant development stops) in various landscape elements and crops important to bees across Europe. The models integrate information on plant composition in different habitat units (Deliverable D3.1) with nectar and pollen production (Deliverable D3.2), and flowering phenology. In the first version of floral resource models, the timing of flowering was related only to temperature. This means that onset, peak and end of flowering were determined based on accumulated GDD. For calculation of daily GDD the following formula was applied:

Daily GDD (°C) = ((Daily Max T °C + Daily Min T °C)/2) – T_b °C

For all wild plant species, GDD were accumulated starting from 1st January and using the base temperature (T_b) of 4°C. For crops we used crop-specific base temperatures, determined from the literature (see Deliverable D3.3, Table 1). For permanent crops (i.e., fruits, olives), GDD were accumulated starting from 1st January while for annual crops it was accumulated starting from the sowing date.

Here we described the updated version of floral resource models, in which calculation of GDD was modified by adding the maximum temperature for growth, above which plant growth is inhibited. In addition, optimization procedures were applied to select the base and maximum temperatures giving the best fitted flowering phenology models according to the root-mean-square error (RMSE). Lastly, corrections related to altitude and latitude were included, and accuracy assessment of the final models performed.

2.1. Input data for modelling of flowering phenology

The following data sources were integrated in the database on floral phenology:

- Pan European Phenology Database (PEP725): http://www.pep725.eu/ (Templ et al., 2018) including observations collected until 2016. The database records observations on phenological development stages of plants using the BBCH-scale. For our purposes only observations with BBCH of 60 (beginning of flowering), 65 (full flowering), and 69 (end of flowering) were selected.
  The majority of data provided by PEP725 is for wild plant species, but some observations are also available for crops, such as oilseed rape (*Brassica napus*), turnip rape (*Brassica rapa*), or alfalfa (Medicago sativa).
  These data are referred to as 'PEP'-data and tables containing these data are named with the prefix 'PEP'.

- Phenological observations collected by the Deutscher Wetterdienst (German meteorological service, DWD) from 1951 to date accessed via Climate Data Centre OpenData server: https://opendata.dwd.de/climate_environment/CDC/. The observations of phenological development stages are described using specific codes of pheno-phases from 1 to 67 (description available at: https://opendata.dwd.de/climate_environment/CDC/help/PH_Beschreibung_Phase.txt), but in most cases the reference to the BBCH-scale is also provided. For our purposes only observations with codes of 5 (beginning of flowering), 6 (full/general flowering), and 7 (end of flowering) were selected.
  DWD provides information for many wild plant species, annual crops (including data on start of flowering of sunflower, corn, potato, green bean, green pea and tomato,

and data on peak of flowering of corn), fruit crops (including data on start, peak and end of flowering of apple, pear, cherry, morello, and plum; and data on start of flowering of apricot, peach, and different kinds of berries), and vine (including data on start, peak and end of flowering of early, middle-late and late ripeness varieties). These data are referred to as 'DWD'-data and tables containing these data are named with the prefix 'DWD'.

- The database on nectar and pollen production (Deliverable 3.2). These data are referred to as 'UJ'-data and tables containing these data are named with the prefix 'UJ'.

- Phenological observations of development stages of selected crops (including data on start and end of flowering of winter oilseed rape) collected by the Polish Official Variety Testing (COBORU) in years 2007-2016. These data are referred to as 'COBORU'-data and tables containing these data are named with the prefix 'COBORU'.

- Phenological observations from the multitaxon database on phenology from the Russian Federation, Ukraine, Uzbekistan, Belarus and Kyrgyzstan (Ovaskainen et al. 2020). The data cover the period 1890–2018, with 96% of the data being from 1960 onwards. The database is rich in plants, birds and climatic events, but also includes insects, amphibians, reptiles and fungi. The database was restricted to plant flowering phenology observations within the spatial and temporal coverage of the E-OBS meteorological data. These data are referred to as 'CNC'-data and tables containing these data are named with the prefix 'CNC'.

- Flowering phenological observations collected by Jachuła et al. (2021) for bee-friendly species. These data are referred to as 'JJ'-data and tables containing these data are named with the prefix 'JJ'.

The current version of flowering phenology database (available in the GitLab repository) includes 8223641 records, 7195055 (87.5 %) of which refer to onset of flowering.

2.2. Optimization and accuracy assessment of flowering phenology models

2.2.1. Optimization of the base temperature

Optimization of base temperature was done based on 7195055 records on the onset of flowering. First, for each record, the day of the year indicating onset of flowering was converted to GDD based on meteorological data from the E-OBS database using a range of base temperatures between 0 and 9 Celsius degrees (range of base temperatures was selected based on literature review). Next, mean GDD needed for onset of flowering were calculated for each species and base temperature being tested. These mean GDD values were used to predict the onset of flowering (as day of the year) for each plant phenological record being analysed. The predicted and actual values for each record were compared using RMSE, and the minimum RMSEs were reported for each species (Appendix A). Summary of the results indicating RMSEs for plant families, and for all records are provided in Table 1.

Zero degrees Celsius was the best performing base temperature (i.e., in terms of minimalizing RMSE) for most of the species (Figure 2), plant families as well as when considering all records together (Table 1). This temperature was therefore applied when generating floral resource curves for ALMaSS to be used in the ApisRAM model.

Table 1. Summary of the accuracy assessment for the onset of flowering (RMSE values). Different base temperatures between 0 and 9 degrees Celsius were tested. Lowest RMSE values for each family, belonging to the most accurate base temperature for that family, are marked in green. If number of observations for a given species was < 3, RMSEs were not calculated and base temperature of 0 degrees Celsius was assumed.

Plant family	No of records	Base temperature									
		0	1	2	3	4	5	6	7	8	9
Actinidiaceae	17	8.92	9.19	9.56	10.15	10.38	10.73	11.12	11.60	11.96	12.47
Adoxaceae	251498	46.76	46.95	47.27	47.90	49.02	50.67	52.50	53.95	54.79	55.38
Amaranthaceae	2	-	-	-	-	-	-	-	-	-	-
Amaryllidaceae	328387	33.41	34.05	34.94	36.58	39.34	43.74	50.76	63.18	85.55	122.81
Apiaceae	499	6.84	6.94	7.11	7.37	7.68	8.03	8.40	8.92	9.44	10.11
Apocynaceae	71	5.43	5.26	5.08	5.01	4.93	4.92	4.91	4.96	5.02	5.33
Aquifoliaceae	1	-	-	-	-	-	-	-	-	-	-
Araceae	20	6.41	6.37	6.29	6.18	6.03	5.89	5.81	5.73	5.96	6.01
Araliaceae	5	19.54	21.22	22.14	23.59	25.55	26.45	28.40	30.21	32.29	37.61
Aristolochiaceae	54	5.52	5.47	5.49	5.58	6.38	6.94	8.03	9.87	10.94	20.01
Asparagaceae	9540	16.76	16.95	17.15	17.46	18.87	19.70	21.05	33.78	35.52	37.29
Asteraceae	73	4.63	4.45	4.41	4.37	4.46	4.60	5.00	5.45	5.96	6.66
Balsaminaceae	13	8.80	9.44	10.03	10.82	11.43	12.16	12.89	13.66	14.59	15.45
Berberidaceae	113	12.42	12.43	12.46	12.59	12.69	12.83	12.83	12.86	12.90	13.15
Betulaceae	605979	39.04	39.44	40.21	42.02	45.96	53.32	64.93	82.36	106.35	153.49
Bignoniaceae	1	-	-	-	-	-	-	-	-	-	-
Boraginaceae	294	7.56	7.41	7.48	7.67	8.86	10.73	13.77	23.45	34.58	35.49
Brassicaceae	1165	18.52	18.66	18.80	18.99	19.22	19.58	20.21	25.65	26.77	36.48
Campanulaceae	205	9.66	9.39	9.27	9.23	9.27	9.33	9.54	9.83	10.20	10.66
Cannabaceae	16	22.04	22.01	22.01	21.89	22.25	22.24	22.41	22.32	22.55	22.84
Caprifoliaceae	100185	21.54	21.48	21.42	21.36	21.32	21.34	21.40	21.52	21.71	22.11
Caryophyllaceae	417	7.34	7.42	7.63	7.97	8.33	8.96	9.87	25.35	25.52	25.84
Celastraceae	266	7.39	7.43	7.59	7.90	8.81	13.25	19.08	25.88	30.80	38.13
Cistaceae	33	11.94	11.94	11.94	12.05	12.08	12.35	12.70	13.08	13.55	14.16
Colchicaceae	124016	24.97	26.18	27.73	29.75	32.11	35.09	38.66	42.75	47.72	53.01
Compositae	651762	27.51	27.70	27.87	28.06	28.41	29.13	30.51	32.89	36.37	41.45
Convolvulaceae	22	14.23	14.21	14.29	14.44	14.67	14.68	15.00	15.37	15.66	15.92
Cornaceae	75158	22.39	22.64	22.99	23.47	24.17	25.70	29.26	35.59	43.44	51.95
Crassulaceae	40	4.51	4.25	4.07	3.92	3.99	3.96	4.15	4.44	4.79	55.58
Cucurbitaceae	24	6.34	6.28	5.80	5.72	5.67	5.42	5.55	5.57	5.43	5.58
Cupressaceae	14	11.97	11.77	11.52	11.52	11.17	11.40	11.56	12.13	12.54	12.96
Cyperaceae	379	8.40	8.81	9.63	10.56	12.11	14.36	18.31	23.56	24.13	53.35
Droseraceae	32	10.84	11.19	11.60	11.99	12.56	12.71	13.18	13.90	14.66	15.54
Elaeagnaceae	11	2.71	2.50	2.22	2.20	2.09	2.54	2.75	3.12	3.46	3.83
Ericaceae	200827	23.53	23.82	24.19	24.66	25.37	26.38	27.82	30.26	33.25	36.79
Euphorbiaceae	64	4.54	4.44	4.42	4.46	4.68	4.88	5.12	5.55	6.29	7.43
Fabaceae	9	5.43	5.31	5.65	5.85	6.01	6.18	6.55	101.90	101.94	101.97
Fagaceae	118954	22.51	22.43	22.31	22.16	22.03	21.94	21.92	21.98	22.17	22.63
Gelsemiaceae	50333	20.46	20.40	20.35	20.30	20.28	20.30	20.35	20.45	20.61	20.84

Plant family	No of records	Base temperature									
		0	1	2	3	4	5	6	7	8	9
Gentianaceae	17	14.91	14.44	14.18	13.81	13.67	13.72	13.87	14.14	14.53	15.11
Geraniaceae	426	20.12	19.94	19.85	19.84	20.02	20.31	21.05	26.69	31.15	36.18
Grossulariaceae	263428	26.34	26.34	26.34	26.33	26.34	26.39	26.53	26.89	27.98	30.84
Hydrangeaceae	173140	24.22	24.32	24.41	24.50	24.60	24.81	25.46	27.07	29.96	34.59
Hypericaceae	169	6.77	6.59	6.53	6.49	6.51	6.58	6.70	6.86	7.14	7.50
Iridaceae	99	9.94	9.68	10.46	11.45	13.11	15.37	169.62	169.65	169.67	169.70
Juglandaceae	569	17.32	17.52	17.80	18.10	18.39	18.55	18.75	19.13	19.67	20.58
Juncaceae	90	8.33	8.25	8.46	8.78	9.31	10.25	14.76	20.85	76.95	219.61
Lamiaceae	757	80.40	80.47	80.57	80.68	80.86	81.08	81.51	82.26	83.76	87.67
Lauraceae	287	181.20	181.21	181.24	181.28	181.32	181.37	181.42	181.49	181.70	182.15
Leguminosae	267440	19.69	19.65	19.56	19.50	19.47	19.47	19.56	19.72	19.98	20.34
Lentibulariaceae	1	-	-	-	-	-	-	-	-	-	-
Liliaceae	236	11.95	11.92	12.26	12.57	13.37	15.03	121.34	121.98	124.76	124.88
Linaceae	120	17.39	17.35	17.39	17.58	17.78	17.87	18.11	18.35	18.56	18.97
Lythraceae	63	17.43	17.72	17.99	18.34	18.51	18.79	18.98	19.10	19.33	19.65
Malvaceae	378743	19.41	19.36	19.33	19.30	19.29	19.33	19.40	19.54	19.76	20.09
Melanthiaceae	54	6.84	6.78	6.72	6.73	6.92	7.08	7.40	7.77	8.22	8.94
Menyanthaceae	78	5.54	5.49	5.35	5.35	5.27	5.21	5.47	5.68	6.15	6.93
Montiaceae	1	-	-	-	-	-	-	-	-	-	-
Moraceae	1	-	-	-	-	-	-	-	-	-	-
Nartheciaceae	1	-	-	-	-	-	-	-	-	-	-
Nymphaeaceae	122	9.99	10.05	10.20	10.48	10.78	11.09	11.48	11.88	12.27	12.80
Oleaceae	593184	24.97	24.92	24.86	24.81	24.80	24.84	25.02	25.60	26.92	29.34
Onagraceae	1846	13.37	13.41	13.54	13.69	14.32	15.45	17.72	19.83	21.48	23.63
Orchidaceae	291	7.65	7.67	7.70	7.79	7.95	8.18	8.45	9.06	10.46	73.69
Orobanchaceae	201	8.45	8.60	8.75	8.90	9.14	21.41	21.65	29.13	29.30	29.53
Oxalidaceae	122	25.00	24.72	24.54	24.40	24.47	24.68	25.19	26.17	28.23	30.64
Paeoniaceae	38	5.84	5.64	5.65	5.58	5.56	5.88	5.90	6.35	7.02	7.40
Papaveraceae	367	11.71	11.82	11.80	12.28	13.19	14.64	29.64	30.06	188.79	203.21
Pinaceae	307275	22.13	22.08	22.00	21.91	21.85	21.87	22.00	22.29	22.86	23.80
Plantaginaceae	266	8.77	9.09	9.36	9.82	10.24	10.63	11.23	37.42	37.64	37.94
Plumbaginaceae	1	-	-	-	-	-	-	-	-	-	-
Poaceae	151893	22.54	22.59	22.67	22.70	22.81	22.97	23.23	23.62	24.14	24.92
Polemoniaceae	3	4.69	3.92	2.45	1.41	1.91	3.16	3.92	4.65	5.00	5.00
Polygalaceae	15	4.59	4.44	4.52	4.62	4.95	5.11	6.51	6.62	7.06	10.70
Polygonaceae	103	7.65	7.81	7.95	8.15	8.37	8.79	9.20	9.55	10.12	10.78
Primulaceae	3730	30.25	31.02	31.97	33.45	35.02	37.28	46.96	49.37	52.20	55.39
Ranunculaceae	147394	28.76	29.00	29.24	29.49	30.02	30.79	31.78	34.36	38.23	44.68
Resedaceae	12	6.42	6.16	6.08	6.26	6.56	6.90	7.43	8.01	8.68	9.24
Rhamnaceae	138	19.64	19.53	19.48	19.47	19.46	19.51	19.58	19.70	19.84	20.12
Rosaceae	1348953	22.61	22.56	22.51	22.46	22.46	22.51	22.66	22.96	23.59	24.99
Rubiaceae	108	5.83	5.60	5.47	5.42	5.56	5.73	6.31	37.80	37.90	38.03
Rutaceae	140	15.51	15.59	15.79	16.04	16.28	16.55	17.00	17.25	17.37	17.53
Salicaceae	299186	27.74	27.99	28.26	28.55	28.93	29.73	31.52	35.31	41.23	49.36

Plant family	No of records	Base temperature									
		0	1	2	3	4	5	6	7	8	9
Sapindaceae	515310	24.06	24.01	23.92	23.82	23.74	23.70	23.74	23.97	24.65	26.18
Saxifragaceae	42	14.55	14.85	15.64	17.54	20.28	26.66	33.48	78.54	107.06	107.31
Scrophulariaceae	77	5.27	5.12	5.05	5.10	5.10	5.29	5.51	5.82	6.33	6.91
Solanaceae	111141	21.37	21.38	21.37	21.35	21.36	21.39	21.51	21.67	21.92	22.58
Thymelaeaceae	211	9.33	9.59	9.96	11.43	14.74	19.58	23.79	46.32	46.67	46.99
Ulmaceae	47	13.49	13.37	13.30	13.09	13.74	13.75	19.17	54.82	58.12	181.86
Urticaceae	94	10.19	10.21	10.19	10.33	10.52	10.77	10.98	11.29	11.72	12.26
Violaceae	9053	18.34	18.76	19.37	20.37	22.17	25.13	29.24	34.85	42.80	52.95
Vitaceae	14995	26.72	26.67	26.59	26.49	26.39	26.31	26.27	26.32	26.45	26.76
ALL	**7112592**	**27.15**	**27.29**	**27.51**	**27.94**	**28.82**	**30.49**	**33.35**	**38.16**	**45.73**	**60.42**

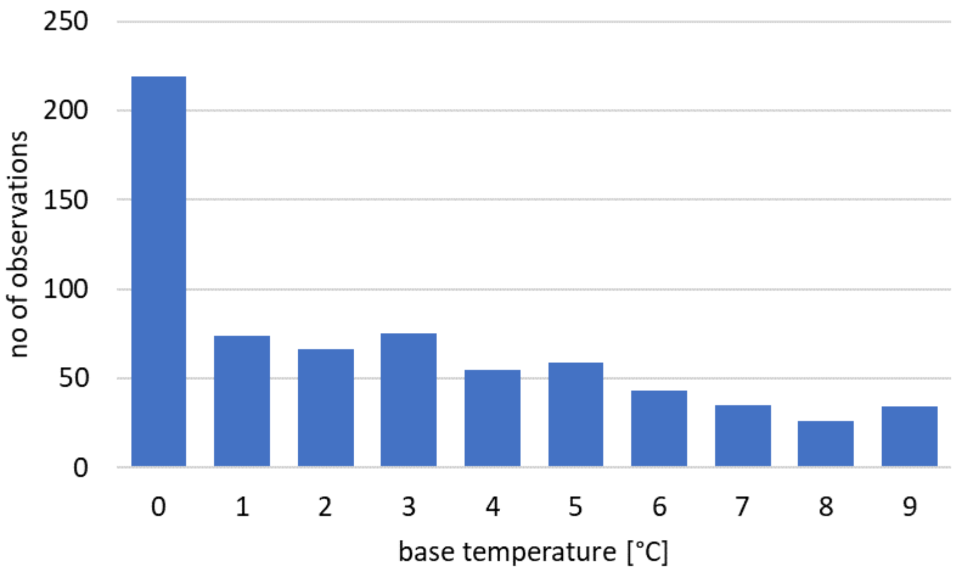


Figure 2. Frequency distribution for the best fitted base temperature for onset of flowering.

2.2.2. Optimization of the maximum temperature

Optimization of the maximum temperature for growth was done based on 320974 records of the end of flowering. First, for each record, day of the year indicating the end of flowering was converted to GDD based on meteorological data from the E-OBS database using a range of maximum temperatures between 15 and 33 degrees Celsius. Next, the mean GDD needed for the end of flowering was calculated for each species and maximum temperature being tested. These mean GDD values were used to predict the end of flowering (as day of the year) for each plant phenological record being analysed. The predicted and actual values for each record were compared using RMSE, and the minimum RMSEs were reported for each species (Appendix A). A summary of the results indicating RMSEs for plant families and for all records is provided in Table 2.

28 degrees Celsius was the best performing maximum temperature (i.e., in terms of minimalizing RMSE) for most of the species (Figure 3), plant families as well as all records (Table 2). This temperature was therefore applied when generating floral resource curves for ALMaSS to be used in the ApisRAM model.

Table 2. Summary of the accuracy assessment for the end of flowering (RMSE values). Different maximum temperatures between 15 and 33 degrees Celsius were tested but here results for temperatures between 18 and 30 degrees Celsius are shown. Lowest RMSE values for each family are marked in green. If number of observations for a given species was < 3, RMSEs were not calculated and max temperature of 28 Celsius degrees was assumed.

Plant family	No of records	Maximum temperature												
		18	19	20	21	22	23	24	25	26	27	28	29	30
Actinidiaceae	16	81.21	55.04	39.24	35.94	7.19	6.63	6.90	6.84	6.96	7.07	7.07	7.07	7.07
Adoxaceae	350	29.70	24.09	20.75	18.30	17.28	16.21	15.89	15.78	15.75	15.74	15.74	15.74	15.74
Amaranthaceae	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Amaryllidaceae	119	10.48	10.19	10.02	10.06	10.15	10.07	10.06	10.05	10.05	10.05	10.05	10.05	10.05
Apiaceae	393	30.46	25.40	21.06	17.05	14.87	11.96	9.69	8.66	8.43	8.00	7.95	7.94	7.95
Apocynaceae	59	39.98	36.67	31.27	26.36	20.80	18.32	16.20	14.23	14.21	14.32	14.42	14.49	14.61
Aquifoliaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Araliaceae	5	50.81	48.13	52.01	48.34	44.33	32.54	24.50	23.30	21.09	21.32	21.42	21.22	21.22
Aristolochiaceae	53	6.96	5.77	5.54	5.53	5.37	5.37	5.38	5.38	5.38	5.38	5.38	5.38	5.38
Asparagaceae	522	30.73	26.23	23.48	22.65	21.46	20.87	20.60	20.50	20.46	20.41	20.41	20.41	20.41
Asteraceae	66	35.28	31.26	25.27	18.92	16.92	12.76	11.30	9.65	8.95	8.86	8.85	8.85	8.81
Balsaminaceae	6	33.76	28.04	24.23	21.40	27.50	36.48	41.63	41.57	41.57	41.57	41.57	41.57	41.57
Berberidaceae	15	14.74	11.22	10.72	10.66	10.66	10.67	10.67	10.67	10.67	10.67	10.67	10.67	10.67
Betulaceae	1095	26.01	25.96	25.94	25.93	25.92	25.92	25.92	25.92	25.92	25.92	25.92	25.92	25.92
Boraginaceae	248	22.01	16.33	12.98	11.03	8.93	8.08	7.70	7.65	7.67	7.67	7.67	7.67	7.67
Brassicaceae	182	22.32	16.30	11.87	10.72	9.50	8.56	8.17	8.12	8.06	8.05	8.05	8.05	8.05
Campanulaceae	94	33.15	26.49	22.68	19.52	17.70	15.62	13.51	13.22	13.20	13.13	13.12	13.12	13.12
Caprifoliaceae	259	29.29	22.94	19.29	16.48	14.26	12.87	12.24	11.88	11.98	12.03	11.99	11.98	11.97
Caryophyllaceae	216	22.79	16.93	12.60	12.49	10.64	9.32	8.77	8.36	8.10	7.62	7.44	7.44	7.44
Celastraceae	184	22.48	14.86	12.21	9.81	8.78	7.96	7.50	7.38	7.45	7.45	7.45	7.45	7.45
Cistaceae	4	67.62	3.61	3.57	2.12	1.73	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Colchicaceae	17	29.05	23.89	25.79	30.03	31.67	39.58	40.34	40.79	41.30	41.45	41.80	41.98	41.98
Compositae	1120	36.26	33.11	31.27	29.92	28.90	28.10	27.38	27.07	27.21	27.22	27.24	27.31	27.34
Convolvulaceae	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Cornaceae	192	21.32	17.98	16.00	15.06	14.56	14.14	13.95	13.88	13.87	13.87	13.87	13.87	13.87
Crassulaceae	37	21.91	18.74	15.34	13.02	12.30	5.84	5.35	5.23	5.19	5.16	5.16	5.16	5.16
Cucurbitaceae	24	13.14	14.13	10.93	8.87	8.64	8.71	8.84	8.54	8.69	8.95	8.95	8.95	8.95
Cupressaceae	14	18.05	15.36	13.95	13.29	12.87	12.51	12.50	12.50	12.50	12.50	12.50	12.50	12.50
Cyperaceae	131	5.04	4.43	4.21	4.16	4.11	4.11	4.11	4.11	4.11	4.11	4.11	4.11	4.11
Droseraceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Ericaceae	555	23.65	19.70	18.03	17.18	16.66	17.10	17.81	17.95	18.08	18.14	18.19	18.19	18.19
Euphorbiaceae	64	21.49	15.75	11.42	9.80	8.24	7.57	6.97	6.95	6.99	6.99	6.99	6.99	6.99
Fabaceae	9	8.44	8.47	8.74	6.77	7.55	10.09	10.65	10.20	9.71	10.02	10.02	10.02	10.02
Fagaceae	543	26.03	25.23	24.86	24.68	24.66	24.63	24.63	24.63	24.63	24.64	24.64	24.64	24.64
Gentianaceae	4	12.16	10.76	3.97	3.94	7.05	6.44	7.84	7.84	7.84	7.84	7.84	7.84	7.84
Geraniaceae	261	34.76	29.69	25.76	23.63	22.43	21.23	20.89	20.83	20.85	20.87	20.87	20.87	20.87
Grossulariaceae	122	9.61	8.23	7.37	6.87	6.91	6.87	6.87	6.87	6.87	6.87	6.87	6.87	6.87
Hydrangeaceae	9	17.09	8.88	5.03	4.03	3.56	2.71	2.71	2.71	2.71	2.71	2.71	2.71	2.71
Hypericaceae	111	33.94	30.89	27.60	26.02	24.39	22.26	21.44	21.15	20.61	20.24	20.06	20.16	20.12

Plant family	No of records	Maximum temperature												
		18	19	20	21	22	23	24	25	26	27	28	29	30
Iridaceae	83	14.07	10.41	8.35	7.17	6.55	6.26	6.16	6.02	6.02	6.02	6.02	6.02	6.02
Juglandaceae	244	18.24	17.95	17.86	17.84	17.88	17.90	17.91	17.91	17.91	17.91	17.91	17.91	17.91
Juncaceae	7	3.53	3.07	3.07	3.07	3.07	3.07	3.07	3.07	3.07	3.07	3.07	3.07	3.07
Lamiaceae	363	32.77	26.58	22.96	19.54	18.05	16.55	15.41	14.95	14.87	14.88	14.89	14.90	14.90
Leguminosae	964	32.80	28.64	24.65	22.64	21.09	19.65	18.90	18.51	18.37	18.22	18.19	18.20	18.19
Lentibulariaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Liliaceae	185	20.18	17.43	14.06	11.37	10.36	9.38	8.13	8.13	8.18	8.16	8.16	8.16	8.16
Linaceae	61	38.70	35.24	31.02	25.96	23.40	21.45	18.39	18.06	17.99	17.92	17.90	17.91	17.91
Lythraceae	46	56.09	45.01	34.53	30.22	24.30	16.65	16.80	16.98	17.16	17.76	18.22	18.85	19.04
Malvaceae	236	35.87	30.68	25.38	20.97	18.43	15.94	14.88	14.76	14.75	14.73	14.74	14.74	14.74
Melanthiaceae	50	29.16	25.90	20.82	17.60	14.98	12.58	11.14	10.91	10.78	10.24	10.02	10.12	10.14
Menyanthaceae	5	8.06	6.29	3.79	3.00	3.00	4.52	4.31	4.47	4.60	4.60	4.60	4.60	4.60
Montiaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Nartheciaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Nymphaeaceae	27	41.21	37.22	30.45	26.77	25.70	24.21	24.11	24.64	24.61	24.81	24.81	24.81	24.81
Oleaceae	578	98.24	96.28	95.56	95.38	95.21	95.18	95.17	95.18	95.17	95.18	95.18	95.18	95.18
Onagraceae	115	35.38	38.03	36.45	36.30	36.00	37.09	37.22	36.88	37.03	37.18	37.17	37.18	37.20
Orchidaceae	4	12.37	11.91	3.28	1.73	1.73	1.73	3.00	3.00	3.00	3.00	3.00	3.00	3.00
Orobanchaceae	70	24.84	14.78	10.59	7.87	5.66	4.27	3.28	3.22	3.37	3.38	3.38	3.38	3.38
Oxalidaceae	10	36.80	36.39	36.17	35.68	35.50	35.50	35.50	35.50	35.50	35.50	35.50	35.50	35.50
Paeoniaceae	38	15.78	9.17	7.11	5.23	3.90	3.22	3.08	3.18	3.18	3.18	3.18	3.18	3.18
Papaveraceae	136	11.12	9.29	8.80	8.18	8.06	7.77	7.77	7.74	7.76	7.76	7.76	7.76	7.76
Pinaceae	173	32.49	31.75	31.16	31.05	31.26	31.34	31.31	31.30	31.30	31.30	31.30	31.30	31.30
Plantaginaceae	153	36.91	30.08	25.27	22.43	21.20	19.11	17.63	16.36	15.90	15.74	15.79	15.91	15.96
Plumbaginaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Poaceae	650	30.03	22.11	17.04	15.07	13.21	11.71	11.01	10.79	10.78	10.77	10.78	10.78	10.78
Polemoniaceae	3	14.73	8.35	7.19	3.79	3.11	2.71	2.71	2.38	2.38	2.38	2.38	2.38	2.38
Polygalaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Polygonaceae	70	21.22	16.83	13.90	12.35	11.80	10.92	11.15	11.34	11.17	11.35	11.35	11.35	11.35
Primulaceae	221	34.13	32.61	32.12	31.90	31.89	31.59	31.50	31.46	31.35	31.27	31.23	31.21	31.21
Ranunculaceae	1310	33.11	31.37	30.24	29.63	29.29	28.80	28.68	28.68	28.67	28.66	28.66	28.66	28.66
Resedaceae	12	19.24	14.47	10.50	9.21	8.50	8.86	8.89	8.79	9.04	9.04	9.04	9.04	9.04
Rhamnaceae	115	19.42	15.64	14.07	12.76	12.05	11.73	11.71	11.57	11.76	11.76	11.76	11.76	11.76
Rosaceae	296142	22.84	22.66	22.59	22.56	22.55	22.55	22.55	22.55	22.55	22.55	22.55	22.55	22.55
Rubiaceae	63	28.54	25.12	20.50	15.16	12.52	10.56	8.47	5.88	5.91	5.91	5.95	5.94	5.93
Rutaceae	65	17.75	16.53	15.88	15.29	15.25	15.13	15.05	15.04	15.04	15.06	15.05	15.05	15.05
Salicaceae	493	29.49	29.41	29.39	29.38	29.38	29.38	29.38	29.38	29.38	29.38	29.38	29.38	29.38
Sapindaceae	341	19.96	15.73	14.09	13.32	12.88	12.66	12.56	12.56	12.56	12.56	12.56	12.56	12.56
Saxifragaceae	28	8.48	6.53	6.36	6.32	6.15	6.08	6.08	6.08	6.08	6.08	6.08	6.08	6.08
Scrophulariaceae	63	33.94	30.54	27.39	24.13	21.48	18.97	17.65	16.72	16.35	15.09	14.97	14.99	14.98
Solanaceae	19	7.97	7.98	7.71	7.71	7.71	7.71	7.71	7.71	7.71	7.71	7.71	7.71	7.71
Thymelaeaceae	60	5.97	5.99	5.95	5.97	5.97	5.97	5.97	5.97	5.97	5.97	5.97	5.97	5.97
Ulmaceae	32	13.59	13.57	13.57	13.57	13.57	13.57	13.57	13.57	13.57	13.57	13.57	13.57	13.57
Urticaceae	92	36.90	32.89	29.08	25.55	23.72	22.88	21.99	20.24	20.32	20.37	20.32	20.32	20.32

Plant family	No of records	Maximum temperature												
		18	19	20	21	22	23	24	25	26	27	28	29	30
Violaceae	177	10.03	7.92	6.85	6.42	6.02	5.99	5.97	5.96	5.96	5.96	5.96	5.96	5.96
Vitaceae	10345	36.80	32.56	30.25	28.65	27.82	27.54	27.45	27.42	27.41	27.40	27.40	27.40	27.40
ALL	320974	**24.07**	**23.53**	**23.26**	**23.11**	**23.03**	**22.99**	**22.97**	**22.97**	**22.97**	**22.97**	**22.97**	**22.97**	**22.97**

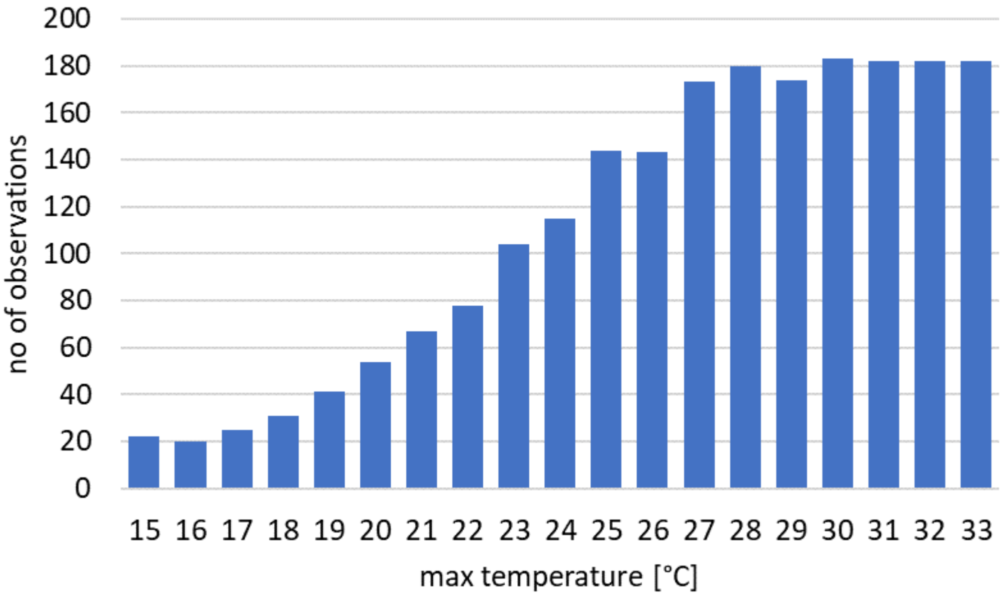


Figure 3. Frequency distribution for the best fitting maximum temperature for end of flowering.

2.2.3. Corrections for altitude and longitude

Flowering patterns can vary within plant species with changing abiotic conditions. In particular, it has been shown that the start of flowering is delayed with increasing elevation (e.g., Bucher et al. 2017; Bucher and Römermann 2020). Populations at higher elevations need less temperature accumulation to start flowering than populations of the same species at lower elevations, but the magnitude of this responses is very species dependent. Also, latitude can influence onset of flowering, which relates to photoperiod (e.g., Cho et al., 2017; White 1995).

Here, GDD for onset of flowering (calculated for base temperature of 0 degrees Celsius and max temperature of 28 degrees Celsius) were analysed against latitude and altitude at the plant family level. Although it was indicated in the literature that the magnitude of a response may be species-specific, we decided to apply correction at the family level as not enough data were available for most of the species to perform correction at the species level. Therefore, for each plant family with more than 10 records on the onset of flowering, based on data pre-processing a second order quadratic surface was fitted using least-squares solution in the SciPy Linear Algebra package in Python 3.7 was applied:

GDD for onset of flowering = $C[4] * ALT^2. + C[5] * LAT^2. + C[3] * ALT * LAT + C[1] * ALT + C[2] * LAT + C[0]$

where C[0[to C[5] are parameters of the quadratic model; ALT and LAT stand for altitude (in meters above sea level) and latitude (in decimal degrees)

For plant families with less than 10 records on onset of flowering, a general surface fitted to all data on onset of flowering was applied. Parameters for fitted surfaces are presented in Table 3, while Figure 4 shows examples of best-fitted surfaces for Colchicaceae and Leguminosae families.

For each record on flowering, a correction for altitude and longitude was then applied as follows. Mean GDD at average altitude and latitude values for a plant family (given by the fitted surface) were compared to the modelled species mean GDD value (see Appendix B), predicting the onset of flowering at a specific altitude and latitude for a given record and the resulting difference was applied as a correction value to that respective record.

Corrected mean GDD values were used to predict the onset of flowering (as day of the year) for each plant phenological record being analysed. The predicted and actual values for each record were compared using RMSE, and the minimum RMSEs were reported for each species (Appendix A). The RMSEs for models with and without the corrections for altitude and longitude were then compared for all species (Appendix A). A summary of the results indicating RMSEs for plant families, and for all records is provided in Table 4.

In general, application of a correction for altitude and longitude slightly lowered the resulting RMSE values (Table 4), suggesting greater accuracy in the models. However, we also found that for some species (e.g., *Alnus incana, Anemone hepatica, Primula veris, Thymus vulgaris*; Appendix A) the corrected flowering phenology models gave much higher RMSEs, which are also reflected in the results from their respective families (Table 4).

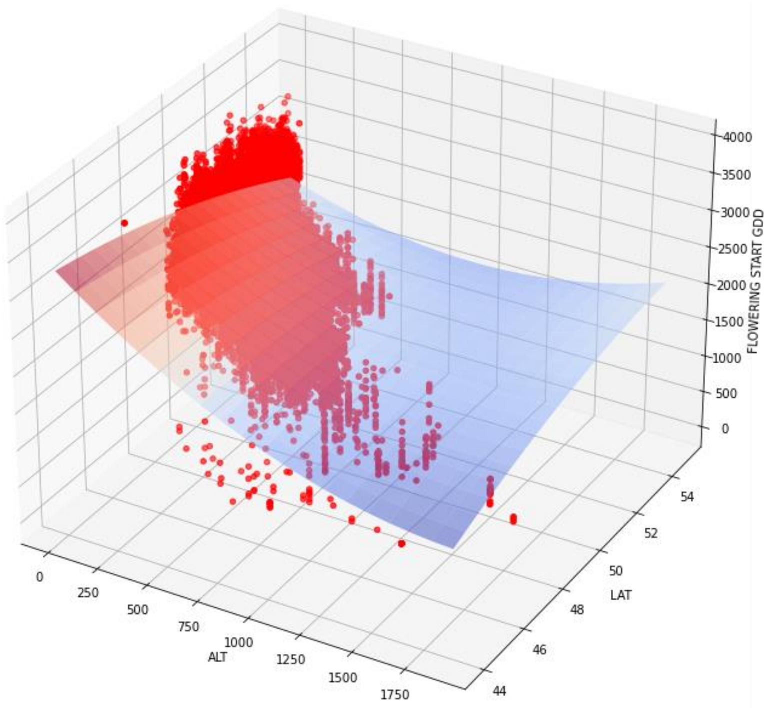
Table 3. Parameters for best-fitted second-order quadratic surfaces to the data on the onset of flowering at the family level.

Plant family	No of observations	C[0]	C[1]	C[2]	C[3]	C[4]	C[5]
Actinidiaceae	17	0.00	0.00	0.02	0.09	0.01	0.70
Adoxaceae	251498	15006.14	-1.59	-548.16	0.03	0.00	5.23
Amaranthaceae	2	-	-	-	-	-	-
Amaryllidaceae	328387	-2448.04	-0.99	108.58	0.02	0.00	-1.14
Apiaceae	499	13696.05	9.05	-390.31	-0.20	0.00	3.00
Apocynaceae	71	-224.24	994.24	-5619.21	-18.39	-0.28	110.18
Aquifoliaceae	1	-	-	-	-	-	-
Araceae	20	0.00	0.00	0.00	0.00	0.01	0.00
Araliaceae	5	-	-	-	-	-	-
Aristolochiaceae	54	0.00	0.00	0.00	0.00	0.01	0.00
Asparagaceae	9540	-3567.30	-2.95	166.56	0.05	0.00	-1.62
Asteraceae	73	1095467.06	1949.31	-48192.01	-39.01	0.21	524.62
Balsaminaceae	13	-5.04	-347.32	-128.02	6.13	0.15	3.88
Berberidaceae	113	-184.66	-12.92	48.34	0.28	0.00	-0.65
Betulaceae	605979	-7300.27	-0.73	303.29	0.01	0.00	-2.98
Bignoniaceae	1	-	-	-	-	-	-
Boraginaceae	294	-45525.57	-6.82	1857.05	-0.45	0.10	-17.77
Brassicaceae	1165	-75.16	-11.05	54.61	0.22	0.00	-0.77
Campanulaceae	205	53474.88	-4.63	-1770.42	0.01	0.00	14.95

Plant family	No of observations	C[0]	C[1]	C[2]	C[3]	C[4]	C[5]
Cannabaceae	16	211379.43	-208.13	-7024.18	4.28	0.00	55.58
Caprifoliaceae	100185	2323.07	-2.34	-25.24	0.04	0.00	0.00
Caryophyllaceae	417	1969.17	-10.74	-19.11	0.19	0.00	-0.02
Celastraceae	266	-30147.80	-4.38	1073.31	0.07	0.00	-9.17
Cistaceae	33	13004.26	-14.97	-551.26	0.35	0.00	6.25
Colchicaceae	124016	771.60	-6.73	198.97	0.11	0.00	-3.17
Compositae	651762	2035.68	-3.44	-45.16	0.06	0.00	0.30
Convolvulaceae	22	781188.56	5.94	-31289.46	-0.22	0.01	313.90
Cornaceae	75158	4087.39	-2.13	-144.77	0.04	0.00	1.36
Crassulaceae	40	-1943.48	23.01	87.29	-0.43	0.02	-0.67
Cucurbitaceae	24	0.00	0.00	0.00	-0.19	0.11	-0.10
Cupressaceae	14	-10239.08	2.80	370.15	-0.04	0.00	-3.13
Cyperaceae	379	56798.87	-20.26	-1885.12	0.42	-0.03	15.60
Droseraceae	32	0.00	0.01	0.01	0.37	-0.13	0.47
Elaeagnaceae	11	0.00	0.00	0.00	0.06	0.04	0.09
Ericaceae	200827	17163.13	-10.57	-396.34	0.17	0.00	2.09
Euphorbiaceae	64	-0.27	-28.00	-6.47	-19.14	2.64	36.98
Fabaceae	9	-	-	-	-	-	-
Fagaceae	118954	1098.04	1.14	9.56	-0.03	0.00	-0.35
Gelsemiaceae	50333	-24267.37	1.14	1005.82	-0.03	0.00	-9.98
Gentianaceae	17	0.16	375.51	18.40	-6.32	-0.27	0.49
Geraniaceae	426	-1227.64	-4.73	118.21	0.09	0.00	-1.46
Grossulariaceae	263428	4651.68	-1.78	-146.35	0.03	0.00	1.26
Hydrangeaceae	173140	10639.12	-3.10	-355.48	0.05	0.00	3.10
Hypericaceae	169	-26594.96	19.02	994.94	-0.35	0.01	-8.90
Iridaceae	99	72180.14	-97.76	-2340.63	1.67	0.02	19.08
Juglandaceae	569	-7999.53	2.54	355.15	-0.06	0.00	-3.49
Juncaceae	90	-2.46	40.75	-127.05	-0.40	-0.06	1.89
Lamiaceae	757	-13881.85	23.25	479.53	-0.48	0.00	-3.49
Lauraceae	287	139504.21	-51.81	-6325.09	1.24	0.00	71.74
Leguminosae	267440	747.38	-0.27	8.77	0.01	0.00	-0.11
Lentibulariaceae	1	-	-	-	-	-	-
Liliaceae	236	123302.37	267.79	-5400.09	-4.31	-0.08	56.57
Linaceae	120	-619906.61	50.97	25091.14	-1.13	0.00	-252.56
Lythraceae	63	1268813.01	9398.70	-65035.86	-240.77	14.54	831.87
Malvaceae	378743	4713.61	-2.96	-103.88	0.05	0.00	0.74
Melanthiaceae	54	0.00	0.00	0.00	0.00	0.05	-0.01
Menyanthaceae	78	-16134.44	-1.62	571.13	0.04	0.00	-4.85
Montiaceae	1	-	-	-	-	-	-
Moraceae	1	-	-	-	-	-	-
Nartheciaceae	1	-	-	-	-	-	-
Nymphaeaceae	122	-27430.83	-1.48	958.87	0.04	0.00	-8.06
Oleaceae	593184	4583.87	-1.23	-153.99	0.02	0.00	1.47

Plant family	No of observations	C[0]	C[1]	C[2]	C[3]	C[4]	C[5]
Onagraceae	1846	9779.17	-3.72	-251.31	0.06	0.00	1.72
Orchidaceae	291	-25786.06	5.87	904.81	-0.09	0.00	-7.67
Orobanchaceae	201	55847.82	-0.36	-1893.68	-0.05	0.00	16.23
Oxalidaceae	122	20714.72	0.48	-668.08	0.01	0.00	5.43
Paeoniaceae	38	0.00	0.00	0.00	0.00	0.01	0.00
Papaveraceae	367	7090.27	5.08	-241.65	-0.11	0.00	2.17
Pinaceae	307275	2657.00	-4.08	-32.76	0.07	0.00	-0.08
Plantaginaceae	266	-14918.03	-41.27	721.38	0.60	0.02	-7.61
Plumbaginaceae	1	-	-	-	-	-	-
Poaceae	151893	15595.57	-2.61	-531.97	0.05	0.00	4.80
Polemoniaceae	3	-	-	-	-	-	-
Polygalaceae	15	0.00	0.01	0.01	0.30	-0.27	0.54
Polygonaceae	103	52982.34	287.69	-2718.01	-6.76	0.24	34.64
Primulaceae	3730	48392.49	-9.21	-1588.23	0.15	0.00	13.12
Ranunculaceae	147394	-1297.68	-1.50	64.07	0.03	0.00	-0.63
Resedaceae	12	0.00	0.00	0.00	0.01	0.04	0.00
Rhamnaceae	138	3947.41	19.87	-121.33	-0.17	-0.05	1.00
Rosaceae	1348953	-1274.44	-0.70	74.26	0.01	0.00	-0.73
Rubiaceae	108	-15765.47	-39.33	739.74	0.22	0.10	-7.35
Rutaceae	140	-17802.44	16.94	755.50	-0.29	-0.01	-7.40
Salicaceae	299186	356.39	-0.98	-1.70	0.02	0.00	-0.01
Sapindaceae	515310	2648.95	-0.62	-70.90	0.01	0.00	0.59
Saxifragaceae	42	-15345.62	7.15	499.91	-0.10	0.00	-3.91
Scrophulariaceae	77	-6307453.68	-5858.14	262010.90	115.61	-0.39	-2710.42
Solanaceae	111141	-1248.91	-3.84	142.47	0.07	0.00	-1.77
Thymelaeaceae	211	-9008.32	2.33	305.53	0.00	-0.01	-2.58
Ulmaceae	47	-4549.21	5.87	154.27	-0.09	0.00	-1.21
Urticaceae	94	0.00	0.00	0.00	0.16	-0.02	0.10
Violaceae	9053	-6134.05	-0.32	228.91	0.00	0.00	-1.99
Vitaceae	14995	-27859.05	7.42	1176.85	-0.16	0.00	-11.81
All	**7112592**	**2038.23**	**-1.56**	**-34.13**	**0.03**	**0.00**	**0.15**

A)



B)

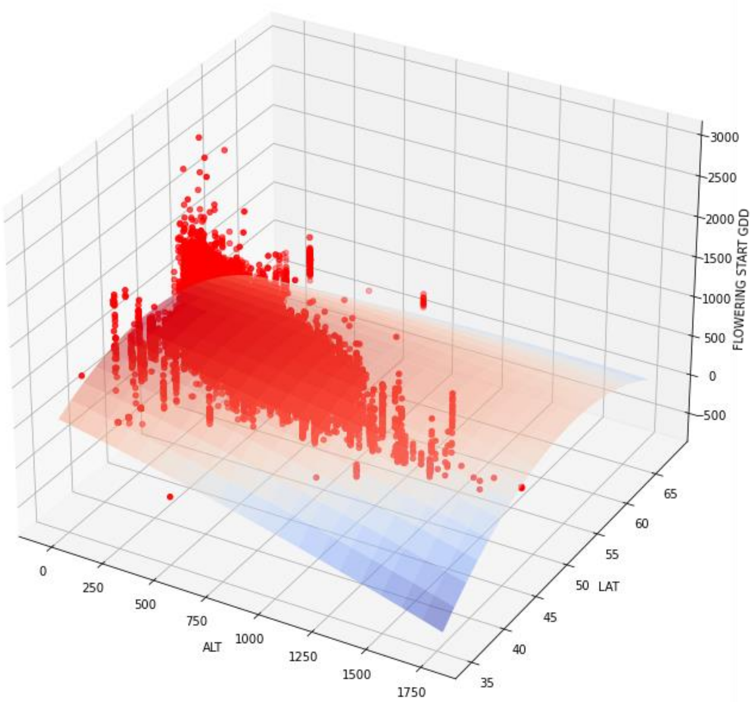


Figure 4. Predicted flowering phenology and its variation with altitude and latitude. Exemplary best-fitted surfaces for (A) Colchicaceae; (B) Leguminosae families. The red dots show GDD values for the onset of flowering plotted against the altitude (ALT) in meters above sea level and latitude (LAT) in decimal degrees.

Table 4. Comparison of the RMSEs for the onset of flowering with and without corrections for altitude and latitude (calculated using a base temperature of 0 degrees Celsius and maximum temperature of 28 degrees Celsius). If number of observations for a given species was < 3, RMSEs were not calculated.

Plant family	No of observations	without correction	with correction
Actinidiaceae	17	8.92	6.51
Adoxaceae	257380	46.45	46.55
Amaranthaceae	2	-	-
Amaryllidaceae	331584	33.42	33.28
Apiaceae	499	6.53	11.27
Apocynaceae	71	5.43	136.31
Aquifoliaceae	1	-	-
Araceae	20	6.41	6.41
Araliaceae	5	19.54	106.53
Aristolochiaceae	54	5.52	5.52
Asparagaceae	9706	16.82	20.89
Asteraceae	73	4.63	22.78
Balsaminaceae	13	8.80	48.58
Berberidaceae	113	12.42	14.34
Betulaceae	608567	39.09	39.40
Bignoniaceae	1	-	-
Boraginaceae	294	7.52	61.94
Brassicaceae	1170	18.51	19.07
Campanulaceae	205	9.66	30.18
Cannabaceae	16	22.04	23.78
Caprifoliaceae	101932	21.57	21.47
Caryophyllaceae	417	6.67	9.45
Celastraceae	266	7.39	125.11
Cistaceae	33	11.94	15.48
Colchicaceae	125718	24.95	19.81
Compositae	657554	27.55	28.16
Convolvulaceae	22	14.21	47.49
Cornaceae	75209	22.38	22.24
Crassulaceae	40	4.51	17.62
Cucurbitaceae	24	6.34	7.71
Cupressaceae	14	11.97	13.02
Cyperaceae	379	8.40	44.00
Droseraceae	32	10.84	25.07
Elaeagnaceae	11	2.71	2.71
Ericaceae	202927	23.55	26.14
Euphorbiaceae	64	4.54	7.60
Fabaceae	9	5.43	27.55
Fagaceae	119251	22.54	22.38

Plant family	No of observations	without correction	with correction
Gelsemiaceae	50333	20.46	20.46
Gentianaceae	15	15.87	183.67
Geraniaceae	426	20.12	27.92
Grossulariaceae	268770	26.41	26.24
Hydrangeaceae	173241	24.21	24.03
Hypericaceae	169	6.81	12.54
Iridaceae	99	9.94	49.22
Juglandaceae	569	17.32	12.75
Juncaceae	90	8.33	119.89
Lamiaceae	759	81.08	83.38
Lauraceae	291	181.52	181.45
Leguminosae	270594	19.67	19.35
Lentibulariaceae	1	-	-
Liliaceae	236	11.95	96.31
Linaceae	120	17.39	34.83
Lythraceae	67	17.21	212.82
Malvaceae	382983	19.42	19.10
Melanthiaceae	54	6.84	31.85
Menyanthaceae	78	5.54	10.99
Montiaceae	1	-	-
Moraceae	1	-	-
Nartheciaceae	1	-	-
Nymphaeaceae	122	9.99	13.44
Oleaceae	599479	25.01	24.85
Onagraceae	1839	13.39	13.69
Orchidaceae	291	7.65	16.40
Orobanchaceae	201	8.45	47.20
Oxalidaceae	122	25.00	25.82
Paeoniaceae	38	5.84	5.84
Papaveraceae	367	11.72	28.93
Pinaceae	309509	22.18	21.72
Plantaginaceae	266	8.68	80.79
Plumbaginaceae	1	-	-
Poaceae	155704	22.42	21.90
Polemoniaceae	3	-	-
Polygalaceae	15	4.59	139.02
Polygonaceae	103	7.65	28.84
Primulaceae	3808	30.23	84.04
Ranunculaceae	150035	28.73	30.27
Resedaceae	12	6.42	6.42
Rhamnaceae	138	19.64	20.26
Rosaceae	1364072	22.64	22.49

Plant family	**No of observations**	**without correction**	**with correction**
Rubiaceae	108	5.54	18.62
Rutaceae	141	15.48	23.23
Salicaceae	302222	27.75	27.10
Sapindaceae	520504	24.10	23.91
Saxifragaceae	42	14.55	93.81
Scrophulariaceae	77	5.27	45.54
Solanaceae	114471	21.40	21.13
Thymelaeaceae	211	9.33	33.05
Ulmaceae	47	13.49	16.44
Urticaceae	94	10.19	10.64
Violaceae	9223	18.34	16.34
Vitaceae	15310	26.64	25.99
ALL	**7191166**	**27.16**	**27.25**

2.3. Field data

2.3.1. Field data collection

The primary goal of field data collection was to gather data that could be used for the validation of floral resources maps and models developed across the various tasks within WP3, and also and to fill specific information gaps during the development of the phenological model. The field-work was conducted in three countries (Portugal, Belgium and United Kingdom) using three field protocols developed under B-GOOD and described in Milestone MS15.

These protocols are part of Tasks 3.1 and 3.3 and serve various purposes. The primary goal of Field Protocol 1: "*Assessment of plant species composition on key landscape elements/habitats important for bees*" was to determine the species composition in selected key plant communities (*i.e.* landscape elements or habitats) important for bees. Field Protocol 1 was used to determine the plant species composition of specific ALMaSS landscape elements and to confirm/validate the plant composition of some BIOEUNIS habitat types, developed in Task 3.1. The main goal of Field Protocol 2: "*Assessment of Phenology of Floral Resources for Bees*" was to determine the flower phenology of targeted plant species to construct flowering phenological curves for targeted plant species. Field Protocol 2 was used to validate the floral resource models developed in Task 3.2 (see Section 2.4). The primary goal of Field Protocol 3: "*Floral resources evaluation (detailed method)*" was to conduct a detailed evaluation of the floral resources in each landscape window with B-GOOD mini-apiaries to map resource availability. Field protocol 3 was divided into two parts: Part 1 - "*Assessment and quantification of floral resources*", aiming to determine the species composition, species cover, and flower abundance, and Part 2 - "*Flowering species characterization*", aiming to quantify the number of flowers per individual plant, and the nectar and pollen production of target plant species. Field Protocol 3 was also used to make a detailed assessment of plant species composition and plant resources at the landscape level, as well as to fill the gaps in knowledge about pollen and nectar production of some target plant species.

Field protocols have been implemented in Portugal, the United Kingdom, and Belgium. Field protocols 2 and 3 were fully implemented at the three countries. However, field protocol 1 was not implemented as a stand-alone field protocol in Portugal and the United Kingdom due to logistic and time constrains primarily caused by the COVID pandemic. However, this does not hamper our ability to obtain landscape-specific plant composition data, because the information gathered in this protocol can be derived entirely from the implementation of the first part of Field Protocol 3. As a result, for Portugal and the United Kingdom, Field Protocol 1 data were derived from the first part of Field Protocol 3. The full dataset gathered by the implementation of these three protocols is upload and available in the B-GOOD data portal (https://beehealthdata.org/datasets/1642b97c-e81e-4fad-b1bd-34c6d4900f99).

As explained above, the field data collected by the implementations of the field protocols could be categorized into three main groups: Plant Species Composition (Field Protocol 1 and Field Protocol 3: Part 1), Phenology of Floral Resources (Field Protocol 2), and Flowering Species Characterization (Field Protocol 3: Part 2). A general overview of data collected from each of these groups is presented below.

2.3.2. Plant Species Composition

One crucial point in the evaluation of the floral resources is determining the species composition and cover of "bee-friendly" plant species present in key landscape elements or habitats important for bees

The information about the species composition was used to derive the plant species composition of specific landscape elements in ALMaSS (*e.g.* roadside verge, field margins), where no information about the species composition existed from BIOEUNIS habitats due to the small scale of these elements. The plant species composition of different landscape elements and habitat types was assessed using the field data obtained from the implementation of field protocol 1 (Belgium) and field protocol 3: part 1 (Portugal and the UK). Additionally, this information may be used to confirm/validate the plant species composition of some BIOEUNIS habitats.

The main plant species composition for the selected habitats of each of the three countries is presented in Figure 5. As expected, there is evidently a clear separation between habitat types within each country and, by association, differences in plant species composition.

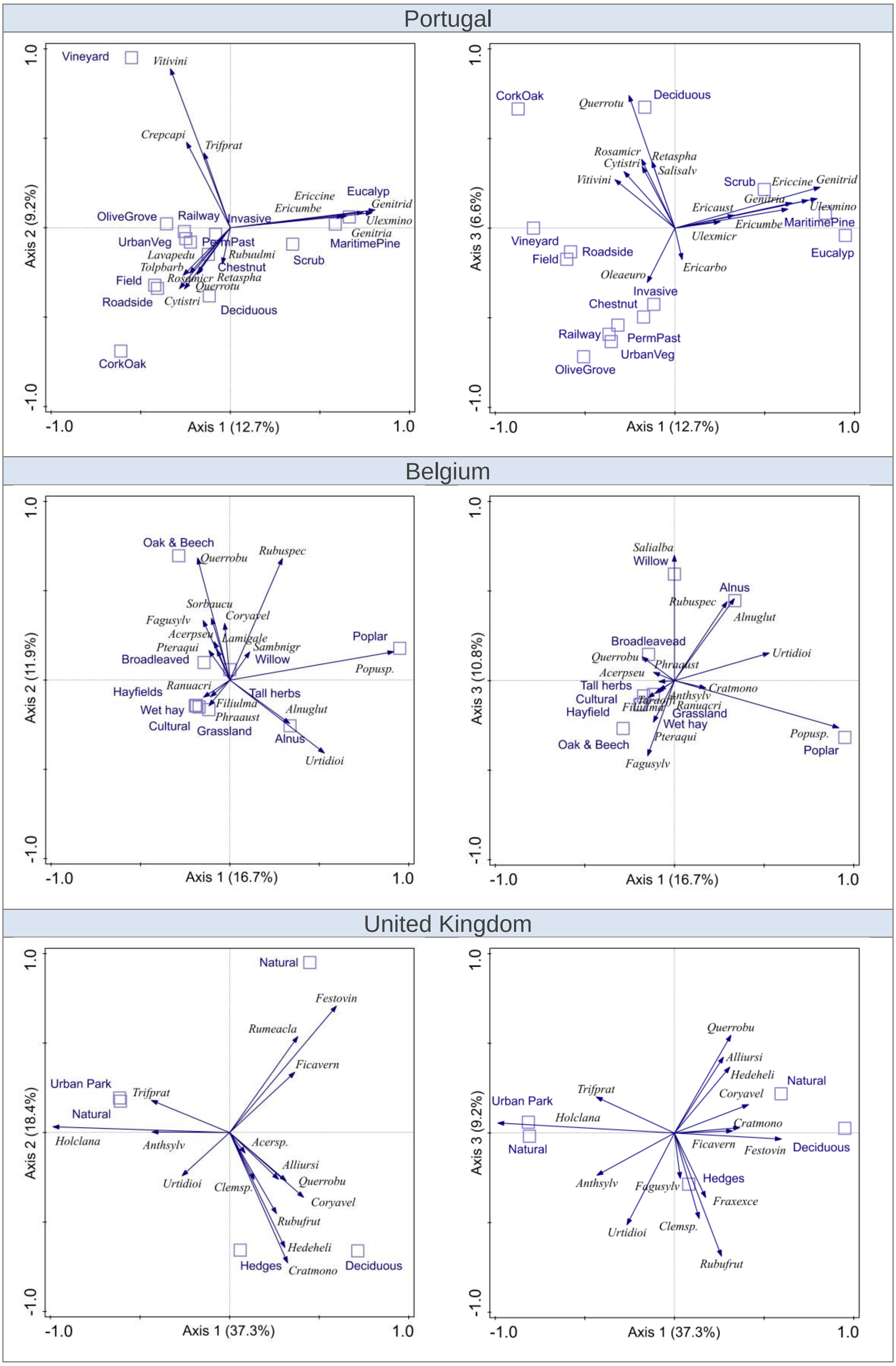


Figure 5. Multivariate ordination (PCA) of the species composition in the surveyed plant communities of Portugal, Belgium, and the United Kingdom. Arrows represent the different plant species, and squares represent the plant communities. Left panels show Axis 1 and 2 and right panels shows Axis 1 and 3 of the PCA. The plant species label is composed of the first four letters of the genus and four letters of the specific epithet. For simplification of the diagrams, only species having a contribution higher than 15% are represented.

2.3.3. Phenology of Floral Resources

Information about the phenology of floral resources, namely bee-friendly plant species, is fundamental to understand the availability of resources for bees over time. Together with the information about the plant species composition, abundance, and coverage, flowering phenology (particularly of those bee-friendly species) allows to determine the floral resources available for bees across both space and time.

The information on the phenology of the floral resources was used to validate the updated flowering phenology models (see Section 2.4.) and was obtained by the implementation of the Field Protocol 2 for previously selected target plant species. In total, there were 94 plant species surveyed in the three countries: 40 species in Portugal, 20 in Belgium and 34 in the United Kingdom. A full list of surveyed plant species by country can be found in Table 5.

Table 5. List of plant species monitored for flowering phenology in Portugal, Belgium, and the United Kingdom.

Country	Species	
Portugal	*Arbutus unedo*	*Erica umbellata*
Portugal	*Calluna vulgaris*	*Eucalyptus globulus*
Portugal	*Carduus tenuiflorus*	*Galactites tomentosus*
Portugal	*Carlina hispanica*	*Genista tridentata*
Portugal	*Castanea sativa*	*Hypericum perforatum*
Portugal	*Chamaemelum sp.*	*Jasione montana*
Portugal	*Cirsium vulgare*	*Lavandula pedunculata*
Portugal	*Cistus crispus*	*Lavandula stoechas*
Portugal	*Cistus ladanifer*	*Lavatera cretica*
Portugal	*Cistus monspeliensis*	*Lithodora prostrata*
Portugal	*Cistus salviifolius*	*Rosmarinus officinalis*
Portugal	*Crataegus monogyna*	*Rubus ulmifolius*
Portugal	*Cytisus multiflorus*	*Salix sp.*
Portugal	*Cytisus striatus*	*Silybum marianum*
Portugal	*Digitalis purpurea*	*Trifolium campestre*
Portugal	*Echium plantagineum*	*Trifolium repens*
Portugal	*Echium tuberculatum*	*Ulex europaeus*
Portugal	*Erica arborea*	*Ulex micranthus*
Portugal	*Erica australis*	*Ulex minor*
Portugal	*Erica cinerea*	*Ulex sp.*
Belgium	*Acer campestre*	*Prunus serotina*
Belgium	*Acer pseudoplatanus*	*Prunus spinosa*
Belgium	*Alnus glutinosa*	*Robinia pseudoacacia*
Belgium	*Castanea sativa*	*Rubus sp.*
Belgium	*Cirsium arvense*	*Salix alba*
Belgium	*Corylus avellana*	*Salix caprea*
Belgium	*Crataegus monogyna*	*Taraxacum officinale*
Belgium	*Frangula alnus*	*Tilia platyphyllos*
Belgium	*Hedera helix*	*Trifolium pratense*

Country	Species	
Belgium	*Prunus avium*	*Vicia cracca*
United Kingdom	*Camellia sp.*	*Hyancinthoides non-scripta*
United Kingdom	*Quercus robur*	*Ilex sp.*
United Kingdom	*Acer sp.*	*Impatiens glandulifera*
United Kingdom	*Achillea millefolium*	*Ligustrum sp.*
United Kingdom	*Bellis sp.*	*Lotus cornicalatus*
United Kingdom	*Borago officinalis*	*Malus domestica*
United Kingdom	*Brassica napus*	*Myosotis arvensis*
United Kingdom	*Buddleia variabilis*	*Prunus avium*
United Kingdom	*Castanea sativa*	*Rubus fruticosus*
United Kingdom	*Centaurea nigra*	*Salix sp.*
United Kingdom	*Cirsium*	*Senecio jacobaeae*
United Kingdom	*Citrus aurantifolia*	*Sorbus sp.*
United Kingdom	*Clematis sp.*	*Taraxacum sp.*
United Kingdom	*Crataegus monogyna*	*Trifolium pratense*
United Kingdom	*Epilobium sp.*	*Ulex europaeus*
United Kingdom	*Filipendula ulmaria*	*Viburnum sp.*
United Kingdom	*Hedera helix*	*Vicia sp.*

A general overview of the floral resources available for bees across the year for each country is presented in Figure 6 (due to the high number of species surveyed, for graphical simplicity purposes, instead of plotting the average percentage of flowers per species, a GAM technique was adopted as a way to visualise the flowering peaks in each country across time, without an aim to make any type of prediction).

It is evident that the flower resources available for bees vary from country to country with a bimodal distribution in Portugal (peaks in spring and autumn) and unimodal distributions in Belgium (peak in spring) and the UK (peak during summer). Resource availability for bees reflects a country's plant species composition and also the result of different environmental factors (*e.g.* rain, temperature, light).

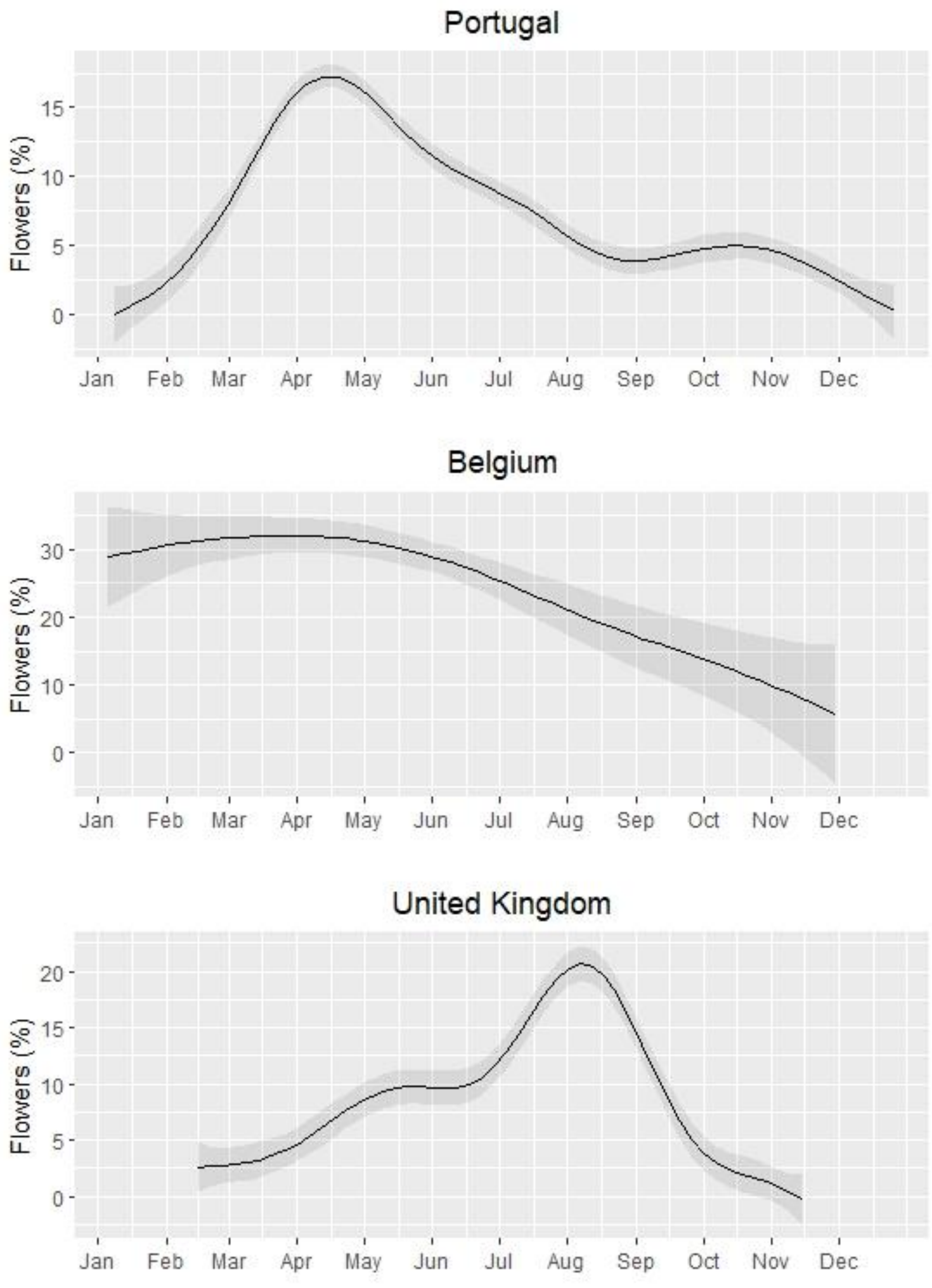


Figure 6. Mean percentage of flowering predicted from a generalized additive model (GAM) of the surveyed plant species in Portugal, Belgium, and the United Kingdom. The grey area represented the 95% confidence intervals of the predicted value.

2.3.4. Flowering Species Characterization

Information about the amount of nectar and pollen available in flowers of each bee-friendly species is essential to quantify the amount of food the floral resources can provide for bees.

Part of the information about the pollen and nectar already exists for some species in the literature and was compiled in Deliverable D 3.2 (Database on Nectar & Pollen Production). However, for several plant species, information is non-existent. For that purpose, for target plant species where information about pollen and nectar was missing or is unreliable, the pollen and nectar contents were measured with the objective of filling these gaps by implementing part 2 of Field Protocol 3.

The main results of the quantification of the pollen and nectar of the selected target species are presented in Table 6. The target plant species selected among the countries is very diverse, with species of different habits/life forms (*i.e.*, trees, shrubs and herbs). It is also evident for some of the same plant species measured in different countries (*e.g. Trifolium*, *Taraxacum*, *Rubus*), that the quantity of pollen and nectar exhibit high natural variation, probably due to environmental factors.

Table 6. Flowering characterization of the target plant species in Portugal, Belgium, and the United Kingdom.

Country	Species	No. of Anthers / flower	No. Of pollen grains / anther	No. Of pollen / flower	No. Of pollen / inflorescence	No. of flowers per flower cluster / catkin	Nectar volume / flower (µl)	Sugar concentration / flower (% Brix)	Sugar concentration / flower (µg)
UK	*Anthriscus sylvestris*	5	37	185			0.5	1	9
UK	*Bellis perennis*	50	31	1550			0.5	0.1	1
UK	*Buddleja davidii*	4	159	636			1	4	41
UK	*Centaurea nigra*	35	111	3885			2	14.8	148
UK	*Cirsium arvense*	45	4	180			1	6.1	62
UK	*Epilobium hirsutum*	8	51	408			2.5	27	301
UK	*Hedera helix*	5	25	125			4.5	48.7	597
UK	*Impatiens glandulifera*	5	124	620			5	216.2	3305
UK	*Ligustrum vulgare*	2	15	30			0.5	6.24	64
UK	*Lotus corniculatus*	10	56	560			1	10.7	111
UK	*Myosotis arvensis*	5	25	125			1.5	16.4	175
UK	*Ranunculus acris*	12	23	276			1	1.1	11
UK	*Rubus fruticosus*	14	30	420			0.5	3.1	31
UK	*Senecio jacobaea*	10	44	440			0.5	3.8	38
UK	*Taraxacum agg.*	40	102	4080			1	1.7	17
UK	*Trifolium pratense*	10	64	640			1	10.8	113
UK	*Ulex europaeus*	10	12	120			0.5	0.7	7
UK	*Vicia sativa*	10	96	960			1.5	26.7	297
BE	*Acer campestre*	8	603.6	65744		13.3	12.07	32.2	
BE	*Acer pseudoplatanus*	8	7610	4898320		80.8	172.03	18.07	
BE	*Alnus glutinosa*	4	1037	3482080		844			
BE	*Castanea sativa*	4	2500	2976400		287	5.79	30.97	

Country	Species	No. of Anthers / flower	No. Of pollen grains / anther	No. Of pollen / flower	No. Of pollen / inflorescence	No. of flowers per flower cluster / catkin	Nectar volume / flower (µl)	Sugar concentration / flower (% Brix)	Sugar concentration / flower (µg)
BE	*Cirsium arvense*	1	3380	332740		98.7	2.19	38.6	
BE	*Corylus avellana*	4	5930	5582400		237			
BE	*Crataegus monogyna*	12	700.5	8406			1.45	11.57	
BE	*Frangula alnus*	5	600.5	3002.5			0.34	14.9	
BE	*Hedera helix*	5	6900	991000		28.3	3.12	35.33	
BE	*Prunus avium*	29.8	7120	212410			0.9	23	
BE	*Prunus serotina*	24	654	15696			0.67	23.23	
BE	*Prunus spinosa*	22	492.4	10832.8			0.73	17.97	
BE	*Robinia pseudoacacia*	10	780.2	7802			0.77	58.03	
BE	*Rubus sp.*	93.3	1030	96751			1.33	19.27	
BE	*Salix alba*	2	3630	7260		224	60	17.4	
BE	*Salix caprea*	2	5370	2761400		258	25.03	17.5	
BE	*Taraxacum officinale*	5	303.6	1518			0.7	39.8	
BE	*Tilia platyphyllos*	32.5	313	10198.9			1.43	38.1	
BE	*Trifolium pratense*	10	258	1986.4			0.23	0.3	
BE	*Vicia cracca*	8	248.3	1986.4			0.6	28.3	
PT	*Andryala integrifolia*			1280	120125	93.4			
PT	*Arenaria montana*						0.09		
PT	*Carthamus lanatus*			3565	70255	20.2			
PT	*Centranthus calcitrapae*	1	275	275					
PT	*Chamaemelum fuscatum*			1370	190385	143.6			
PT	*Cichorium intybus*			3050	49215	16.3			
PT	*Cladanthus mixtus*			3535	456010	130.3			
PT	*Crepis capillaris*			2745	112350	40.5			
PT	*Cytisus multiflorus*	9.57	991.84	9642.86					
PT	*Cytisus striatus*	10	10837.5	108375					
PT	*Delphinium gracile*						0	0	0
PT	*Diplotaxis catholica*	6	520.83	3125					
PT	*Echium plantagineum*						0.48	41	
PT	*Erica arborea*	8	21375	2671.88					
PT	*Erica australis*	8	1431.25	11450					
PT	*Erodium moschatum*	5	300	1500					
PT	*Fumaria muralis*	4.6	109.75	495					
PT	*Geranium molle*	10	120	1200					
PT	*Geranium purpureum*	10	117.5	1175					
PT	*Gladiolus illyricus*	3.1	6766.67	20700			0.39	29.3	
PT	*Glandora prostrata*	5	12860	64300			0.68	31.68	
PT	*Hirschfeldia incana*	6	4945.83	29675			0.05		
PT	*Hypericum perforatum*	64.3	658.92	42350					

Country	Species	No. of Anthers / flower	No. Of pollen grains / anther	No. Of pollen / flower	No. Of pollen / inflorescence	No. of flowers per flower cluster / catkin	Nectar volume / flower (µl)	Sugar concentration / flower (% Brix)	Sugar concentration / flower (µg)
PT	*Jasione montana*	4.2	4732.08	18475					
PT	*Lavandula pedunculata*						0.45	29	
PT	*Leopoldia comosa*	5.6	191.67	1075					
PT	*Linaria spartea*	4	32600	130400					
PT	*Linum bienne*	5	262.5	1312.5					
PT	*Papaver dubium*	120.9	8230	1003260					
PT	*Raphanus raphanistrum*	6	6175	37050			0.15	33.5	
PT	*Rosmarinus officinalis*	2	1875	3750					
PT	*Scolymus hispanicus*			3025	177255	57.6			
PT	*Senecio vulgaris*			295	10155	34			
PT	*Silene gallica*						0.11	15	
PT	*Silene portensis*	10	1310	13100					
PT	*Simethis mattiazzi*	6	6701.67	39600			0.31		
PT	*Sonchus oleraceus*			405	41525	94.2			
PT	*Spergularia purpurea*	9.6	625.95	6175					
PT	*Tolpis barbata*			1985	142315	72.7			
PT	*Trifolium campestre*	10	22.5	225					
PT	*Trifolium pratense*	10	36.5	365					
PT	*Trifolium repens*	8.4	322.74	2600					
PT	*Trifolium resupinatum*	10	66.5	665					
PT	*Verbascum virgatum*	5	11560	57800			0	0	

2.4. Validation of flowering phenology models with field data

Validation of flowering phenology models was performed based on field data gathered in Belgium, Portugal and the UK (see section 2.3.3). For Belgium it was possible to validate flowering phenology models for all 20 species investigated in the field. In case of the UK, some assumptions regarding species had to be applied as some records had only information at the genus level (e.g., all records reported for *Acer* sp. were assumed to represent *Acer campestre* and all records reported for *Ilex* sp. were assumed to represent *Ilex aquaifolium*; see Appendix C). These assumptions were based on species distribution maps from the Online Atlas of the British and Irish Flora (https://plantatlas.brc.ac.uk/). As the *Clematis* genus is very broad and flowering time differs considerably between species from this genus, we decided to not include these records in the validation process. In a nutshell, it was possible to validate flowering phenology models for 33 of 34 species investigated in the field. Although the number of species for which flowering phenology was investigated in Portugal was the highest among all three countries (N=40), it was possible to validate flowering phenology models for only 12 of them. The rest of the species had no flowering phenology models due to no records available in the current version of the flowering database. To overcome this aspect, it is planned to increase the phenological database with phenological data for southern European species using data gathered from the Portuguese Flora-on project (https://flora-on.pt/).

For each of the records gathered in the field we predicted the flowering period based on the species name, year of observation and information about latitude, longitude and altitude according to our optimized flowering phenology models (with base temperature of 0 degrees Celsius and maximum temperature of 28 degrees Celsius) corrected and un-corrected for altitude and latitude. We then assessed if the flowering period observed in the field remained within the range predicted by the flowering phenology model (mean GDD +/- SD; Appendix C).

In general, we were able to predict the onset of flowering much better than the end of flowering. Flowering phenology models corrected for altitude and longitude predicted better the end of flowering but were less able to predict the start of flowering (Figure 7).

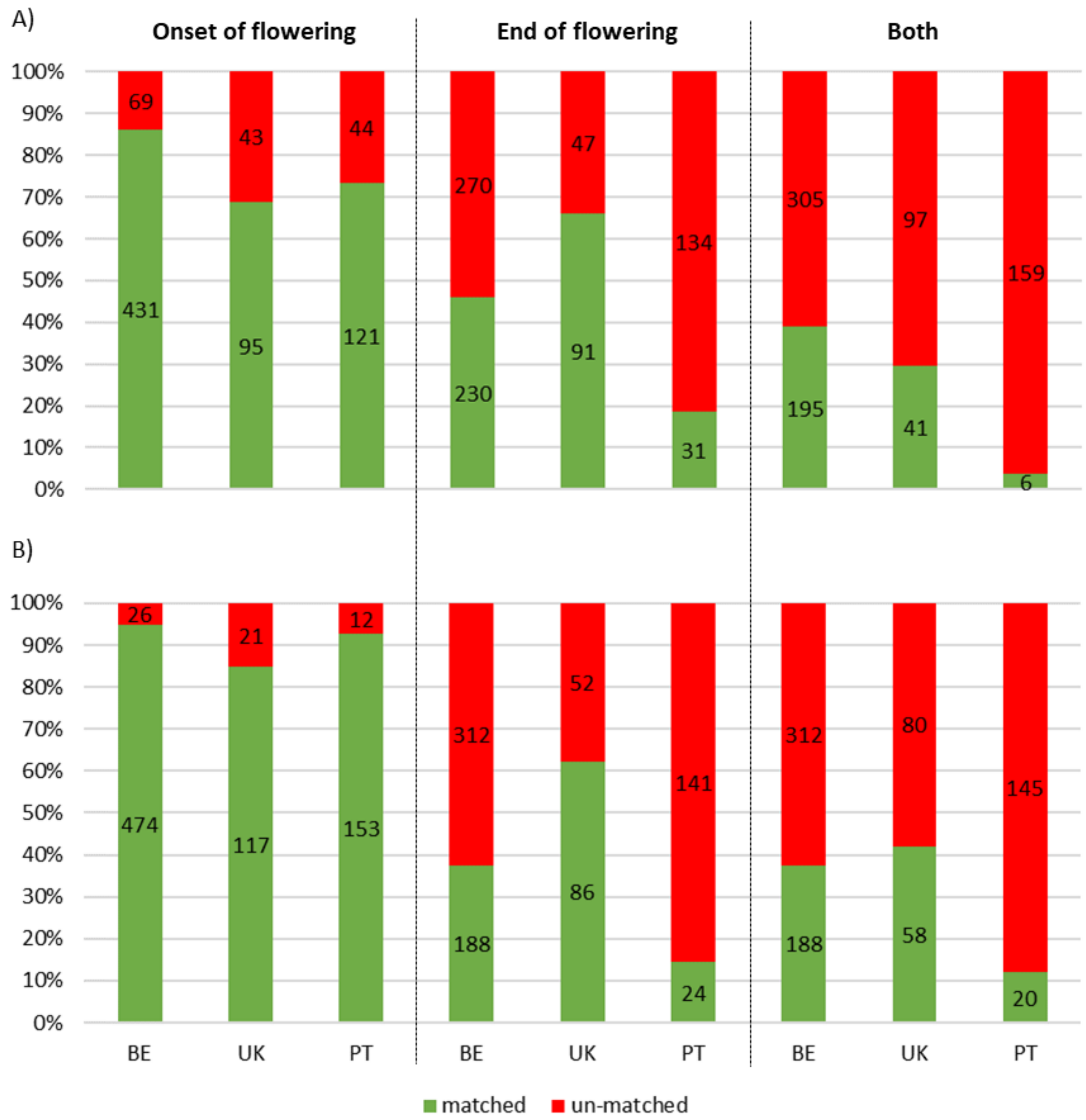


Figure 7. Results of validation of flowering phenology models with field data. Numbers indicated number of observations correctly or un-correctly predicted within the range of flowering period (mean GDD +/- SD) by the optimized flowering phenology models (with base temperature of 0 degrees Celsius and maximum temperature of 28 degrees Celsius) corrected (A) and un-corrected (B) for altitude and latitude.

2.5. Important remarks and discussion of the results

The floral resource models can be considered 'living' models and are designed in such a way that they can be easily updated when more/additional data on pollen, nectar or sugar production, phenology of bee-friendly species or plant species composition in landscape elements important for bees, are made available. It is the intention that any new data be added to the database during and also after the project finishes.

The accuracy assessment and validation of flowering phenology provided in this deliverable are based on the current version of the flowering database. The next step includes generating the flowering phenology models for important southern European 'bee-friendly' species for which no records are available in the phenology database. This will be done based on data from the Flora-On (https://flora-on.pt/) portal coordinated by the Portuguese Botanical Society. That, however, requires applying a special methodology to deal with more general data on flowering phenology, as most of flowering records gathered in the Flora-On portal have no information of flowering stage. This new methodology will allow one to use the rest of field data on phenology of floral resources gathered in Portugal in the validation process.

The correction for altitude and longitude applied to the flowering resource models was based on the surfaces generated at the plant family level, which for some species did not improve the models' accuracy. It seems that for same families / species the number of observations was too low to generate the well fitted models. We plan to further investigate the dependence of flowering on altitude and latitude at the species level.

The validation of the flowering resource models based on gathered field data showed that, although we are good in predicting the onset of flowering, the end of flowering is rather poorly predicted to be too early than observed. The poorer prediction of end of flowering compared to onset of flowering could be related to the number of records based on which this stages of flowering are being modelled (320974 records on the end of flowering compared to 7195055 records on the onset of flowering). The other reason may be related to the fact that most of the flowering records in the phenology database come from the Continental pedo-climatic zone while validation was performed in the Atlantic and Mediterranean zones. We are therefore in the process of generating separate flowering resource models for each pedo-climatic zone to see if that improves accuracy assessment and validation results.

3. List of appendices

Appendix A: Results of accuracy assessment for flowering phenology
[Accuracy_assessment_flowering_phenology.xlsx]
Appendix B: Parameters for final floral phenology models [Flowering_phenology.xlsx]
Appendix C: Validation results [Validation_results.xlsx]

Appendices are available in a GitLab Repository:
(https://gitlab.com/ALMaSS/floral_resource_models).

4. References

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