

Predicting the effect of sowing flowering field margins on bumblebee abundance: Using the BEE-STEWARD model.

RESEARCH REPORT
ERNST MILTENBURG



Author:

Ernst Miltenburg

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Predicting the effect of sowing flowering field margins on bumblebee abundance
Using the BEE-STEWARD model

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Summary

Pollination is globally important for food production. However, pollinator numbers are declining and species diversity is under threat. This is the result of many factors, most of which are landscape related. Bumblebees are used as a flagship species representing pollinators, as they are both well-known and arguably the most important pollinator group. A stronger case for landscape scale measurements aimed at improving pollinator numbers and diversity can be made if their effects and efficiency can be predicted more accurately. In line with the aims of the international BEESPOKE project, a stochastic model providing such predictions has been studied. This model, the BEE-STEWARD model, is publicly available and open source. It models both foraging behaviour and in-colony dynamics. The BEESPOKE trial locations were modelled as research area and different applications (or lack thereof) of flowering field margins were modelled as the input variable. This research had 2 goals: Firstly, to identify predicted increase per unit area of BEESPOKE seed mixture and discuss influences on this. Secondly, to identify optimal popular application structure and discuss why this is optimal.

An area of 1km² around the BEESPOKE trial sites was modelled in BEE-STEWARD. A base/control scenario based on 2019 crop data was compared to results of the same areas but with a variety of added flower rich habitat. This variety consisted of 4 main groups: one group following the exact application as applied in the BEESPOKE trials, one application of varied 3 meter wide margins, one group of varied 6 meter margins and one group wherein entire fields had been replaced with flowering habitat instead of only adding margins. Each combination of research location and base/experimental scenario was run 7 times, with 7 unique predetermined random seeds. Each run lasted 5 simulated years. The initial bee species and their relative abundances were based on field observations in Fryslân, a northern province of the Netherlands.

This led to a final total of 1603 simulations, outputting slightly below 3 million data points. The cover of flower rich habitat in the simulations varied from 0% to near 40%. In the application as applied in the BEESPOKE trial, each hectare of flower rich area was predicted to lead to 400.0 (95% C.I. 150.9 – 649.3) adult bumblebee queens after 5 years. This is roughly double the amount as was predicted for the base/control situation. In this scenario, flower rich cover was a significant predictor of total adult queens ($W=9.903$, $df=1$, $p=.002$). The 3 and 6 meter wide margin scenarios scored higher than the other scenarios with a predicted number of queens per hectare of 795.9 (95% C.I. 558.1 – 1033.6) and 766.3 (95% C.I. 593.0 – 939.6) respectively. Both these predictions cannot be explained by pure chance (3m wide: $W=60.367$, $df=1$, $p<.001$, 6m wide: $W=75.138$, $df=1$, $p<.001$). For full field replacements this number was the lowest at 228.0 (95% C.I. 159.2 – 296.8). In the full field replacements, flowering habitat cover was also a significant predictor ($W=42.214$, $df=1$, $p<.001$). The species distribution reliably changed during the 5 year runs. The 2 most abundant species declined in numbers (*B. terrestris* and *B. pascuorum*), 2 other species took over as most dominantly abundant species (*B. lapidarius* and *B. hortorum*). The other species (*B. pratorum*, *B. hypnorum* and the *Psithyrus* spp.) started at a relatively low abundance and further declined during the 5 year simulations. This led to the extinction of *Psithyrus* spp. in all simulations.

Margins (both 3 and 6 meters wide) were predicted to be the most efficient per unit area. It is hypothesised that this is due to the resources being more evenly spread out over the area when compared to entire fields of flower rich area. A more even distribution leads to lower average foraging distances when colony placement is random. The BEESPOKE trial had an efficiency in the middle of the whole fields and the margins. This makes sense, as the BEESPOKE application consists of a mixture of some floral fields and floral margins. Crop rotation also played a role, especially when the amount of added flower rich area is relatively low (<0.1ha/km²).

The species distribution at the end of modelling runs differed from expected. This is likely due to an

underestimation of early season floral resources, as well as a lack in species specific differentiation of life history traits. This was both due to the nature of this specific research (nesting was unlimited) and due to a lack of sources on species specific traits: Only 4 out of 21 life history variables available in BEE-STEWARD are currently differentiated between species, the rest follows data for *B. terrestris*. The possibility of multiple colony cycles in a single season is not (yet) incorporated in the BEE-STEWARD model. In contrast to the other bumblebee species, cuckoo bees are modelled with different mechanics than they adhere to in real life.

The BEE-STEWARD model provides a powerful tool for estimating the carrying capacity in an area and how this capacity is affected by changes in the landscape. Crop rotations likely have an important effect on pollinator populations. It is concluded that the more heterogeneously spread margins are more efficient than the more concentrated floral patches.

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1. Introduction

1.1. Pollination and pollinator decline

What was the last supper that you've had? Chances are that that meal would not have been possible without pollinating insects; from the 124 leading food crops, at least 87 rely on animal pollination. This translates to at least 35% (weight by weight) of the global yearly food production. These globally leading crops are pollinated by 47 different species of bees, with 8 other insects and 2 bird species also providing important pollination services. (Klein, et al., 2007) Unfortunately, pollinator populations are declining. (National Research Council, 2007) (Kosior, et al., 2007) (Nieto, et al., 2014)

Pollinator populations are declining as a result of multiple factors acting together. These include, but are not limited to: Agricultural intensification, livestock farming (over-grazing), urban development and pollution (including pesticides and herbicides). Within European bee species, intensification of agriculture together with a decrease in landscape complexity is the most common threat to already endangered and not currently endangered species alike. (Nieto, et al., 2014) (Potts, et al., 2010) (Carrié, et al., 2017) To preserve biodiversity and protect our own food supply, action is needed to mitigate these threats to pollinating insects.

Planting flowering field margins around agricultural fields is a proposed solution to increase pollinator populations in agricultural landscapes. This increases landscape complexity and provides necessary floral and habitat resources that land used for intensified agriculture does not provide. Currently these field margins are seeing good results at a pilot scale. However, there is uncertainty about the area of flowering field margins necessary on a landscape scale to increase pollinator populations. (Hackett & Lawrence, 2014) (Wiepkema, 2019) (Frans, 2015) (Marja, et al., 2018) (Feltham, et al., 2015) Another option is the use of intercropping systems, whereby multiple crop species are farmed in the same plot. This also increases landscape complexity and provides more resources within the agricultural fields themselves. As with flowering field margins, there are no predictions on exactly how much needs to change on a landscape scale to rejuvenate pollinator populations. (Van Apeldoorn, et al., 2018) (Hodgkiss, et al., 2019) (Van Apeldoorn, et al., 2017) (Marion, n.d.) (Van Wijk, et al., 2015) De-intensification of agriculture in the form of food forests is also currently being explored. This is a more extreme approach that rebuilds agricultural systems from the ground up. Although food forests could be modelled in the same way as will be discussed in the methods, they are outside the scope of this research.

Although there is a lot of research about field margins and intercropping, these measures aren't widely used yet. With a clear prediction of what is necessary for a significant increase in pollinator numbers, policy makers will gain a more compelling argument to invest resources into these measures and therefore into biodiversity.

1.2. Modelling approaches for measuring success of flower strips

In many fields of work (e.g. bioreactor design, weather forecasts, traffic flow analysis, crowd management, (genetic) population management), mathematical models are already used to provide quantitative predictions before any real life changes are implemented.

In a review by Becher et al. (2013), it became apparent that there have been many models analysing and predicting (the effects of) honeybee foraging behaviour, colony dynamics, *varroa* infestation and pesticide exposure. However, there was no method of analysing the complete system, consisting of all these aspects and their interactions combined. This led to the development of the BEEHAVE model, later adapted to the BEE-STEWARD model for use with bumblebee species. (Becker, et al., 2018) The BEE-STEWARD model stochastically determines the behaviour of the simulated bees on every simulated day, based on whether or not certain stimuli are higher than the threshold for a given behaviour (with all behaviours evaluated in order of importance).

There is also a model creating relative abundance numbers for different habitats of pollinators (implicitly defined as wild bee species): the Lonsdorf model. (Lonsdorf, et al., 2009) This model has a purely mathematical basis and calculates floral and habitat suitability's as a ratio (between 0% and 100% suitable). It also calculates relative pollinator abundances based on the spatial distribution of the floral and habitat suitability's.

Besides these, there exists a partial (foraging only) model for solitary bee species (SOLBEE). (Everaars & Dormann, 2014)

Creating a complete model for all pollinating species is not currently feasible within the time and effort constraints of this research, especially since important pollinator groups lack complete (or even partial) models (e.g. Diptera spp. and solitary bees). Therefore this research will focus on applying the already existing models. The BEE-STEWARD model is the most detailed of the existing models and will be used for this research.

1.3. Current Dutch and international pollinator initiatives

To fully understand what modelling output will be most beneficial for solving the problem of pollinator decline, it is good to know what initiatives are already operating in this field.

In the Netherlands, pollinator decline is combatted by a multitude of varying initiatives. The ministry of agriculture, nature and food quality identified over 70 initiatives, by 43 organizations, in their national bee strategy plan: “Bed and Breakfast for bees”. Relevant for farmers are the national subsidies available for herb rich field borders (allocated by the governmental organization “Bij12”, based on the “Agraric Nature and Landscape management (ANLb)” as part of the “Subsidy structure Nature and Landscape (SNL)”). (Ministerie van Landbouw, Natuur en Voedselkwaliteit, 2018) (Bij12, n.d.) In the national bee strategy plan the government also formulates a focus on improving the European Common Agricultural Policy (CAP) in regards to pollinators.

Besides the European CAP, there are also a number of other international initiatives relevant to pollinators. These include, but are not limited to: The EU Pollinators Initiative (European Union), FAO's Global Action on Pollination Services for Sustainable Agriculture (United Nations Food and Agriculture), the International Initiative for the Conservation and Sustainable Use of Pollinations (Convention on Biological Diversity) and BEESPOKE (EU, specifically the North Sea Regional Development Programme). All these projects and policies have similar goals, emphasizing the importance of knowledge, awareness and effective actions. They differ in their scale and their mix between focussing on policy, science and/or awareness raising.

This research report is produced in the framework of the BEESPOKE project. BEESPOKE is a project from the EU North-Sea Region programme, initiated after, and in line with, the 2018 European Commission pollinator initiative.

1.4. The BEESPOKE project

BEESPOKE stands for: Benefitting Ecosystems through Evaluation of food Supplies for Pollination to Open up Knowledge for End users. The BEESPOKE project is an international project supported by the North Sea Programme of the European Regional Development Fund of the European Union. Its goal is to increase levels of pollinators and crop pollination at local and landscape scales by providing land managers and policy makers with new expertise, tools and financial knowledge to create more sustainable and resilient agro-ecosystems.

An important part in generating the new expertise, tools and financial knowledge is to measure the effect of proposed ideas in a set of trial locations. In the eight Dutch trial locations a specific flower rich seed mixture for application in field borders will be tested. Using BEE-STEWART, the Dutch trial locations will be modelled, with a variety of seed mixture applications. In this way the predictions can, in a later report, be referenced to the actual real life results of the trials. The exact scenarios that will be modelled are explained in chapter 2.3. and 2.4. (p. 16-18).

Using the BEE-STEWART model fits in the BEESPOKE project as a means to better predict the effectiveness of the BEESPOKE seed mixture and different application scenarios thereof. Within the BEESPOKE project, a team at the University of Gent has implemented the Lonsdorf model to better predict pollinator services and the effect of management thereon. The Lonsdorf model focusses on several species of wild bees, grouped by similarities in lifestyle (mainly nesting choices).

These two sub-projects will provide future opportunity to compare the different predictions made by the two (BEE-STEWART and Lonsdorf) approaches and thereby assess validity and complementarity.

1.5. Bumblebees as a flagship species group

Although pollination is done by a range of different animal species, bumblebees are generally assumed to be a very important group with in these pollinators. They have been shown to compromise the greatest number of links in ecological pollinator networks. (Memmott, et al., 2004) Bumblebees outnumber other pollinating species groups in terms of interactions with flowers. (Brosi, et al., 2017) Bumblebees are also important species in buzz pollination, where flowers only release pollen when stimulated by vibrations. The relatively large size of bumblebees creates higher amplitude vibrations, leading to more pollen released per flower visit. (Vallejo-Marín, 2018) (Larson & Barret, 1999) (De Luca, et al., 2013) (McIntyre, et al., 2008) For all these reasons bumblebees seem the logical candidate to be a flagship species group to model the pollinator guild¹.

With the BEE-STEWARD model, the effect of flowering areas on bumblebee populations will be quantified. This will provide new information on the conditions in terms of area of flowering field margins necessary for successful positive change in bumblebee populations.

¹ A guild is defined as the group that encompasses all species that make use of similar resources in a similar way within their ecosystems. [A specific resource strategy as such is also called an ecological niche, a guild is defined as all species within the same ecological niche.]

1.6. Conceptual model

The conceptual model in figure 1 shows the place of predictive modelling in the management of bumblebee populations. Different drivers influence landscape management decisions. These decisions affect the amount of floral resources and suitable nesting sites in an area and thereby affects the bumblebee population. Predictive modelling can increase the quality of evaluating the biodiversity aspects of proposed management plans. This strengthens conservation arguments and there effect on management decisions. Furthermore, predictive modelling can help to optimally apply conservation measures, leading to reductions in cost per effect size, however, modelling does take effort (as opposed to not doing it). Therefore the effect between “profit” and “predictive modelling” is double sided.

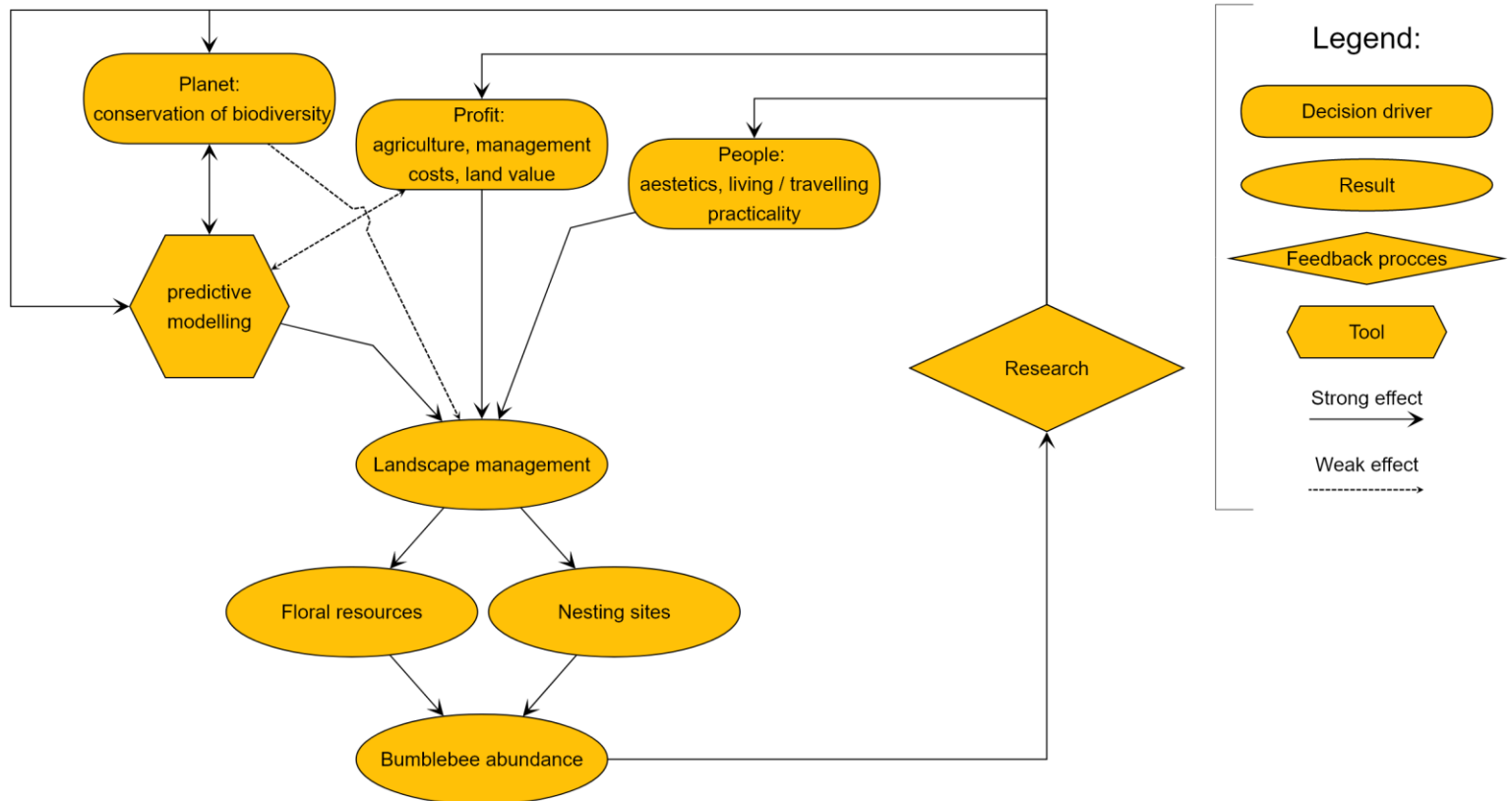


Figure 1: Conceptual model showing the placement of predictive models in management of bumblebee populations.

1.7. Goals & research questions

The primary goal of this research was to apply the current modelling knowledge of BEE-STEWARD to the BEESPOKE seed mixture and analyse the predicted effect of this flower rich habitat. The BEESPOKE seed mixture was modelled in a number of different ways, varying both implementation and area. These modelling scenarios are described in chapter 2.3. (p. 16&17). The goal of these modelled scenarios is to make the quantitative effects on pollinators insightful, in terms of increase per unit area and optimal application structure of flowering areas.

This leads to the following goals and resulting questions:

Research goals:

- Identify predicted increase per unit area of BEESPOKE seed mixture and discuss influences on this.
- Identify optimal application and discuss why this is optimal.

Primary research question:

- What is the predicted quantitative effect of applying BEESPOKE seed mixture on the modelled number of Bumblebees per unit area in the trial locations in different scenarios using the BEE-STEWARD model?

Sub questions:

- What is the quantitative effect of BEESPOKE seed mixture per unit area?
- What is the optimal application?

2. Methods

2.1. Modelled locations

There are eight areas in the Netherlands where application of the BEESPOKE seed mixture takes place (see appendix A for the exact contents of the BEESPOKE seed mixture). The areas lie in the north-east of the province Fryslân. All eight areas are shown in figure 2. These areas are all rural areas, centred on the farms where the BEESPOKE trial locations are. They have a clay soil with ample ditches for water management. These ditches and their edge vegetation provide nesting habitat for bumblebee species, as banks and tussocks are generally important aspects in bumblebee nest sites. (Kells & Goulson, 2003) The cyan circles in figure 2 signify an area of 1km², centred on the BEESPOKE trial locations. These 1km² areas are the research areas that were modelled in BEE-STEWARD.



Figure 2: The location of the eight BEESPOKE trial locations in the north-east of province Fryslân in the Netherlands. The 1km² research areas surrounding the locations are also drawn.

Area size

Literature on the foraging range of Bumblebees is conflicting. Flight ranges for *B. terrestris* are reported up to 1.5 km (with number of visits declining after roughly 500 m) by Osborne et.al. (2008). A maximum of 631 m (mean 275,3 +/- 18,5 m) is reported by Osborne et.al. (1999). A maximum flight distance mean of 257 +/- 125 m is reported by Woodgate et.al. (2016).

In the BEE-STEWARD model the detection probability of a floral patch for every colony is defined as $P = e^{\lambda*d}$ where P is the detection probability, λ is -.005 and d is the distance to the colony in meters. The detection probability is set to zero for any distance beyond 758 meters. Lambda (λ) can be experimentally defined using the Beescout program and is by default set to -.005. (Becher, et al., 2016) The resulting graph of distance influencing the detection probability is shown in figure 3. In this research a circle with a radius of 564 m around the BEESPOKE locations was assumed to be sufficient space to model bumblebee foraging. This led to a modelled area of 1km² per location. These 1km² areas were modelled in BEE-STEWARD based on the 2019 crop data of the yearly updated database of all agricultural fields and crops that farmers within the Netherlands fill in. This database is owned by the Dutch ministry of economic affairs and climate. It is publicly available through PDOK, the government platform for geographic datasets. (Ministerie van EZK, n.d.)

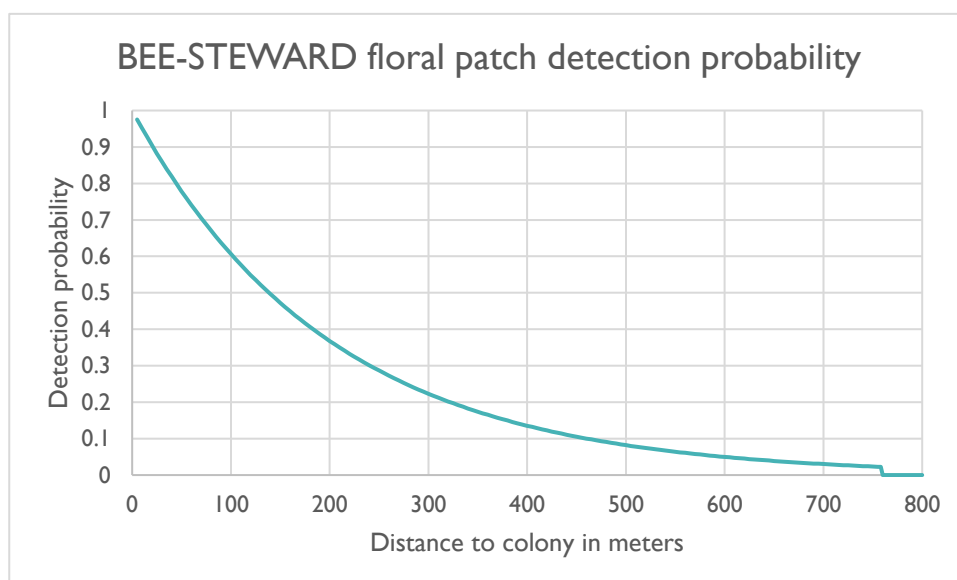


Figure 3: Floral patch detection probabilities as used within the BEE-STEWARD model, based on distance to the bumblebee colony.

2.2. Creating BEE-STEWARD input maps

The BEE-STEWARD model requires a specific map of the area to be modelled. Such a map consists of areas that are colour coded for different habitats. Netlogo (the programming language that BEE-STEWARD is written in) can only recognize a limited set of colours. A “colour map” showing this set of colours and what habitats they code for was used as a guide and legend for creating and understanding the input maps. The colour map of this research is shown in figure 4.

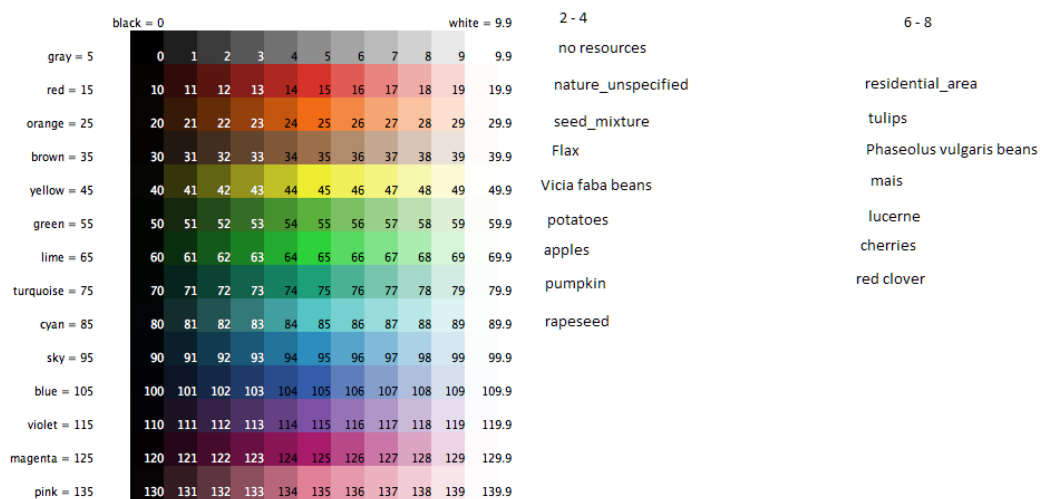


Figure 4: Colour map describing the Netlogo colours and what habitat they code for within the BEE-STEWARD input maps. The habitats listed under “2-4” are coded by the colour with a number ending in 3 in the same row as the habitat. The “habitat input file” is setup to interpret the three colours ending in 2, 3 or 4 in that row as that habitat type. The habitats in column “6-8” are coded in a similar way, only using the (end-)numbers 6, 7 and 8 instead.

An example of an input map created with this colour coding in ArcGIS is shown in figure 5. The circular area in figure 5 that has defined colours is one of the circular areas in figure 2 (the map of all eight areas) after being coloured in according to the GIS data, using the corresponding colours of the colour map (figure 4). Each of the colours corresponds to one distinct floral habitat for bumblebees, being either a type of crop grown by a farmer or a more general habitat (for example “residential areas”, which includes buildings and gardens).

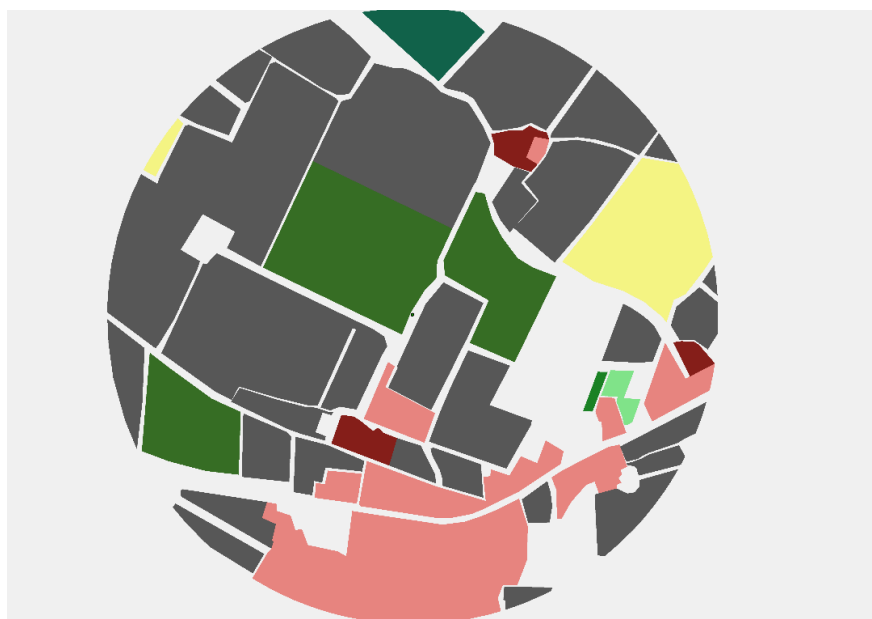


Figure 5: Colour coded habitats as created with ArcGIS. Every colour in the map codes for a different habitat, according to the colour map (figure 4).

This colour coded map is then scanned and interpreted by BEE-STEWARD when the map is loaded into the program. This happens according to a user defined "habitats input file". The map in figure 6 is the interpreted version of the map in figure 5. (Note the much lower quality in terms of pixels per area. BEE-STEWARD can be forced to interpret in higher resolutions than this standard setting, but this dramatically increases the computation time of the interpretation step.)

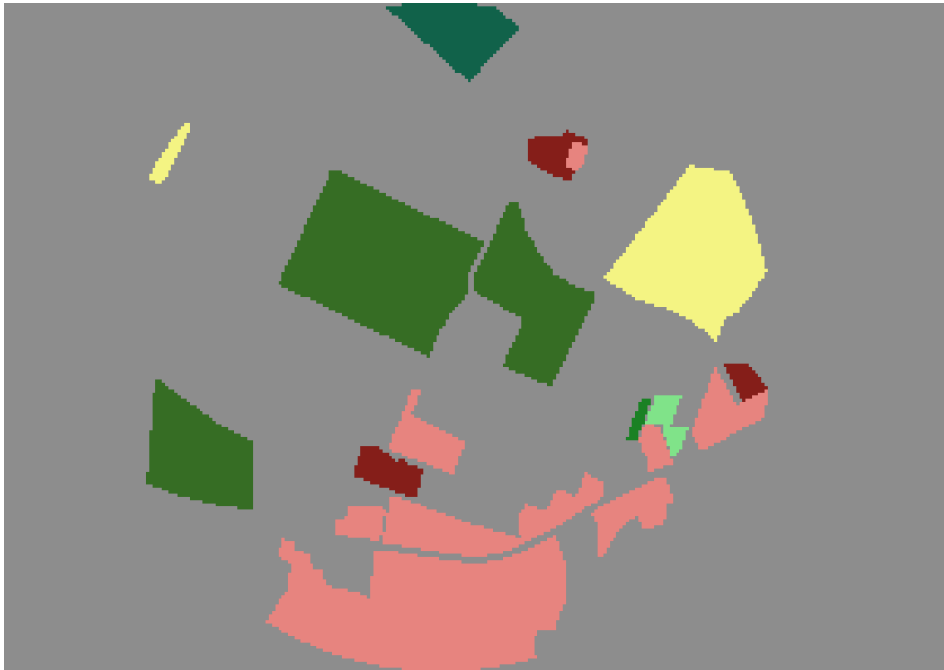


Figure 6: Example map as interpreted by the BEE-STEWARD model. This is the same map as figure 5, after interpretation by BEE-STEWARD.

2.3. Modelling scenarios

In the Netherlands the regional collectives of farmers can acquire a subsidy for herb rich field borders. The subsidy provides for borders with a width in multiples of 3 meters and an option for 1,5 meter wide borders. The 3 and 6 meter wide borders are applied most often. (BoerenNatuur, 2019) (Agrarisch collectief Waadrâne, n.d.) (Arjen Strijkstra, personal communication, 2020).

To determine the predicted effect of seed mixture applications, a wide variety of scenarios were modelled. The most realistic way is modelling the application of 3 and 6 meters wide borders or complete fields, as these are applied most often by farmers. Furthermore it is interesting to see how the model responds to a large range of input variation. This has provided a comparison between the effectiveness of applying flower rich habitat in 3 or 6 meter wide strips or in complete fields.

Each application leads to a number of scenarios, each of which was defined in an input map for the BEE-STEWART model. Each of these input maps was then run in 7 unique simulations. The creation of the input maps is outlined in chapter 2.2, the number of runs per input map is defined in chapter 2.6.

There were 5 application structures used:

The base situation

In this scenario no seed mixture was applied. Crops were based on the 2019 governmental GIS database. (Ministerie van EZK, n.d.) Applied flower rich conservation habitats that were already in the base situation are highly variable in plant species that they can contain. Therefore, they were modelled as containing the same floral values as the BEESPOKE seed mixture. The already existing “agricultural nature areas” are aimed at increasing the numbers of meadow-birds. This is partly achieved by providing excellent habitat for insects (as food for the birds). (Agrarisch collectief Waadrâne, n.d.) (Bij12, n.d.) These areas can be expected to be less beneficial for bumblebees than the BEESPOKE seed mixtures. By modelling these areas the same as the BEESPOKE mixture areas, they were essentially given the benefit of the doubt, overestimating bumblebee numbers in the base situation. The base situation had 8 input maps, one for each modelled research area (as defined in chapter 2.1.).

The BEESPOKE application

In this structure seed mix was applied as carried out for the Dutch trial locations of the BEESPOKE project. Some crops were also changed compared to the 2019 data. The full list of changes to the 1km² research areas is based on information of the local agricultural nature collective (Agrarisch collectief Waadrâne, n.d.) and is as follows:

The Fokkema trial location had .84 ha changed from wheat to flax and .87 ha from beets to BEESPOKE equivalent area (Agricultural bird species conservation habitat, “vogelakker” in Dutch). It also gained 2 flower strips totalling 0.17ha. Together with the BEESPOKE equivalent area this ends up at 1.04ha added florally rich habitat.

The Hoekstra area had .41ha changed from potatoes to barley. It also gained 1 flower strip of .06ha.

The Minnema trial location gained one flower strip of .07ha.

The Roersma trial location had 1.40ha changed from maize to *Vicia faba* beans. 6.46ha was changed from maize to beets and wheat fields. 18ha was changed from maize to a strip of BEESPOKE seed mixture.

In the Sipma trial location .91ha was changed from wheat to *Vicia faba* beans. 3.44ha was changed from onions to potato. The field changed to BEESPOKE mixture was already bespoke equivalent “agricultural nature mixture” (agrarisch natuurmengsel in Dutch) before.

In the SPNA trial location .44ha was changed from potatoes to a flower strip.

The Venema trial location had a BEESPOKE seed mixture strip of .07 ha applied. A field of .66 ha was changed from potatoes to wheat.

At the Zuidema area .64ha was changed from potatoes to rapeseed crops. A BEESPOKE strip of .10ha was added.

In total, 8.19ha of somewhat attractive area was changed to unattractive area for bumblebees. A total of 9.45ha of BEESPOKE seed mixture and agricultural nature areas were available in the BEESPOKE application simulations. This flower rich area consisted of 10 new BEESPOKE floral areas (a total of 1.58ha, mostly margins) and 9 already existing “agricultural nature areas” (a total of 7.87ha, mostly whole fields). The BEESPOKE application had 8 input maps, one for each modelled trial location.

The 3 meter margin application

In this application structure an incremental amount of fields gained a 3 meters wide margin of BEESPOKE seed mixture, until all fields (that have a larger minimal radius than 3 meters) had this border applied. Each incremental step was modelled as a separate input map in BEE-STEWART. A total of 70 borders (and thus input maps) were generated in this way.

The 6 meter margin application

In this application structure an incremental amount of fields gained a 6 meters wide margin of BEESPOKE seed mixture, until all fields (that have a larger minimal radius than 6 meters) had this border applied. Each incremental step was modelled as a separate input map in BEE-STEWART. In this application a total of 66 borders (and thus input maps) were generated. This is a bit less than the amount for the 3 meter wide borders, as some areas were too small for a 6 meter wide border, but not for a 3 meter wide border.

The Full Field application

In this application structure an incremental amount of fields was fully replaced by an equally sized field of BEESPOKE seed mixture, until all agricultural fields were replaced. Each incremental step was modelled as a separate input map in BEE-STEWART. A total of 76 fields were incrementally changed, leading to 76 unique input maps that were simulated.

2.4. Implementation of scenarios in BEE-STEWARD

In BEE-STEWARD there are options to change the colour of a field in an input map. This changes the habitat and can then be saved as a new map without changing the original. In this way it is possible to create many input maps with an incremental amount of fields converted to BEESPOKE seed mixture. Fields were selected (and converted) in order of closest distance to the centre of the modelled area. Only fields that provided at least some form of floral resources can be changed in this way. This method was used to implement the Full Field scenarios. Since only fields that actually provide some value in the base scenario can be changed, the highest maximum floral cover of any single area was around 40% of the total surface area. The lowest maximum cover in a single research area was around 18% of the total surface area.

A similar option (under “Stewardship options”) allows the same manipulation as described above, but instead adding margins of any width on the inside edges of any (agricultural) field instead of changing colour. This was used to model the 3 and 6 meter margin structures. The same limitations for selecting fields apply as in the full field scenarios. This time the lowest maximum was around 1.5% and 2.5% for the 3 and 6 meter scenarios respectively. The highest maximum cover of a single area was around 6% for both 3 and 6 meter margins. These maximum percentages are equal for the 3 and 6 meter margins because some smaller fields were not capable of housing a 6 meter margin, but could accommodate a 3 meter margin.

The BEESPOKE scenarios were edited in ArcGIS and then converted to BEE-STEWARD maps in the same way as described for the base situation in chapter 2.2. (p. 14&15).

The 8 modelled areas had between 7 and 12 agricultural fields in each of them. In every area the agricultural fields were incrementally altered with 3 and 6 meter margins of, or completely replaced with, BEESPOKE seed mixture. This led to the creation of 221 individual input maps. A further 16 input maps were loaded for the base and BEESPOKE scenarios combined, for a total of 237 input maps.

At each step in the creation process of these input maps, the area of the added Bespoke seed mixture area was viewed using the “Identify” option (both in BEE-STEWARD or ArcGIS) and then copied to an Excel file for use in result comparisons by square meters of applied flower rich habitat.

2.5. Creating BEE-STEWARD input files

Besides input maps, BEE-STEWARD needs two user defined files to operate. The “habitats” input file and the “flowerspecies” input file.

The habitat input file specifies a number of details about the colour encoded habitats in a table format. This habitat file contains one row for each type of habitat. It contains columns for specifying which colour range the program will interpret as that habitat (see figure 4). Furthermore it contains one column for every plant species that is defined in the “flower species file”. Every cell in a plant species’ column has a number specifying the amount of flowers per square meter that there are within the specified habitat (row). An example is given in table 1.

Table 1: Excerpt of the habitats input file. Columns necessary for correct reading of the file by BEE-STEWARD, but not conveying modelling input information have been left out. All plant species after the first two have also been left out. The triple dotted cells indicate where the table continues listing plant species. The numbers in the “colour” columns indicate the colours as defined in the colour map (figure 4). The numbers underneath the plant species (D. carota & A. millefolium in this example) indicate the number of flowers per square meter in the corresponding habitat.

habitatColourID	colourRangeMin	colourRangeMax	habitatType	<i>Daucus_carota</i>	<i>Achillea_millefolium</i>	...
23	22	24	seed_mixture	2.8	1.6	...
53	52	54	crop_potato	0	0	...
57	56	58	crop_lucern	0	0	...
13	12	14	nature_low_value	0	0	...
47	46	48	crop_mais	0	0	...
33	32	34	crop_flax	0	0	...

The “flowerspecies” input file contains data about the plant species that are listed in the habitats input file. This file is also in a table format and is shown in table 2. It specifically contains data on the nectar and pollen resources that are provided on a per flower, per day basis. Together with the number of flowers per square meter, specified in the habitats input file, this defines the resource production per square meter for the habitats.

Table 2: Excerpt of the flowerspecies input file. The rows specify each specific plant species or a habitat for which defining exact species is impossible (e.g. residential area and nature). The nectar per flower per day and the pollen per flower per day are calculated based on the 0 to 5 scores for each species. The proportion of protein within the total pollen, the concentration of sugar within the nectar and the corolla depth are based on the average of all default plant species of the BEE-STEWARD model. The starting day of flowering and the stopping day of flowering are directly based on the flowering months listed in the sources providing the 0 to 5 nectar and pollen scores. The inter-flower time is kept at the default that BEE-STEWARD uses for all its default plant species. The inter-flower time determines the time bees spend flying between single flowers of the same patch.

Flowerspecies	pollen_g /flower	nectar_ml /flower	proteinPollen Proportion	concentration_mol /litre	startDay	stopDay	corollaDepth in mm	intFlowerTime in seconds
<i>Daucus_carota</i>	0.00015625	0.0008	0.2	1	152	304	0.7	0.6
<i>Achillea_millefolium</i>	0.00015625	0.000266667	0.2	1	150	250	0.7	0.6
<i>Centaurea_cyanus</i>	0.01	0.0216	0.2	1	152	243	0.7	0.6
<i>Centaurea_jacea</i>	0.000625	0.0024	0.2	1	152	243	0.7	0.6
<i>Trifolium_pratense</i>	0.0025	0.0024	0.2	1	121	304	0.7	0.6
<i>Zea_mays</i>	0.01	0	0.2	1	152	243	0.7	0.6

The creation of the flowerspecies input file was complex, as there is no strict data on the pollen and nectar production of many plants and these values are also dependant on surrounding (a-biotic and biotic) conditions. (Jacobs, et al., 2010) (Waser & Price, 2016) (Mu, et al., 2016) (Adgaba, et al., 2017) There is, however, data for most plants consisting of a 0 to 5 score of pollen and/or nectar production, which can be used to calculate input data. This score is based on different factors depending on the specific source. In the “beeplants guide” from the royal Flemish beekeepers association, the score is based on an estimation of the pollen/nectar yield per hectare. (Jacobs, et al., 2010) In the work of Van der Steen & Cornelissen (2015) the score is based on a number of (book) sources, likely referring mostly to the “attractiveness” of the flowers to honeybees. In this research the average score (rounded down to the closest integer) between Jacobs et.al. and Steen & Cornelissen was used to value plant species on a 0 to 5 scale.

The 0 to 5 pollen and nectar scores were then used to determine the pollen and nectar production per plant per day. To do this, the plant species that are originally in the model (and thus have full data available thanks to the small scale field study that was done specifically for testing of the BEE-STEWARDS model) were analysed on their production per day. There were many plants with a relatively low production, some plants with a higher production and only a few plants with very high production. This roughly follows an exponential increase (see appendix B for figures showing this roughly exponential increase). Based on this estimated exponential increase, the input values for BEE-STEWARDS were calculated. These compiled data are shown in table 3 and table 4:

Table 3 shows the translation of the 0 to 5 scores for pollen to protein production per flower per day. This is based on the estimated exponential increase of protein production between more and less productive species (see appendix B). This protein production was then multiplied by the average protein proportion in pollen to get the total pollen production per flower per day in grams.

Table 3: pollen production values per production score. The protein production and estimated protein proportion in the pollen is used to calculate the total pollen production per flower per day. All estimations are based on the values of the default plant species that are in the BEE-STEWARDS model. The possible score of 0 is not in the table, this score simply means no production at all.

SCORE	EXPLANATION	PROTEIN PRODUCTION	PROTEIN PROPORTION	POLLEN TOTAL IN GRAMS
1	very low	0.00003125	0.2	0.00015625
2	low	0.000125	0.2	0.000625
3	medium	0.0005	0.2	0.0025
4	high	0.002	0.2	0.01
5	extreme	0.008	0.2	0.04

In table 4 the translation of 0 to 5 scores for nectar to sugar production per flower per day is shown. This is based on the estimated exponential increase of sugar production between more and less productive species (see appendix B). This sugar production in moles was then multiplied by the average sugar concentration in moles per litre of nectar to get the total nectar production in litres. This was divided to get to millilitres per day per flower, which is the input BEE-STEWARD uses.

Table 4: Nectar production values per production score. The sugar production and the estimated concentration per litre were used to calculate the total nectar production in ml per flower per day. All estimations are based on the values of the default plant species that are in the BEE-STEWARD model. The possible score of 0 is not in the table, this score simply means no production at all.

SCORE	EXPLANATION	SUGAR PRODUCTION IN MOL	SUGAR CONCENTRATION IN MOL/L	TOTAL NECTAR IN LITRE	TOTAL NECTAR IN ML
1	very low	0.000000266667	1	2.66667E-07	0.000266667
2	low	0.0000008	1	0.0000008	0.0008
3	medium	0.0000024	1	0.0000024	0.0024
4	high	0.0000072	1	0.0000072	0.0072
5	extreme	0.0000216	1	0.0000216	0.0216

Finally, for the habitats input file, the number of flowers per square meter is also widely variable based on environmental conditions. The 0 to 5 scores that production per flower is based on, do not take the amount of flowers per area into account. Therefore, the habitat file should have an equal number of flowers per area for every species. This number is assumed to be 20/m² in total for each habitat. With this generalization the 0-5 production scores following Jacobs et.al. (2010) and Van der Steen & Cornelissen (2015) were the only variables at play. However, the flowers/m² can definitely impact the floral resources over the entire area. Jacobs et.al. gives an estimated yield in kg per season per hectare for every score that they attribute to the plant species. With the knowledge that sucrose is the main sugar in nectar (Wolff, 2006) (Chalcoff, et al., 2006) and 1 mole/L sucrose in water solution has a density of 1.127g/ml, the values used in the simulation can be converted to the same units as reported in Jacobs et.al. (2010). In table 5 this comparison between yields is made. A score of 2 led to an underestimation of resources compared to estimations of Jacobs et.al., both for pollen and nectar. The high end of pollen scores overshoot the estimated range. All other values used in this research fell within the estimations of Jacobs et.al. (2010).

Table 5: Nectar and pollen yields over the duration of a flowering season compared between this research and numbers by Jacobs et.al. (2010). "Simulation" notes the numbers as were used in the simulations in this research. Note that the yields for a pollen score of 5 have been left out, as this score was not assigned to any plant species in this research.

SCORE	NECTAR IN KG/HA, JACOBS. ET.AL.	NECTAR KG/HA, SIMULATION	POLLEN KG/HA, JACOBS ET.AL.	POLLEN KG/HA, SIMULATION
1	1-25	6	1-25	3
2	26-50	18	26-50	13
3	51-100	54	51-100	50
4	101-200	162	101-150	200
5	201-500	487	—	—

Both Jacobs et.al. (2010) and Steen & Cornelissen (2015) state flowering periods (per month) of every plant species. In this research the first day of the first month of flowering till the last day of the last month of flowering is taken as the flowering period, as the model requires input in days of the year (0-365) instead of months. Where the sources don't agree on flowering period the average day of the year is taken as input. For example, start of the flowering period in March (day 60) and in April (day 91) in the sources would average to start on day 76 (roughly halfway March).

When data for the flower resources or flowering period was missing from both sources, assumptions were made. This was the case for 4 plant spp., namely: Common yarrow (*Achillea millefolium*), Potato (*Solanum tuberosum*), Smooth hawksbeard (*Crepis capillaris*) and German chamomile (*Matricaria chamomilla*). For Smooth hawksbeard only the nectar score was missing. This was assumed to be equal to the non-missing pollen score for this plant species. For Common yarrow and Potato, the flowering periods are missing. These have been assumed to start on day 150 and stop on day 250, these are the rounded average values of the default plant species. For German chamomile, all data was missing. Resource scores have been set to 2 (below average, the average score of all species is 2.3 for both pollen and nectar). Flowering period has been set to day 150 till day 250.

In Appendix C the full list of flowering species used in this research is shown. Missing data/assumptions can also be found there. Many agricultural species that do exist in the research areas are not shown on this list. These are all species that are harvested (or otherwise incapacitated) before they bloom.

There were 2 habitats that could not be modelled by using individual plant species. These were general nature areas and residential areas. Nature and residential areas contain many different plant species. Since these areas are widely variable, it is impossible to define an accurate and generally applicable specific value for these areas. However, residential areas provide decent to good resources for bumblebee species. (Theodorou, et al., 2020) (Gunnarson & Federsel, 2014) (Nakamura & Kudo, 2019) It was assumed that the broad spectrum of species in nature areas and in residential areas (gardens etc.) leads to a low to medium amount of resources for a large portion of the year. In explorative BEE-STEWARD runs it became clear that flowering resources earlier in the year are important to allow the bumblebees to establish. These earlier resources are mainly provided by the relatively broad flowering period of nature areas and residential areas. It was assumed that resources can be found in nature and residential areas from day 75 till day 325. Nature areas and residential areas were assumed to provide a low to medium amount of resources and have therefore been set to a score of 2 out of 5 for both pollen and nectar.

The inter-flower time found in table 2 (the flowerspecies input file) is defined as the time an individual bee spends flying from one flower to the next within the same flower patch. Based on the depletion of the flower patch the individual modelled bee might need to fly multiple instances before finding a new non-empty flower. This is stochastically determined: the model does not keep track of every flower, it merely calculates the chance that any particular flower is full based on depletion of the total flower patch.

Beside the habitat and flower species input files, a Bumblebee species input file is also used. All values in this file were left at the default, with the exception of the list of suitable nesting habitats. This list was expanded to include all newly defined habitats from the Habitats input file, as none of the original habitats were used. Nesting availability was assumed to not be a limiting factor in this research. The contents of the bumblebee species file can be found in appendix D.

2.6. Behaviourspace setup

Besides input maps and files, BEE-STEWARD has some settings that need to be defined before running the model. These settings can be defined for a number of runs at once using Netlogo's "Behaviourspace". The settings that need to be addressed in Behaviourspace include the maps and files you want to use as input. Besides these, the random number generator of the BEE-STEWARD model requires a seed to start the algorithm. This seed was defined by getting a random number between 1 and 100 from random.org for each run. This website uses atmospheric radio noise to create their random numbers. (Haahr, n.d.) The random numbers that were used as seeds can be found in the results (figure 9, p. 27).

After the RNG seed, the number of initial bees needed to be set. By default the model spawns 500 *B_terrestris* individuals in its digital world. The model comes with support for 5 other species as well, namely: *B_hortorum*, *B_hypnorum*, *B_lapidarius*, *B_pascuorum* and *B_pratorum*. There is also an option to model a general cuckoo bee, *Psithyrus sp.*

In this research the model has been run with an initial mix of bees that is based on field observations as compiled in the database of "Waarnemingen.nl". This data for the 6 species and the combined cuckoo bees can be found in appendix E. An experimental run at fully default settings has been done to estimate current carrying capacity². This resulted in a carrying capacity estimation of roughly 4000 bees per km². Based on that preliminary run, all experimental runs were started with 4000 bees, divided as shown in figure 7, based on the field observations. Due to rounding resulting from this distribution, the total number of individual bumblebee queens at the start of every experimental run was actually 3996.

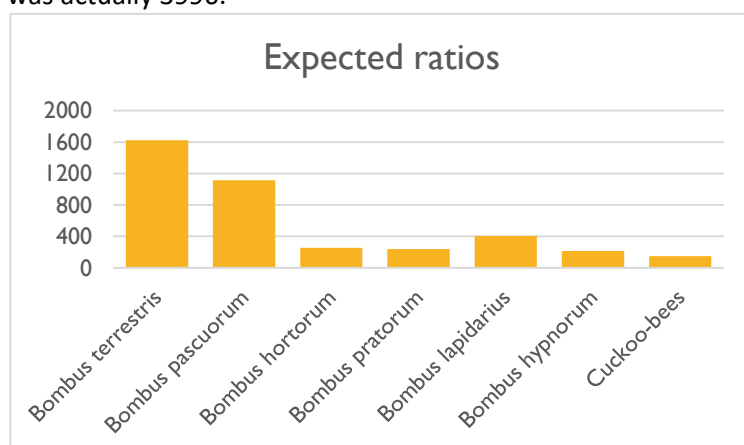


Figure 7: Ratios as observed in Fryslân in the wild, calculated for 4000 bees total.

Lastly the number of runs needed to be specified. The number of runs has been determined by a-priori power analysis using the program G*power. (Faul, et al., 2007) This made sure that the dataset created by the modelling will be large enough to provide statistically significant evidence, but not any larger than is necessary. Calculation using G*power, based on the 245 total expected scenarios led to the conclusion that 7 runs will be necessary per scenario. This leads to a total of 1715 experimental BEE-STEWARD runs. A more complete explanation of the G*power input and output can be found in appendix F.

² Carrying capacity is defined as the maximum number of individuals that a given area can support indefinitely. This is dictated by many variables, such as food availability, nesting availability and predation pressure. In BEE-STEWARD all non-food related variables are approached stochastically by subjecting all modelled bumblebees to a background mortality rate when outside of the colony/nest.

At a later moment 8 more scenarios were added to simulate the exact BEESPOKE trial plans, as presented on the site of the agricultural nature collective Waadrâne (Agrarisch collectief Waadrâne, n.d.) This led to an expected 253 scenarios and 1771 experimental BEE-STEWART runs. The expected numbers of runs and scenarios differs slightly from the reported number of input scenarios/maps and number of experimental runs in the results and other parts of the methods. The actual numbers are slightly lower than the expected numbers, because some (partial) agricultural fields at the edge of the modelled areas were too small to contain a 3 or 6 meter wide border. When this was the case, these fields were left unaltered and a new input map was not created.

Any settings or other options that have not been addressed here have been kept at the default settings. The rationale for the default assumptions and settings in BEE-STEWART is detailed by Becher et.al. (2017) & (2016).

2.7. Data analysis

The data from the different modelled scenarios in BEE-STEWARD is generated as a comma delimited text file. This file contained close to 3 million lines, therefore it had to be opened with a database management program. To do this, Microsoft access was used. The resulting database was then imported into IBM's SPSS Statistics (version 22). All analysis was carried out from within SPSS or on a subset of the data imported in Excel.

The results were analysed in 2 main parts:

In the first part the dependent variable was the total number of adult queens at the end of the modelling runs and the input/experimental variable was the percentual and hectare area cover of BEESPOKE seed mixture. This correlation was analysed per application structure. The different trial locations are also relevant and were individually coloured in each analysis. Statistical modelling was used to supply an exact increase per hectare of seed mixture area with a 95% confidence interval. This analysis was based on an identity linked negative binomial model, as found in the generalized estimating equations option within SPSS. The statistical model was adjusted for research area. The residuals³ are also shown in the results and can help in visualizing model fit and potential outliers. A perfect model would be expected to have an equal amount of residual points above zero and below zero. The distribution of these residual points is also expected to be independent of any variable: the magnitude and sign of the residuals should not be correlated with the cover percentage of BEESPOKE seed mixture or with trial location/research area.

In the other part the predicted ratio between the different bee species was analysed per trial location. Some information on the location and a figure showing both the base situation input map as well as an aerial photo were presented.

Besides these main parts, the RNG seeds used were shortly examined to assure that they were not affecting the results.

³ Residuals in statistics are the difference between the expected value (as predicted by a statistical model or test) and the observed value (the actual results of the experiment). Here the Pearson residual is used, which are those raw residuals divided by the expected (standard) deviation to obtain a dimensionless number.

3. Results

3.1. General results

The experimental BEE-STEWARD batch ran 1603 simulations, returning 2.899.069 data points. Almost all simulations ran fully and without any complications, only a few input maps from the Fokkema area did not fully run. In table 6, these missing values are visualized. Any map that ran fully returned 1826 data points (one per modelled day) for each of 7 runs, with unique RNG seeds. This led to a total of 12782 data points per completely ran map. Fokkema Full Field simulation 1, 2 and 3 returned a much lower count. Fokkema FF simulations 5 and 8 did also not run fully, but to a less extreme extent. The Fokkema FF 1, 2 and 3 simulations were excluded from further data analysis.

Table 6: Number of data points (frequency) and percentage of all the data points represented for the Fokkema area full field replacement simulations.

MYMAP

	Frequency	Percent of all data points
"FOKKEMA FF1.PNG"	388	.0
"FOKKEMA FF10.PNG"	12782	.5
"FOKKEMA FF11.PNG"	12782	.5
"FOKKEMA FF2.PNG"	2593	.1
"FOKKEMA FF3.PNG"	8890	.3
"FOKKEMA FF4.PNG"	12782	.5
"FOKKEMA FF5.PNG"	11402	.4
"FOKKEMA FF6.PNG"	12782	.5
"FOKKEMA FF7.PNG"	12782	.5
"FOKKEMA FF8.PNG"	12628	.5
"FOKKEMA FF9.PNG"	12782	.5

For statistical analysis, the final number of queens at the end of the 5 year runs was used. A histogram of these 1577 data points is shown in figure 8. The data roughly follows a logarithmic distribution.

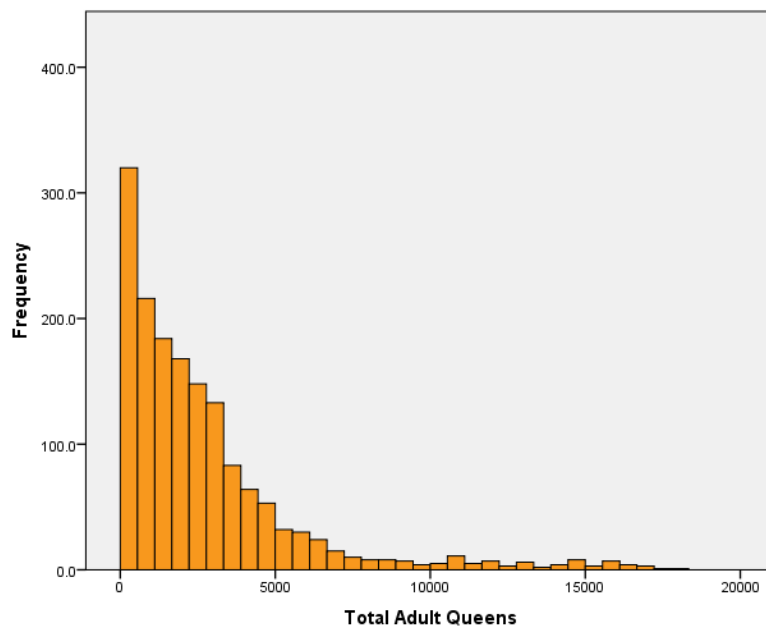


Figure 8: Histogram of total adult queens per run, at the end of all runs. $n=1577$

3.2. RNG seed

The numbers used to initialize the random number generator of the BEE-STEWARD model should not produce outlier cases or have any correlation with the results. The relation between RNG seed and total adult queens at the end of the runs has been visualized in figure 9. This figure shows the quartiles of the data points per RNG seed. These quartiles are fully overlapping, as expected when there is no effect of RNG seed on bumblebee abundance.

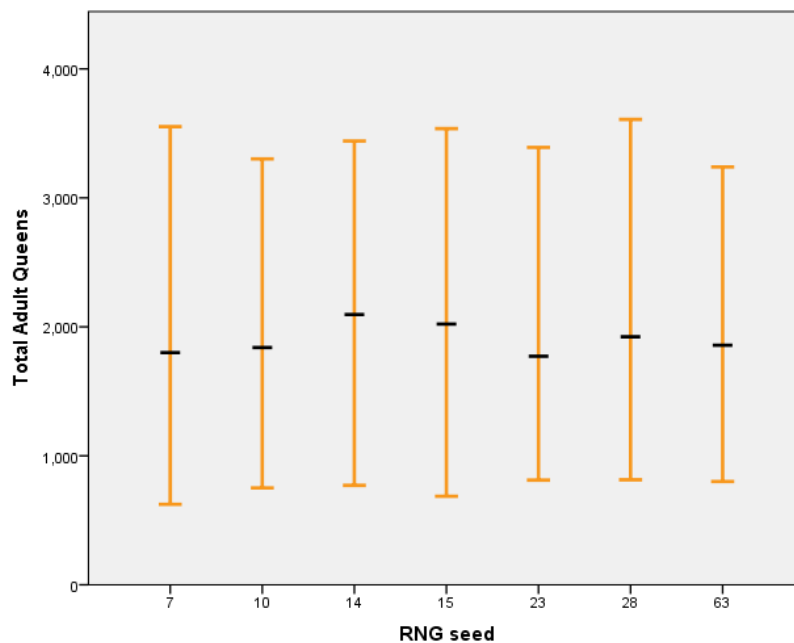


Figure 9: RNG seeds versus total adult queens at the end of each run. Bars represent the first to third quartile. The black line on the bars represents the median (this is also the second quartile).

3.3. Effect of seed mixture on bumblebee abundance per application structure

Base structure (no seedmix applied)

There was only a limited amount of data ($n=56$) on the base situation and many areas had no seed mixture at all. A graph of the results can be found in figure 10. The statistical model predicts values along a slope of $m=204.0$. The 95% confidence interval for the slope is 55.9 – 352.1. Seedmix cover was a significant predictor of the number of queens at the end of the experimental runs, when adjusted for research area ($W=7.293$, $df=1$, $p=.007$). The residuals for this analysis are shown in figure 11. The Venema area had all its data points below expected. However, all the data points were still relatively close to the expected value.

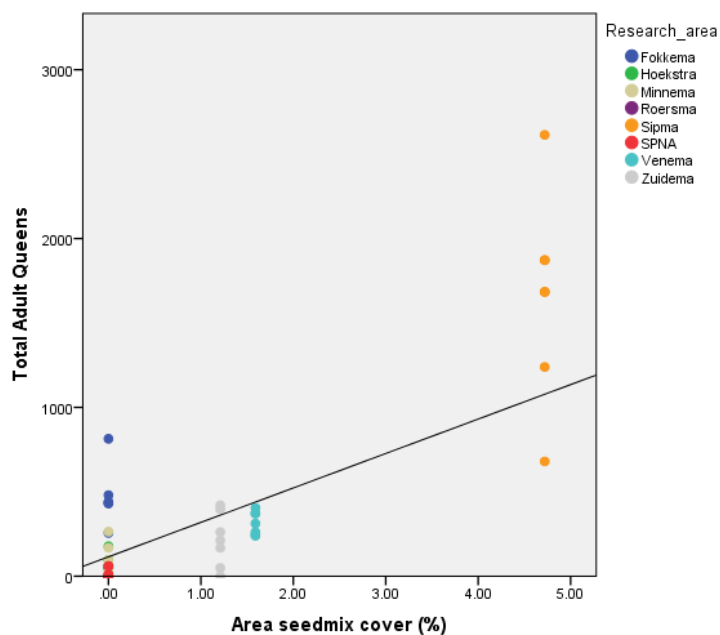


Figure 10: Number of queens vs the cover of seed mixture in percentages, with the predicted line of the statistical model. $n=56$, $m=204.0$

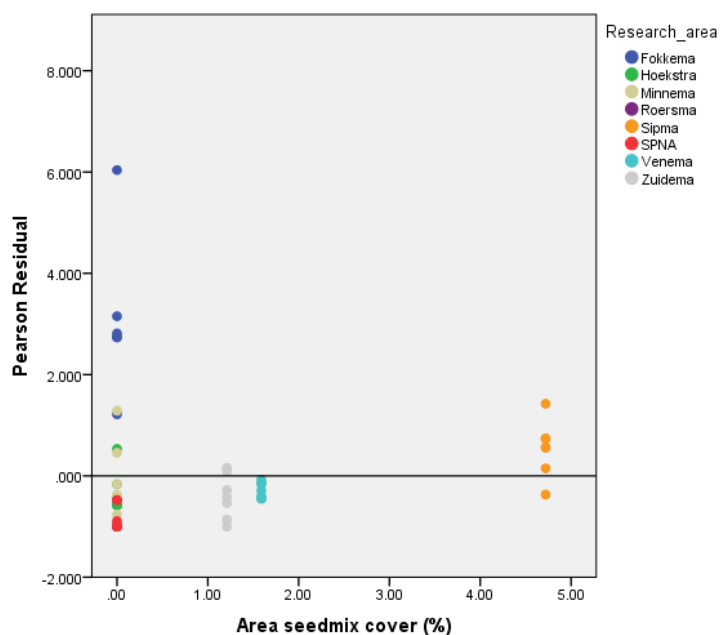


Figure 11: Pearson residuals for the results of the base structure. $n=56$

BEESPOKE application

In figure 12 the data for the BEESPOKE test sites is shown. In figure 12 C, the original data and predicted values are shown. The predictive line has a slope of $m=400.0$, the 95% confidence interval for the slope is 150.9 – 649.3. The area covered by seed mixture was a significant predictor of total adult queens ($W=9.903$, $df=1$, $p=.002$).

The residuals (figure 12 D) of the Hoekstra and Venema areas both are below expected and relatively far from the predicted value. The residuals of the other areas are more evenly dispersed. This points in the direction of the Hoekstra and Venema areas possibly being outlier cases, even after the statistical model has adjusted for the effect of research area.

To further investigate, the same statistical model was used again, but this time excluding the Hoekstra and Venema areas. The results after this exclusion are shown in figure 12 A, with the new residuals shown in figure 12 B. In the analysis excluding the Sipma area, seedmix cover was also a significant predictor for total adult queens after 5 years ($W=18.177$, $df=1$, $p<.000$). The predicted values of the statistical model have a slope of $m=413.7$. The 95% confidence interval for this slope is 223.5 – 603.8.

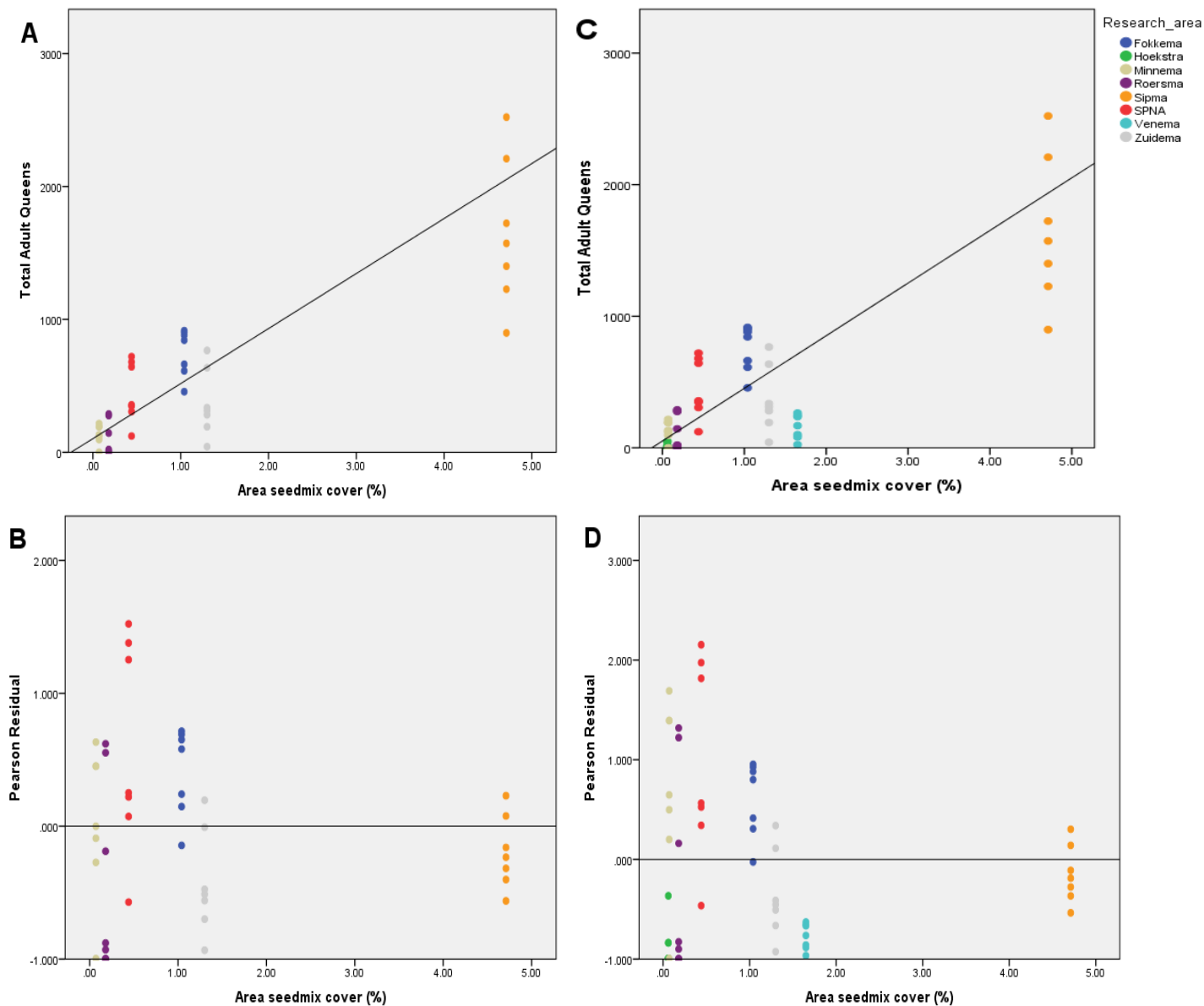


Figure 12: Number of queens and the cover of seed mixture in percentages, with predicted line and resulting residuals, of the BEESPOKE application modelling. A and B show analysis without the Hoekstra and Venema areas, respectively for total adult queens and Pearson residuals. C and D show analysis of all areas of total adult queens and Pearson residuals respectively. $n=56$, $m_A=413.7$, $m_C=400.0$

3 meter wide margins

In figure 13 the data for 3 meters wide borders is shown. In figure 13 C, the original data and predicted values line is shown. The predicted line has a slope of $m=720.8$, the 95% confidence interval for the slope was $486.7 - 954.9$. The area covered by seed mixture was a significant predictor of total adult queens ($W=36.416$, $df=1$, $p<.000$).

However, the Sipma area is completely separated from the other data points in the graph. Of the residuals of the Sipma area (figure 13 D) only a single data point is (a tiny bit) above expected. All other data points are decidedly under expected. The residuals of the other areas are more evenly dispersed. This points in the direction of the Sipma area being an outlier case, even after the statistical model has adjusted for the effect of research area.

To further investigate, the same statistical model was used again, but this time excluding the Sipma area. The results of this are shown in figure 13 A, with the resulting residuals shown in figure 13 B. In the analysis excluding the Sipma area, seedmix cover was also a significant predictor for total adult queens at the end of each model run ($W=60.367$, $df=1$, $p<.000$). The predicted values of the statistical model have a slope of $m=795.9$. The total adult queens increase by 796 for every added percent of seedmix cover. The 95% confidence interval for this increase is $558.1 - 1033.6$.

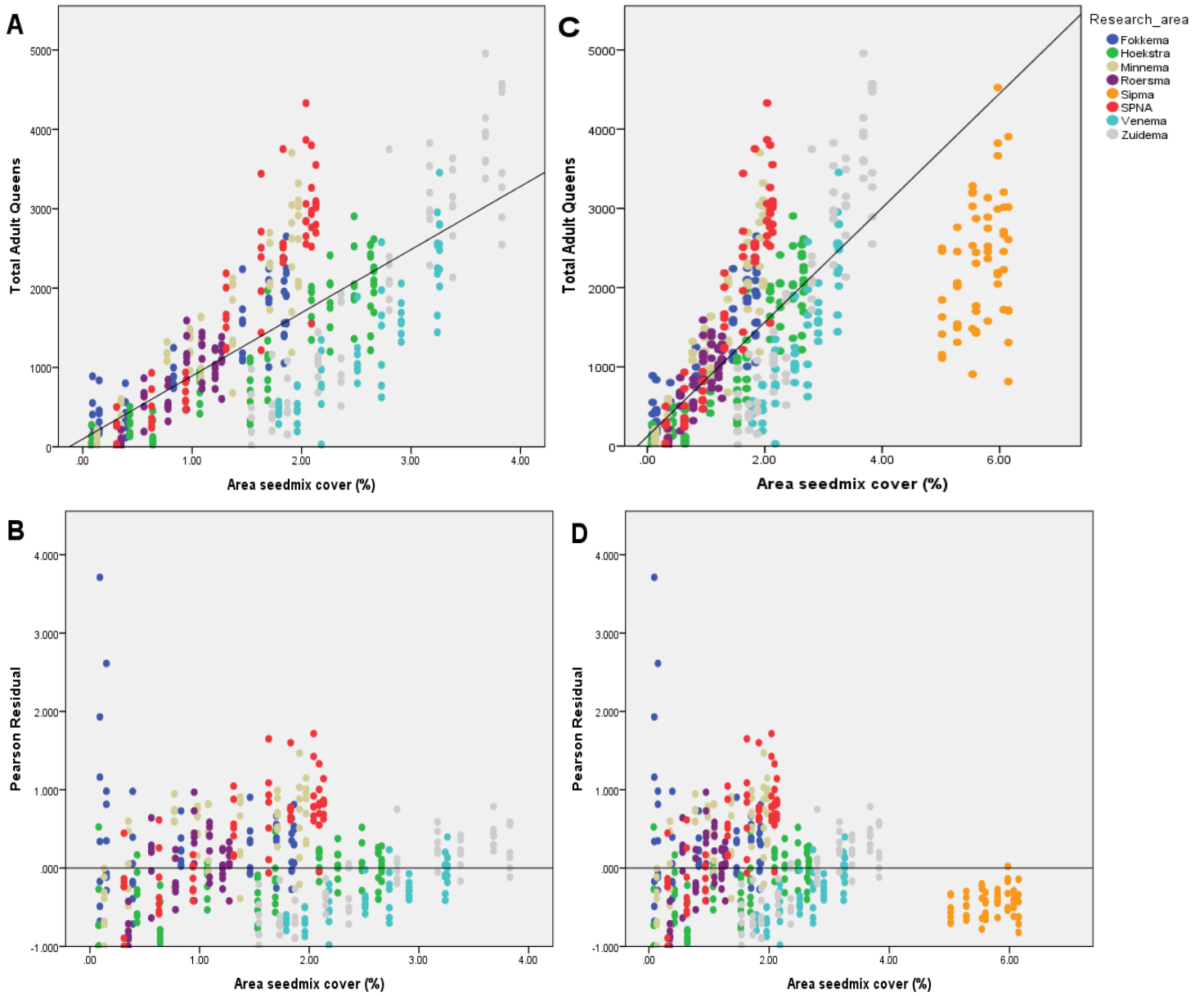


Figure 13: Number of queens vs the cover of seed mixture in percentages, with predicted line and resulting residuals, of the 3 meter margin runs. A and B show analysis without the Sipma area of total adult queens and Pearson residuals respectively. C and D show analysis of all areas of total adult queens and Pearson residuals respectively. $n=490$, $m_A=795.9$, $m_C=720.8$

6 meter wide margins

In figure 14 the data for 6 meters wide borders is shown. In figure 14 C the line predicted by the statistics is also shown, this line has a slope of $m=718.6$. The 95% confidence interval for this slope is 545.3 – 891.9. Seedmix cover was a significant predictor of total adult queens ($W=66.034$, $df=1$, $p<.000$).

Similar to the 3 meter margin graphs, the Sipma area is completely separated from the other data points and might be an outlier. The residuals of the Sipma area (figure 14 D) are all below expected. The residuals of the other areas are more evenly dispersed.

To further investigate, the same statistical model was used again, but this time excluding the Sipma area. The results of this are shown in figure 14 A and B, for total adult queens and residuals respectively. In the analysis excluding the Sipma area, seedmix cover was also a significant predictor for total adult queens at the end of each model run ($W=75.138$, $df=1$, $p<.000$). The predicted values of this statistical model follow the slope $m=766.3$. The 95% confidence interval for the increase per percentage is 593.0 – 939.6.

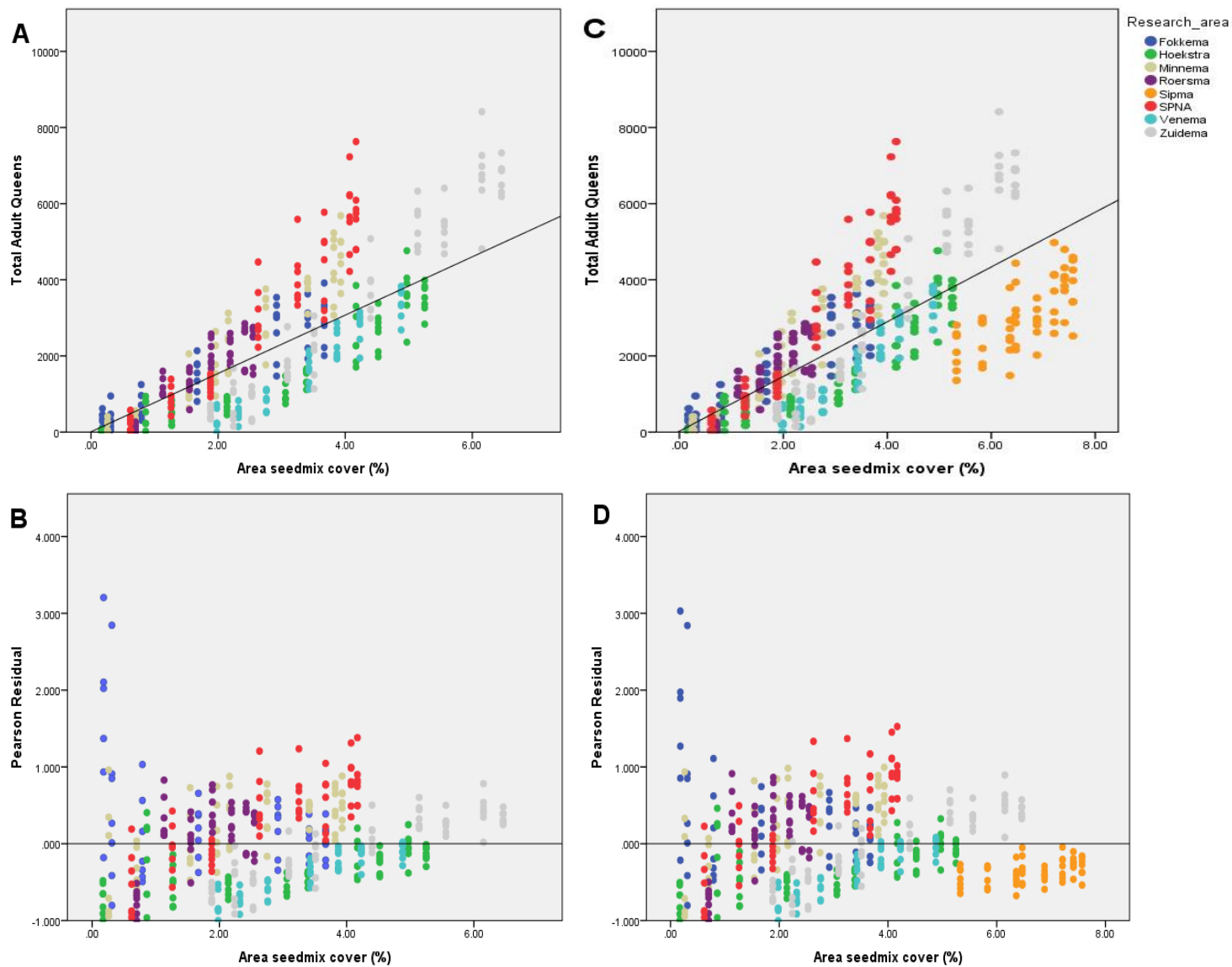


Figure 14: Number of queens vs the cover of seed mixture in percentages, with predicted line and resulting residuals, of the 6 meter margin runs. A and B show analysis without the Sipma area of total adult queens and Pearson residuals respectively. C and D show analysis of all areas of total adult queens and Pearson residuals respectively. $n=462$, $m_A=766.3$, $m_C=718.6$

Full fields

The results for the full field applications are shown in figure 15. The line of predicted values has a slope of $m=228.0$. The 95% confidence interval for the slope is 159.2 – 296.8. The amount of seed mixture in the areas was a significant predictor of total adult queens after 5 years ($W=42.214$, $df=1$, $p<.000$).

The residuals are shown in figure 16. All areas provide points on both sides of the predicted values, although some areas are skewed to one side or the other.

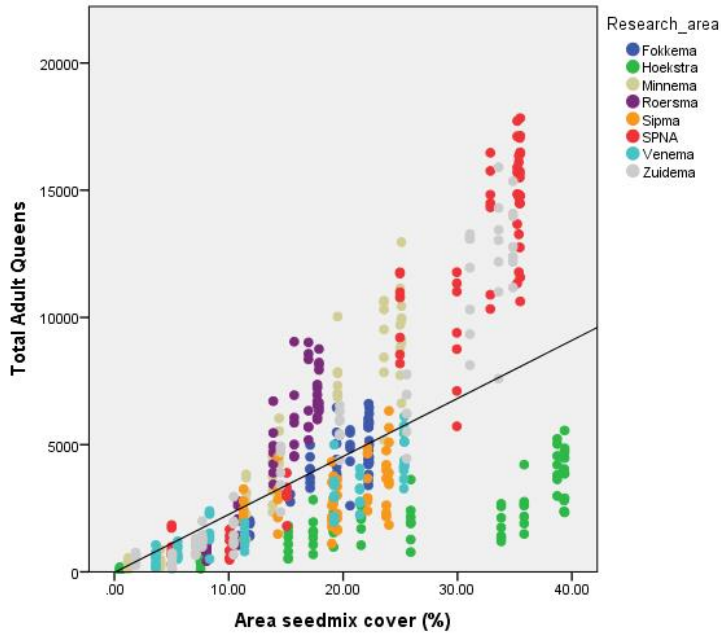


Figure 15: Number of queens at the end of the full field modelling runs, compared to the area of seed mixture in percent. $n=505$, $m=228.0$

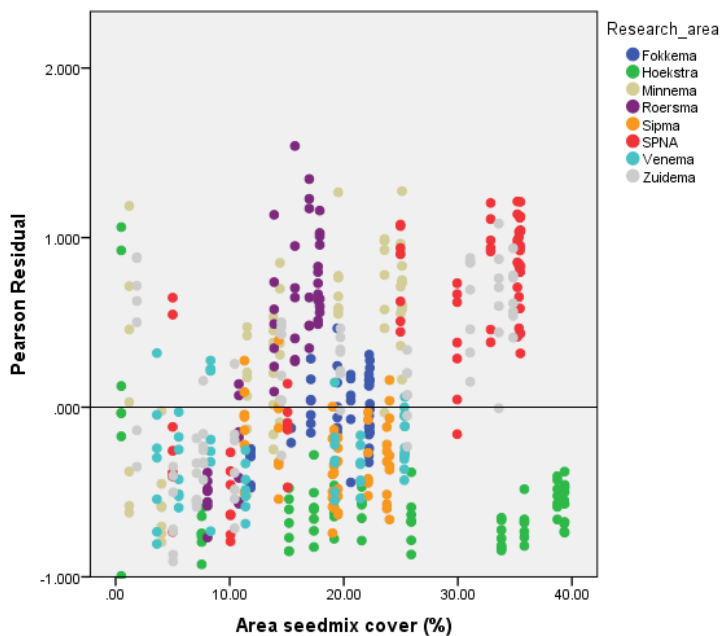


Figure 16: Pearson residuals for the results of the full field scenarios. $n=505$

All structures summarized

In figure 17 the predictions per hectare of seed mixture for each application structure have been summarized. The 3 meter margins scored the best. The 6 meter margins confidence interval fully falls within the interval of the 3 meter margins. The same is true between the base and full field structures. The BEESPOKE application falls in between these 2 groups, and its confidence interval partially overlaps with those of every other structure.

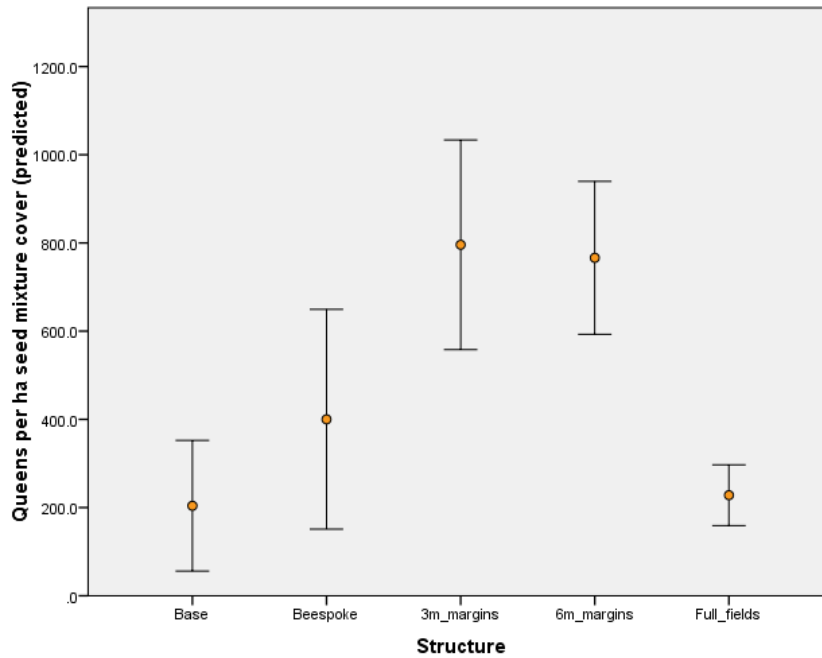


Figure 17: The number of queens expected to be gained from 1 hectare of seed mixture in the different application structures. The lower and upper bounds of the 95% confidence intervals for these predicted increases is also shown. Possible outliers have been included or excluded as discussed in chapter 4 (p. 45).

3.4. Modelled bumblebee species distribution per research area.

The Fokkema area

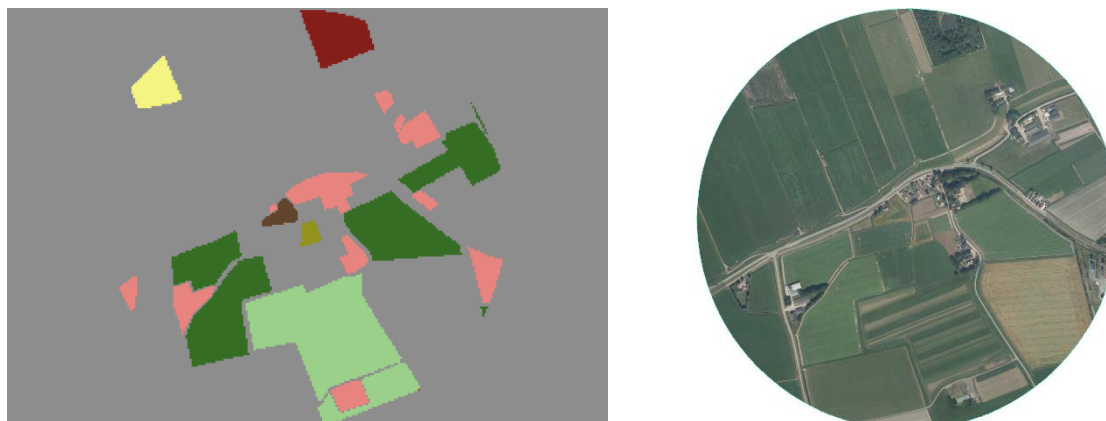


Figure 18: Comparison of the BEE-STEWARD input map (left) and an aerial photo (right) of the Fokkema area. In the BEE-STEWARD input map: residential areas are pink, potato is dark green, alfalfa/lucern is light green, maize is yellow, nature areas are red, flax is brown and *Vicia faba* beans are darkened yellow.

In figure 18 the Fokkema area is shown. The Fokkema area had a relatively large number of modelled habitat types at 7. There were no BEESPOKE seed mixture equivalent areas in the base situation. Residential areas were relatively dispersed and there was a large amount of lucern (alfalfa) crops in this area.

In figure 19 the average of every individual modelled bumblebee species is plotted against time. The ratio between species changes drastically over the modelled years. At the start *B. terrestris* and *B. pascuorum* accounted for 68% of all queens. At the 5 year mark these two species only account for 14% of the queens. *B. lapidarius* and *B. hortorum* on the other hand, continuously grew. They began at a combined 17% and ended at 84%. *B. pratorum* and *B. hypnorum* constantly declined from their initial amount. Species of subgenus *Psithyrus* also constantly declined, completely dying out after 4 years.

There was a pattern of increase in *B. lapidarius* and *B. hortorum* ratio with a simultaneous decrease of all other species in all research areas. This includes the eventual extinction of *Psithyrus* spp. and a slight increase or only mild decrease of average *B. terrestris* queens in the first year. Because of the large similarity in results among areas, the other areas have less information regarding species distribution, instead referring to this paragraph.

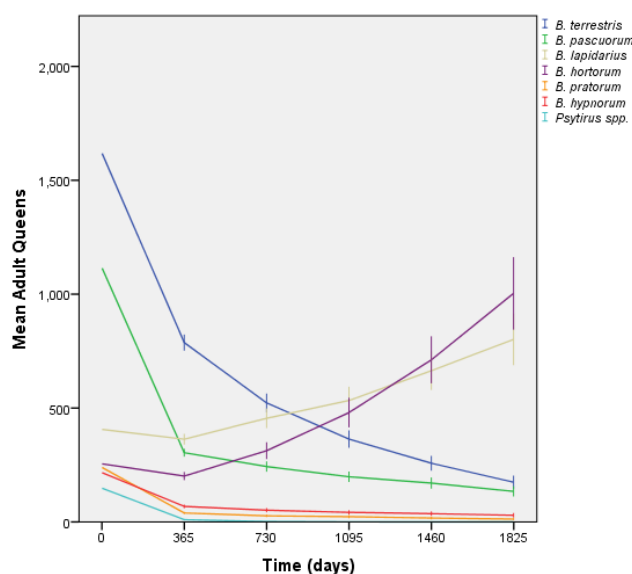


Figure 19: Average of the different species in the modelling runs versus time in days. Vertical lines represent the 95% confidence interval for the average.

The Hoekstra area

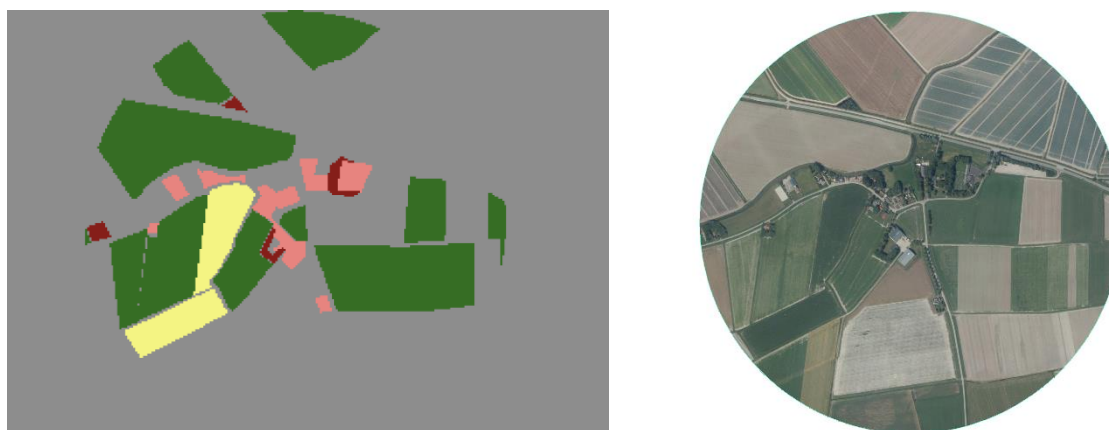


Figure 20: Comparison of the BEE-STEWARD input map (left) and an aerial photo (right) of the Hoekstra area. In the BEE-STEWARD input map: residential areas are pink, potato crops are green, maize crops are yellow and nature areas are red.

In figure 20 the Hoekstra area is shown. This area had a relatively low diversity in modelled habitats at 4 types. Potato crops were prevalent in this area.

In figure 21 the average of every individual modelled bumblebee species is plotted against time. This figure follows the same trend as all other areas, see paragraph “The Fokkema area” for more information. Of noteworthy difference is that *B. hortorum* ended up as the most prevalent species, instead of *B. lapidarius*. This was also the case for the Fokkema and Sipma areas, but not for any of the other 5 areas.

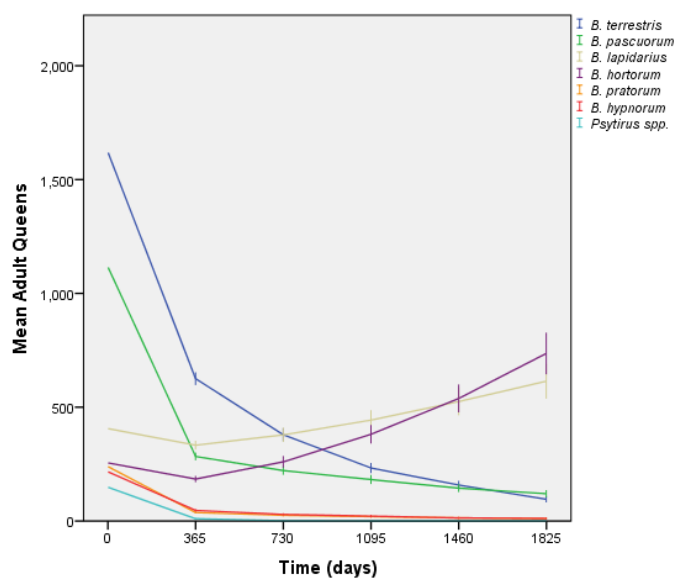


Figure 21: Average of the different species in the modelling runs versus time in days. Vertical lines represent the 95% confidence interval for the average.

The Minnema area

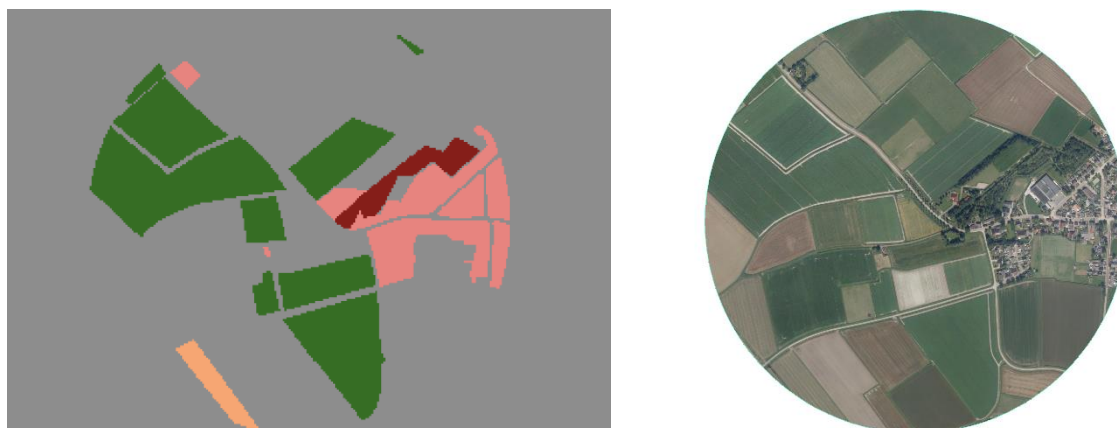


Figure 22: Comparison of the BEE-STEWARD input map (left) and an aerial photo (right) of the Minnema area. In the BEE-STEWARD input map: residential areas are pink, potato crops are green, tulip fields are orange and nature areas are red.

In figure 22 the Minnema area is shown. This area had a relatively low diversity in modelled habitats at 4 types. There were a large amount of potato crops and a relatively large block of residential area to the west. There was also a field of tulips in this area.

In figure 23 the average of every individual modelled bumblebee species is plotted against time. This figure follows the same trend as all other areas, see paragraph “The Fokkema area” for more information.

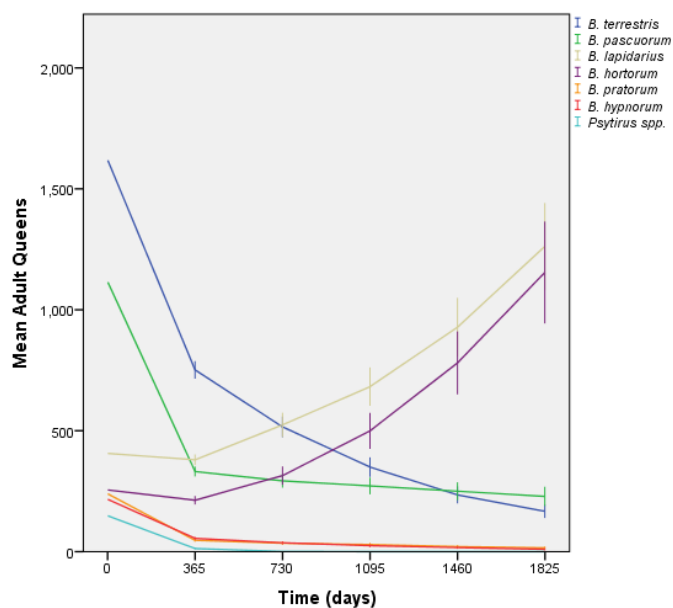


Figure 23: Average of the different species in the modelling runs versus time in days. Vertical lines represent the 95% confidence interval for the average.

The Roersma area

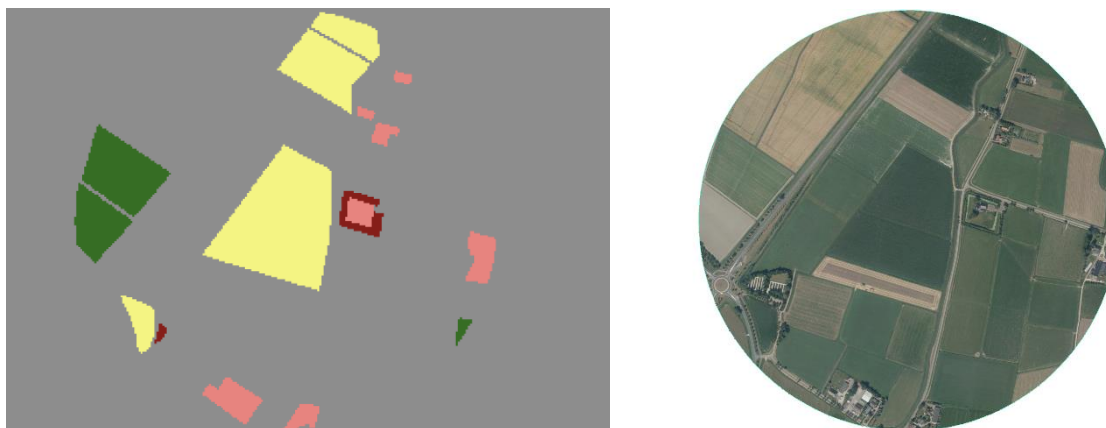


Figure 24: Comparison of the BEE-STEWARD input map (left) and an aerial photo (right) of the Roersma area. In the BEE-STEWARD input map: residential areas are pink, potato crops are green, maize crops are yellow and nature areas are red.

In figure 24 the Roersma area is shown. This area had a relatively low diversity in modelled habitats at 4 types. There was an abundance of maize crops in this area. Residential areas were small and dispersed.

In figure 25 the average of every individual modelled bumblebee species is plotted against time. This figure follows the same trend as all other areas, see paragraph “The Fokkema area” for more information.

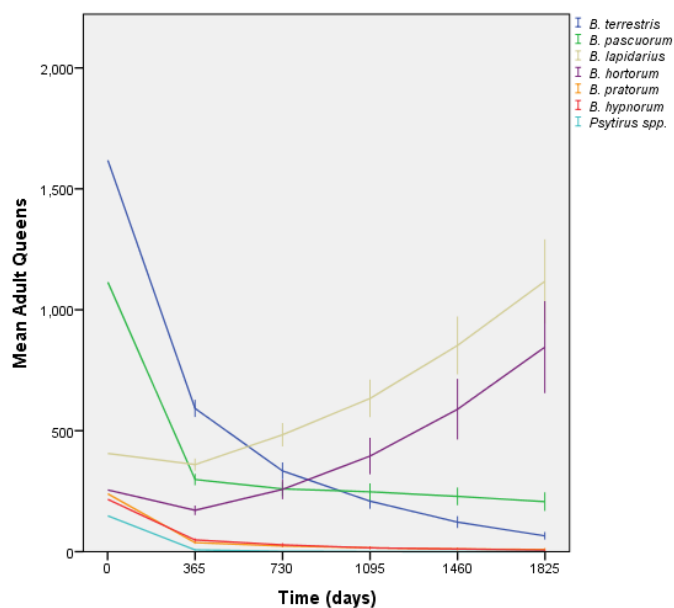


Figure 25: Average of the different species in the modelling runs versus time in days. Vertical lines represent the 95% confidence interval for the average.

The Sipma area

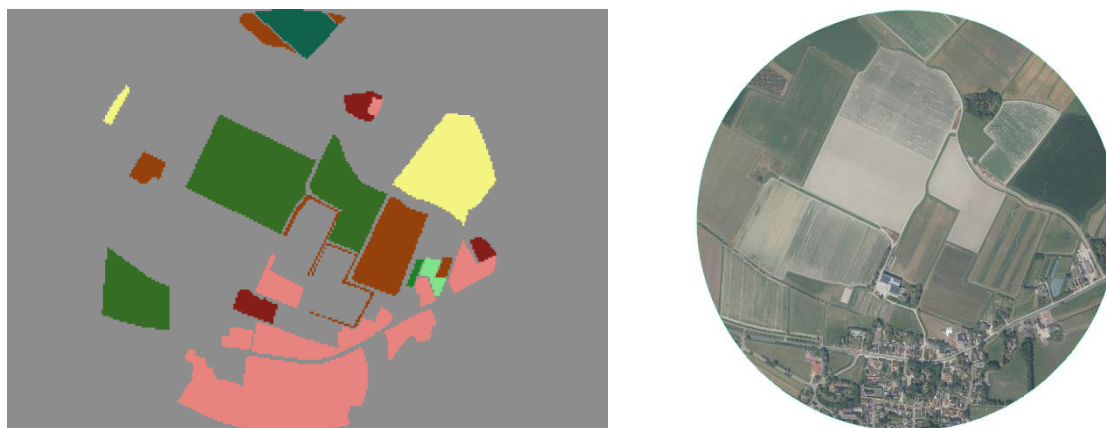


Figure 26: Comparison of the BEE-STEWARD input map (left) and an aerial photo (right) of the Sipma area. In the BEE-STEWARD input map: residential areas are pink, potato crops are green, maize crops are yellow, pumpkin crops are blue-ish green, nature areas are red and BEESPOKE seed mixture equivalent areas are orange.

In figure 26 the Sipma area is shown. This area had a lot of “BEESPOKE seed mixture equivalent habitat”. This habitat consists of “Agricultural nature mixture (agrarijsch natuurmengsel in Dutch)” according to the governmental GIS dataset. The “nature area” slightly southwest of the middle actually is a food forest. The Sipma area also contained a relatively large patch of residential area to the south.

In figure 27 the average of every individual modelled bumblebee species is plotted against time. This figure follows the same trend as all other areas, see paragraph “The Fokkema area” for more information. Of noteworthy difference is that *B. hortorum* ended up as the most prevalent species, instead of *B. lapidarius*. This was also the case for the Fokkema and Hoekstra areas, but not for any of the other 5 areas.

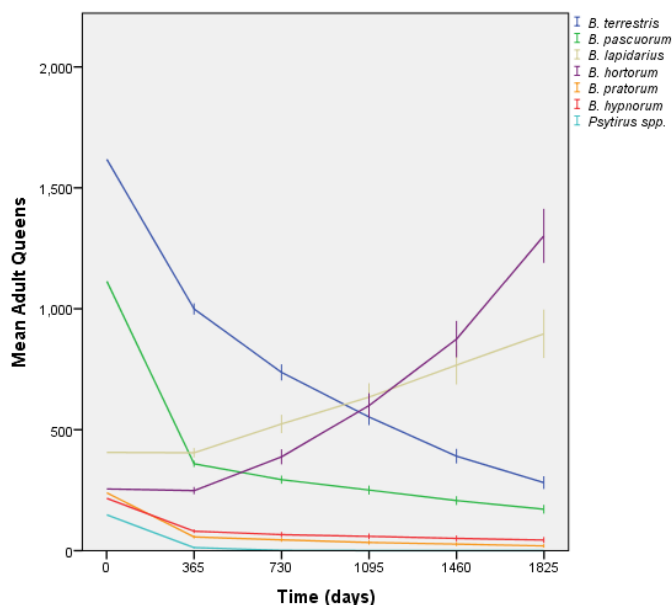


Figure 27: Average of the different species in the modelling runs versus time in days. Vertical lines represent the 95% confidence interval for the average.

The SPNA Area

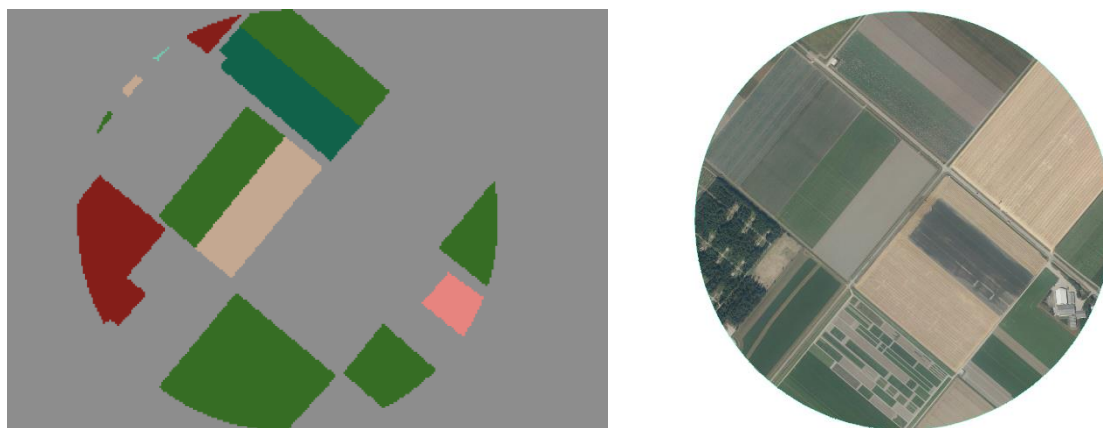


Figure 28: Comparison of the BEE-STEWARD input map (left) and an aerial photo (right) of the SPNA area. In the BEE-STEWARD input map: residential areas are pink, potato crops are green, pumpkin crops are blue-ish green, nature areas are red, *Phaseolus vulgaris* beans are light brown and red clover is blue.

In figure 28 the SPNA area is shown. This area contained a relatively large amount of potato crops. There was a significant amount of *Phaseolus vulgaris* bean crops. A tiny sliver of a red clover field existed to the far northwest.

In figure 29 the average of every individual modelled bumblebee species is plotted against time. This figure follows the same trend as all other areas, see paragraph “The Fokkema area” for more information.

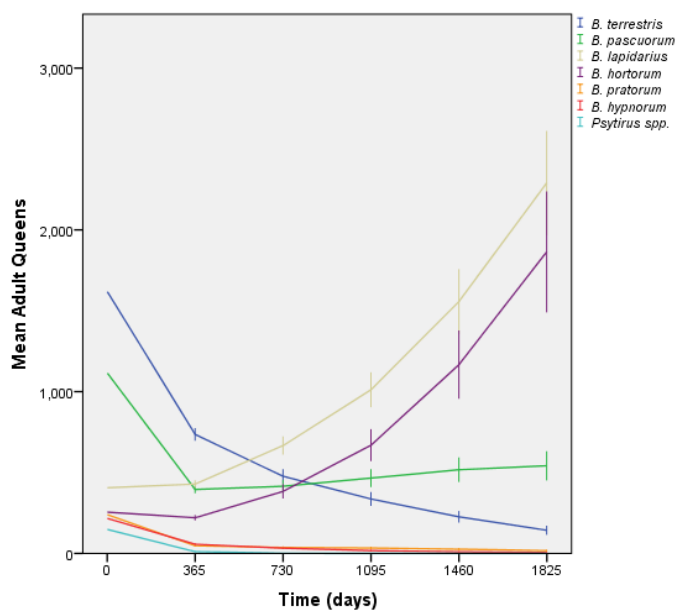


Figure 29: Average of the different species in the modelling runs versus time in days. Vertical lines represent the 95% confidence interval for the average.

The Venema area

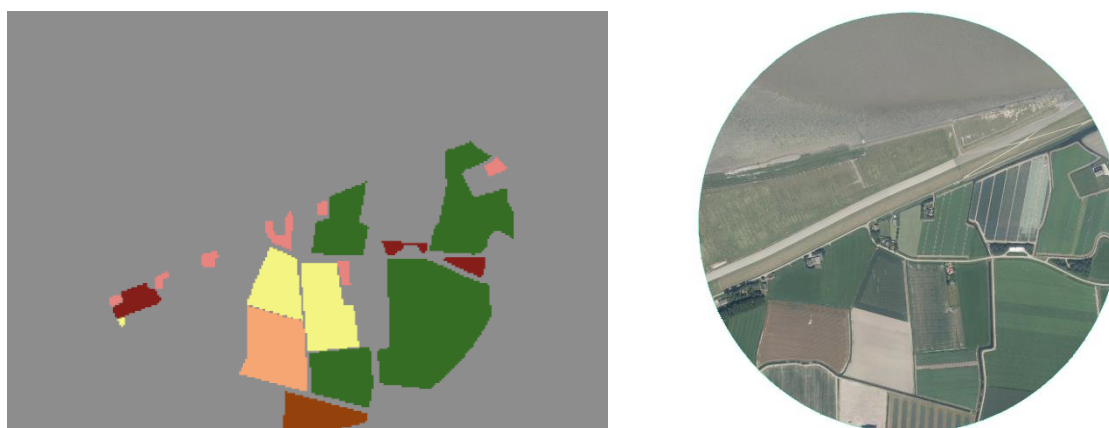


Figure 30: Comparison of the BEE-STEWARD input map (left) and an aerial photo (right) of the Venema area. In the BEE-STEWARD input map: residential areas are pink, potato crops are green, tulip fields are light orange, nature areas are red, maize crops are yellow and “BEESPOKE seed mixture equivalent” areas are dark orange.

In figure 30 the Venema area is shown. Part of this area consists of sea and flats outside the sea levee. These (mud-)flats were not included in the agricultural GIS data from PDOK.

This area also included a relatively large tulip field. To the south there was also a field of “Agricultural nature mixture (agrarisch natuurmengsel in Dutch)”.

In figure 31 the average of every individual modelled bumblebee species is plotted against time. This figure follows the same trend as all other areas, see paragraph “The Fokkema area” for more information.

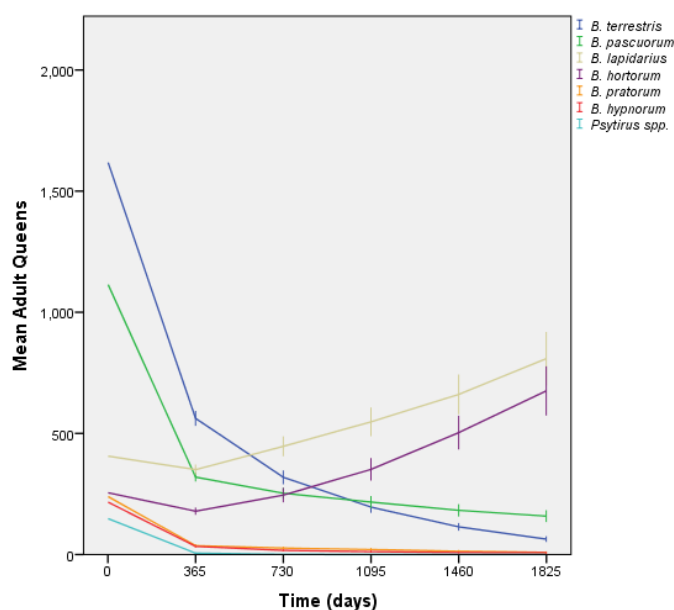


Figure 31: Average of the different species in the modelling runs versus time in days. Vertical lines represent the 95% confidence interval for the average.

The Zuidema area

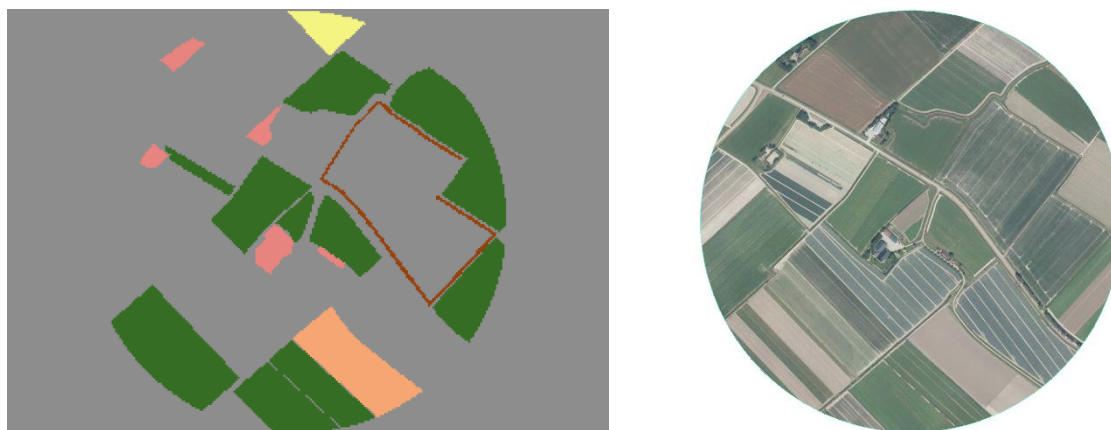


Figure 32: Comparison of the BEE-STEWARD input map (left) and an aerial photo (right) of the Venema area. In the BEE-STEWARD input map: residential areas are pink, potato crops are green, tulip fields are light orange, maize crops are yellow and “BEESPOKE seed mixture equivalent” areas are dark orange.

In figure 32 the Zuidema area is shown. This area had a large amount of potato crops. It also had a thin strip of “BEESPOKE seed mixture equivalent” area in the form of agricultural nature mixture (agrarisch natuurmengsel in Dutch)”. The Zuidema area also featured a tulip field.

In figure 33 the average of every individual modelled bumblebee species is plotted against time. This figure follows the same trend as all other areas, see paragraph “The Fokkema area” for more information.

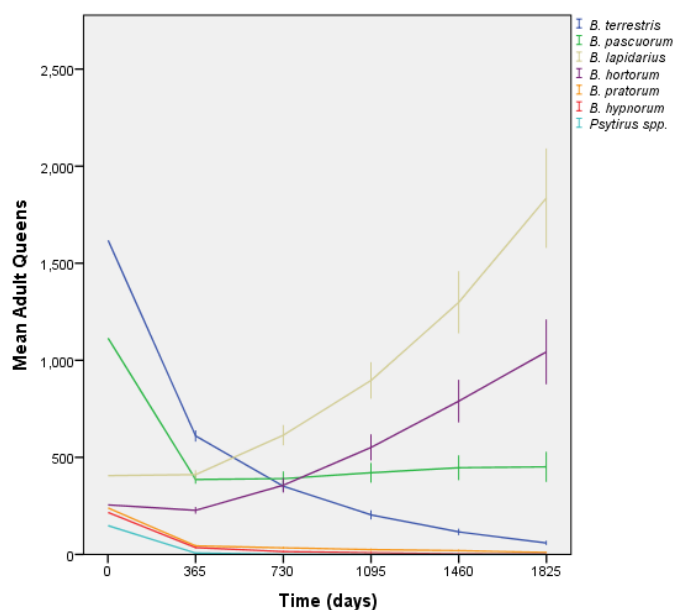


Figure 33: Average of the different species in the modelling runs versus time in days. Vertical lines represent the 95% confidence interval for the average.

3.5. Modelled bumblebee abundance and distribution in the base situation.

In figure 34 the bumblebee species distribution over time is shown. In the situation without any added BEESPOKE seed mixture areas, the distribution still differed from observed, in the same way as demonstrated in chapter 3.4. (p. 37-44).

In figure 35 the predicted bumblebee abundance is shown per area. Both the base and BEESPOKE situation are shown. The Hoekstra and Venema areas had a lower abundance in the BEESPOKE situation compared to base. The Fokkema, Roersma, SPNA and Zuidema areas were predicted to gain a large amount of bumblebee queens in the BEESPOKE scenario. The Minnema and Sipma areas did not differ by a large amount in these two scenarios. None of the areas came close to the initial 4000 bees after 5 years in these two scenarios.

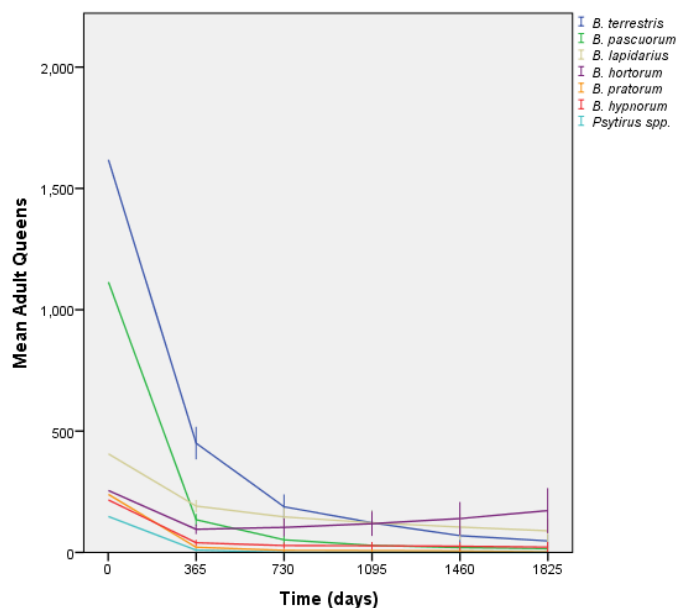


Figure 34: Average of the different species in the modelling runs versus time in days. This graph is based on the base situation (no applied seed mixture) for all areas. Vertical lines represent the 95% confidence interval for the average.

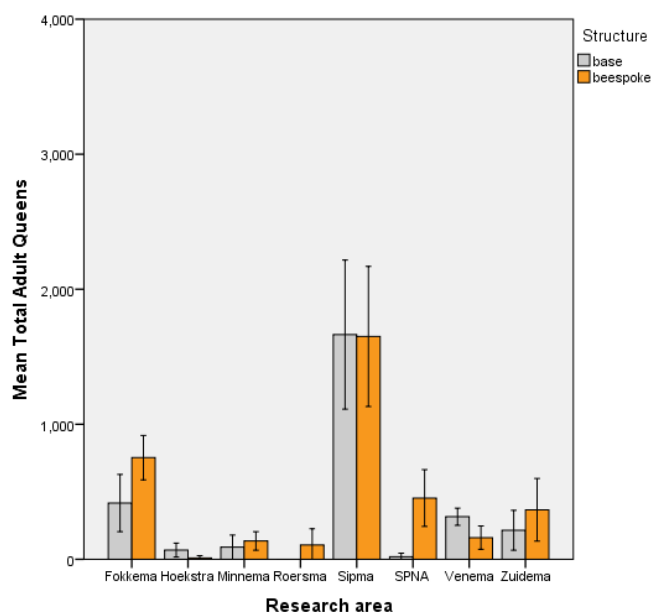


Figure 35: Predicted abundance of total bumblebee queens for the current situation and the planned BEESPOKE situation. Bars are given per trail location, vertical lines represent the 95% confidence interval for the average.

4. Discussion & Conclusion

A lot of data has been generated: almost 3 million data points from 1603 simulations. The data from some areas might potentially be outliers. This was the case for the Hoekstra and Venema areas when analysing the seed mixture application of the BEESPOKE trails. In the BEESPOKE trials the Hoekstra area gained a small bit of flower rich margins (0.06ha), but had an entire field of potatoes (0.41ha) changed to barley. Barley is not attractive to bees at all. Potatoes on the other hand, provide a limited amount of pollen to bees. Similarly, the Venema area gained a small flower rich margin (.07ha), but lost a field of potato (.66ha) to wheat. Wheat is completely unattractive to bees. These two areas already scored lower compared to the other areas throughout all results. It seems that changing part of the potato crops to unattractive crops is not compensated for by adding a small bit of flower rich habitat. Therefore they score even lower compared to expected in the BEESPOKE scenario as compared to the other scenarios. This however, was a result and should not be interpreted as an outlier. Figure 12 C and D (including the Hoekstra and Venema area), and the numbers associated with them, were used to discuss the results further on in this chapter.

The Sipma area could have been an outlier for the 3 meter wide margins and the 6 meter wide margins. In both these structures the Sipma area provided less queens than is expected across all data points. The Sipma area already had a large amount of seed mixture equivalent agricultural nature (4.72ha) in its base situation. The biggest part of these seed mixture equivalent areas was in the form of full fields (4.07ha). This made the Sipma area as a whole uncharacteristic of the applications of margins. For this reason the Sipma area was treated as an outlier for discussion of the 3 and 6 meter margin results.

4.1. Bumblebee abundance

General pattern

The 4 different application structures predicted different effects of adding BEESPOKE seed mixture area. The most efficient application was in 3 and 6 meter wide margins, with a predicted increase of 796 and 766 bumblebee queens per hectare of BEESPOKE seed mixture land cover respectively (figure 17). The 95% confidence interval of bumblebee increase per hectare of the 6 meter margins overlapped completely with the same confidence interval for the 3 meter wide margins.

The base situation and the full field applications scored the worst. Their predicted increases per hectare of seed mixture were 240 and 228 queens respectively. This suggests that most agricultural nature seed mixtures in the base situation are applied as fields. There are 3 areas that contained significant agricultural nature mixtures in their base situation, these are Sipma, Venema and Zuidema. Within 2 of these 3 areas the seed mixture was indeed predominantly applied as whole fields (Sipma and Venema). Furthermore, as explained in chapter 2.3. "The base structure", the floral resources in the "agricultural nature mixtures" were overestimated. This means that the base situation is expected to perform even worse in real life.

The better score of margins when compared to application as whole fields can be attributed to a wider distribution through the modelled landscape. The average distance to (close by patches of) the BEESPOKE seed mixture will be higher when this seed mixture is concentrated in a few whole fields instead of spread out (in relatively thin margins) over a large part of the area. Applying in whole fields thus leads to a higher energy cost of foraging, since larger distances are (on average) flown and the average detection probability of the seed mixture patches will be lower (*chapter 2.1., p. 13*). The assumption of random nest site location is a simplification of reality, but likely a reasonable one, as ditches (specifically the banks and tussocks/small scale dense vegetation on their edges) provide good nesting opportunity for bumblebee species. (Kells & Goulson, 2003) Such ditches are extremely

common in the Frisian agricultural landscape. This accounts for 4 of the 6 simulated species, the other 2 being *B. hypnorum* and *B. pratorum*. *B. hypnorum* usually nests in elevated places, like abandoned bird nests or bird boxes and cavities in trees or in buildings. (BWARS, 2015) (Waarneming.nl, n.d.) Agricultural ditches often (though not always) have a line of trees besides them, so these ditches and neighbouring vegetation might still provide nesting opportunities for this species. Residential areas might also provide nesting opportunities. *B. pratorum* nests both above and under ground, in a wide variety of places. (BWARS, 2012) Their nesting behaviour is similar to *B. pascuorum* (SoortenBank.nl, n.d.), which is associated with “Tussock” type vegetation according to Kells & Goulson (2003). The widely spread agricultural ditches are therefore likely good nesting habitat for this species.

As for the results of margins versus whole fields: Distribution of specific habitat types has not been studied extensively, but landscape heterogeneity and complexity have been positively correlated with bee species abundance. (Carrié, et al., 2017) (Morrison, et al., 2017) (Martin, et al., 2019) The distance dependant effect of foraging efficiency diminishes at very small foraging habitat sizes, no matter how well distributed the foraging habitats are over the area. (Preliminary BEE-STEWARD runs, unpublished results, 2019) At too small foraging habitat sizes, the modelled bees deplete the habitats fast. This leads them to switching foraging patches often and causes more time (and thus energy resources) to be spent on searching for new foraging habitat as opposed to exploiting known floral patches. If the found foraging habitats are again very small, this will become energetically unfavourable. Thus there is a bottom cap in BEE-STEWARD modelling to how small foraging habitats can be to still have a positive effect on bumblebee abundance.

This suggests the existence of an optimum size and number of patches for a given amount of foraging habitat (assuming fully chance based or fully homogenous distribution of the patches). In real life however, habitats can rarely be changed freely and optimized for just a single purpose.

The effectiveness of the BEESPOKE application fell in the middle of the margins and the whole fields, with a predicted increase of 400 queens per hectare of BEESPOKE seed mixture. The 95% confidence interval partially overlaps that of every other application structure (figure 17). In the BEESPOKE scenario, seed mixture is applied as 6 meter wide strips at every trial location except for the Sipma area. However, a number of crops were also changed compared to the 2019 data used as the base for all other scenarios/structures (*chapter 2.3., p. 16&17*). 8.19 hectare was changed from at least somewhat attractive to unattractive crops for bumblebees. Compared to the 6 meter margin scenarios, the BEESPOKE scenario applies a relatively low amount of seed mixture. This possibly reduces the positive effect of application in margins as compared to fields: At the small areas of application in the BEESPOKE scenario, often there are only a single or a few 6 meter margins per area. This means that the seed mixture is still applied in a relatively concentrated way, as opposed to more dispersed as in the 6 meter margin scenarios. This leads to only a minor difference when comparing this application versus a full field application of equal area of BEESPOKE seed mixture. These reasons explain the lower predictions as compared to the 6 meter wide margins, which would otherwise be expected to be nearly identical to the BEESPOKE scenario.

BEESPOKE scenario

The BEESPOKE application has been run for every individual trial location. The results of this (figure 35) are varied.

Areas with increased carrying capacity

The Fokkema, Roersma, SPNA and Zuidema areas were predicted to increase in bumblebee abundance.

The Fokkema area had 0.17 hectare of BEESPOKE mixture added. However, a further 0.84ha was changed from wheat to flax and 0.87ha was changed from beets to “bird-field” (Vogelakker in Dutch). These bird-fields are designed as a herb rich grassy area, increasing nesting habitat for birds and nesting and foraging habitat for their food species, namely flying insects and mice. These areas have been tested for their effect on soil quality and biodiversity. The results of Wiersma et.al. (2019) indicated a “very strong” increase in numbers of the insect niche of “pollinators and flower visitors” in these areas (compared to agricultural plots). These “Bird-field” areas were rated equally to the less specific “agricultural nature mixture” areas and the more specific BEESPOKE floral seed mixture areas. All of the above led to an almost doubling of predicted number of adult queens in the Fokkema area.

The Roersma area gained a 0.18 hectare strip of BEESPOKE seed mixture. Besides this it had maize fields changed to 6.46ha of beets and wheat fields and a further 1.40ha from maize to *Vicia faba* beans. The Roersma area has been predicted to only house a small amount of bumblebee queens in the BEESPOKE scenario (<400, figure 35). Nevertheless, this small amount is of a fundamental difference from the base situation, wherein the prediction was it would not contain any bumblebees at all.

In the SPNA area one of the largest BEESPOKE seed mixture strips has been added, as .44ha was changed from potatoes to a flower strip. This leads to a great increases in Bumblebee numbers, compared to an almost zero carrying capacity in the base situation.

In the Zuidema area a strip of 0.10hectares was added. A field of 0.64ha was also changed from potatoes to rapeseed. An increase in predicted bumblebee numbers was observed (figure 35). Bumble bee numbers still stayed relatively low after this increase.

Areas that stayed at similar carrying capacity

The Minnema and Sipma areas were predicted to stay similar to how they already were. For the Sipma area this makes complete sense, as the BEESPOKE trial field will be placed in the spot where there already was agricultural nature mixture in the 2019 data. Therefore not much changed. In the case of the Minnema area, only 0.07 hectares of seed mixture was added. This makes the overall increase in bumblebee queens quite small.

Areas with decreased carrying capacity

The Hoekstra and Venema areas were predicted to actually lose bumblebee abundance. The Hoekstra area gained 0.06 hectares of BEESPOKE seed mixture. At the same time 0.41 hectare was changed from potatoes to barley compared to 2019. This change was of a relatively big enough scale compared to the amount of seed mixture added that the total carrying capacity actually went down. A similar situation was the case at the Venema area. Here, 0.07 hectares of BEESPOKE mixture was added and 0.66 hectares of potatoes were changed to wheat.

Conclusions

3 and 6 meter wide margins were a more effective application structure for floral rich habitat compared to large fields. This was likely due to a better spread throughout the landscape, reducing the energy expenditure of the bumblebees when foraging. The areas where carrying capacity increased in the BEESPOKE scenario all gained a relatively large amount of BEESPOKE seed mixture (≥ 0.10 ha), often combined with positive changes in agricultural crops regarding floral resources. The areas that remained stable or decreased all gained only small BEESPOKE seed areas (≤ 0.07 ha) often accompanied with negative crop changes regarding floral resources. As numerous researchers have pointed out before (e.g. Carrié et.al. (2017), Nieto et.al. (2014), Potts et.al. (2010)) agricultural practices have a great effect on bumblebee populations and diversity. Therefore it is not surprising that a change of crop species can have an impact similar or greater than that of an added small amount of flower rich habitat.

4.2. Bumblebee species distribution

The distribution of the different bumblebee species varied during the modelling runs. As input the ratios as observed in nature were used. During the runs, the 2 most abundant species declined in numbers (*B. terrestris* and *B. pascuorum*), 2 other species took over as most dominantly abundant species (*B. lapidarius* and *B. hortorum*). The other species (*B. pratorum*, *B. hypnorum* and the *Psithyrus* spp.) started at a relatively low abundance and further declined during the runs. This led to the extinction of *Psithyrus* spp. within 5 years in all modelling runs. In the BEE-STEWARD model there are 4 differences between species: moment of queens emerging from hibernation (mean day of the year and standard deviation), proboscis length (minimum and maximum), batch size (eggs laid by the queen per day) and Developmental weights (minimum weight to go from larva to pupa, minimum weight to go from larva to pupa for a queen). Furthermore, *B. hypnorum* has a unique minimal development age of 19 days instead of 23.8 days for all other species. This is due to a shorter time spent as a pupa (6.1 days instead of 10.9 days).

Of the 4 main differences, only 3 impact this research, as flower corolla depth was assumed to be a low value (.7 mm) and thus was not a limiting factor. Only *B. hortorum* has a very different proboscis length in the BEE-STEWARD files (minimum of 11.3 mm and a maximum of 15.6 mm). The other species all have very similar proboscis lengths (minimum ranges from 6.2 to 7.3, maximum from 10.2 to 11.9). Possible explanations for the species distribution developing differently from expected are explored per individual bumblebee species below.

***Bombus terrestris*, the buff-tailed bumblebee**

B. terrestris sharply decreased in all model runs. In contrast, it is the most observed bumblebee species in the wild. In comparison to the other species, *B. terrestris* emerges very early in the season. The average day of emerging being 91 ± 28 , compared to the average of all species of 117 ± 18 (Appendix D). The only common habitats providing floral resources so early in the season are the nature and residential areas. Less common habitats that provide resources at or before day 91 are rapeseed, tulips, apple trees and cherry trees. It is likely that these early season floral resources were low enough to significantly decrease survival of early established colonies. *B. terrestris* is by far the most affected by this out of all the species. In real life there might be more (early season) resources than modelled. Stelzer et.al. (2010) observed *B. terrestris* individuals successfully foraging throughout the winter in London, England. This points in the direction of there being more early-season (and perhaps late-season) resources than estimated in this research. In addition, *B. terrestris* is capable of staying active later in the season compared to most other bumblebee species, something not modelled here. (BWARS, 2009) (Dafni, et al., 2010) (Stelzer, et al., 2010) Furthermore, most sources note the long foraging distances of *B. terrestris*. This was also not modelled, as both

the (distance dependant) detection probability of floral patches and the species specific “search length” were equal for all species.

B. terrestris in the model also required a very high developmental weight of 590 mg before queen larva can pupate. Only *Psithyrus* spp. have an equally high queen larva weight threshold, the other species all have a threshold lower than 400 mg. This might be a limiting factor for queen production of *B. terrestris*.

***Bombus pascuorum*, the common carder bee**

B. pascuorum also performed poorly in the modelled areas. This species emerges at day 136 of the year with a standard deviation of 14.5 days. At this moment in the season there was an abundance of floral resources. The only restrictive species specific trait is the low batch size: Only 7 eggs are produced per queen per day. For *B. pratorum* this number is 10, for all other modelled species it is 12. This resulted in a slower colony growth of *B. pascuorum*. Late emergence and a slower colony growth leads to a less favourable competitive position: A smaller amount of bees will be able to gather less resources before a floral patch is depleted by all bumblebees combined. The developmental weight thresholds of the pupa of *B. pascuorum* are the lowest of any species. In theory this means that they can thrive in areas with a lower amount of floral resources. However, this might not be enough to overcome the worse competitive position in the modelling runs. *B. pascuorum* stays relatively stable (after the initial drop in numbers) in every area, but always at a lower relative level than expected from real world observations.

***Bombus lapidarius*, the red-tailed bumblebee**

Bombus lapidarius emerges the latest of all species (day 143 ± 20.5). Developmental weights are average. *B. lapidarius* performed very well in the modelling runs. In real life they make up about 10% of all observed bumblebees in Fryslân (Appendix E). No adequate literature was found to explain what is limiting to wild *B. lapidarius* populations or which parameters have been overestimated in the BEE-STEWARD model. Differences in bumblebee species performance under different climates and differing preferred/optimal foraging times over the day have not been taken into account during the modelling runs. This could explain real life trends in the abundance of specific bumblebee species. (Williams, 2005)

***Bombus hortorum*, the small garden bumblebee**

This species performed very well in the simulated runs. *B. hortorum* has slightly below average pupation weight threshold and emerges at an average date (day 120 ± 8). In real life this species makes up about 6% of observed bumblebees in Fryslân (appendix E). *B. hortorum* has a significantly longer tongue length than the other modelled species. However, differences in tongue length were not taken into account in this research. In nature short and long tongued bees rarely overlap in their foraging preferences. However, when less diversity in plant species is available, species readily overlap in their food sources. (Lye, et al., 2010) In the simulation, *B. hortorum* is always competing for the exact same resources, as they are not differentiated by proboscis length. The increased competitive pressure that this led to did not hamper *B. hortorum*. Differences in bumblebee species performance under different climates and differing preferred/optimal foraging times over the day have not been taken into account. This could explain real life trends in the abundance of specific bumblebee species. (Williams, 2005)

***Bombus pratorum*, the early-nesting bumblebee**

B. pratorum has a batch size of 10 eggs/day instead of the more usual 12. It has a wide spread of emergence dates, slightly early in the season, although not as early as some other species (day 110 ± 30.5). These 2 factors, combined with an already low number of initial queens, led to poor

performance in the modelling runs. In real life this species accounts for 6% of Frisian observations. This species has a relatively short colony lifecycle and (especially in southern parts of its range) often goes through multiple of these cycles in a single season: The new queens produced by early colonies don't hibernate, but instead start a new colony. (Roos, n.d.) (Edwards, 2012) (NatureSpot, n.d.) Polycyclism has not been modelled in BEE-STEWARD.

***Bombus hypnorum*, the tree bumblebee**

B. hypnorum emerges early in the season (day100±10) and performed poorly in the model runs, just like the other early species (*B. terrestris* and to a lesser extent *B. pratorum*). *B. hypnorum* also requires a relatively high weight for larva to pupate, at a minimum of 112.4 mg (the average for all species is around 82 mg). *B. hypnorum* accounts for 5% of the bumblebee observations in Fryslân. In nature this species is strongly associated with forested and urban habitat. (Roos, n.d.) (Crowther, et al., 2014) (Edwards, 2015) This suggests that this species mainly thrives outside of direct competition with other bumblebee species, by nesting and foraging in habitats less attractive to other bumblebees. This might explain why this species performed very poorly in these model runs, where nesting was nearly unlimited and equal for all species. Flight distances for foraging were also equal for all species, while in nature not all species forage far outside the nesting habitat (mainly *B. terrestris* is known for long flight paths). (knight, et al., 2005) Thus it is possible that only a limited amount of species would compete over the same resources that *B. hypnorum* uses.

***Psithyrus* spp., cuckoo bees**

Cuckoo bees died out in every modelling run within 5 years, even though they were modelled as generalists that could attack any other bumblebee species' colonies. *Psithyrus* spp. require the highest developmental weight to pupate, for both regular and queen larva. Regular larva require a minimal weight of 140 mg, while the average for all species is just 82 mg. The next highest species is *B. hypnorum* with 112.4 mg. For queen larva they share the highest value with *B. terrestris*, at a minimum of 590 mg. The average over all species for queens larva pupation is 388 mg, with the second to highest being *B. hortorum* at 371 mg. This means that *Psithyrus* spp. larva require a substantial amount of resources more than any of the other species to mature. As might be noticed above, surprisingly, not all *Psithyrus* spp. eggs become queens, although this is the case in nature. In BEE-STEWARD, queens are *only* produced from eggs laid up to a few (and at maximum 5) days before the switchover point of the *colony*, irrespective of the species that the eggs belong to. From the switchover point onward, only haploid eggs (developing into males) are produced. Invaded *Psithyrus* spp. queens produce eggs during the entire life cycle of the colony, leading to the existence of *Psithyrus* "workers". However, these "workers" do not engage in any activities.

The chances that a *Psithyrus* spp. queens successfully invades a nest is dependent on a number of chances. Firstly the cuckoo bee needs to find a nest. The probability of this happening in BEE-STEWARD is 5% per available nest (multiplicative). If a nest is found, there is a 25% chance the *Psithyrus* queen will gain access to the nest. When this is successful, there is another 25% chance the *Psithyrus* queen will get killed by the resident queen of the invaded nest. Once this is successful the nest is invaded and the *Psithyrus* queen becomes part of the colony. When a *Psithyrus* queens successfully becomes a member of a colony, there is a 50% chance that the original resident queen is killed. If both queens survive this string of chances, they will not fight again. As stated in the (detailed) model description, these chances are arbitrarily defined and not yet based on empirical evidence. If the *Psithyrus* queen is unsuccessful, but surviving, she will continue searching and will be subject to the same background mortality as social queens are when searching for a suitable nesting site.

As summarized in the review by Lhomme & Hines (2018), bumblebees of subgenus *Psithyrus* in nature have a (summarized) life cycle as follows: Females emerge from hibernation after their host species does, depending on the specific species this difference can be up to a few weeks. They find the nest of their target host(s) by smell and then judge whether the found nest is of suitable quality (favourable host species, stage of development, and nest size being important aspects). If the nest is deemed suitable, she infiltrates it. The response of the host species is varies among species. In some cases the cuckoo bee is not recognized as an intruder, in other cases a violent effort is made to expel the cuckoo bee. This is rarely effective, however, as *Psithyrus* species have morphological adaptations that favour them in combat. Colony size does affect this, larger colonies have a drastically higher chance of defeating the invading cuckoo bee. The inquiline *Psithyrus* queens deploy a mix of strategies to be accepted in the hosts nest. These strategies can be separated in chemical and behavioural classes. Chemically, either mimicry is used, or a complete absence of identifiable (volatile) chemicals to evade rejection. Behaviourally, strategies range from hiding in the nest for a while to attain the smell of the hosts, to aggressively dominating the host species workers. Most of the time the *Psithyrus* queen eliminates the host queen, although peaceful coexistence also occurs. The inquiline queen replaces the brood of the host queen with eggs of her own, which the host species workers take care for. It is unsure how long the cuckoo bee stays within the host colony. This might range from just long enough to lay a few batches of eggs to until the cuckoo bee dies. Once the new larva have develop into adults, they leave the host nest. The females do not return to the nest, nor make orientation flights as observed in non-cuckoo bumblebees. The males exhibit patrolling behaviour very similar to other (non-cuckoo) bumblebee species. Mating behaviour is poorly documented. After mating, females will look for a suitable hibernation site. Because they enter hibernation sooner and emerge later, *Psithyrus* spp. hibernate almost a third longer than other bumblebee species. Exactly how they are capable of doing this is yet unknown.

It stands to reason that current modelling of cuckoo bees in BEE-STEWARD produces incorrect results, as large parts of their life cycle is modelled very different from reality.

Conclusions

In general, the species distribution was affected by a likely underestimation of early season resources. Cuckoo bees were not modelled realistically. Further differences in bumblebee species distribution might be explained by different species specific performance responses to temperature and other weather effects that were not modelled. Furthermore, the capability of the model to differentiate on a further 17 species specific variables (Appendix D) was not used due to a lack of data to base these differentiations on. Nesting sites were also assumed to be nearly unlimited (ditches widely present in agricultural landscapes provide ample nesting opportunity, see chapter 2.1., p.12) and thus equal for all species. More detailed species specific data has the potential to significantly increase the predictive qualities of the BEE-STEWARD model when it comes to the ratio of abundance between different species.

4.3. Floral resource assumptions

A number of assumptions has been made in this research to create the flower and habitat input files. The production of protein and sugar of flowers was assumed to differ along an exponential distribution for different flower species. This was based on the default model species for which precise data is known. The protein content and sugar content in the pollen and nectar respectively was then assumed to be equal for all species and the (rounded) average value of the default species was used. In this way, only the (exponential) production scores were affecting resource availability. These production scores could then be related to Jacobs et.al. (2010) and Van der Steen & Cornelissen (2015) to acquire input data for a wide range of plant species. Of course it is not guaranteed that the default plant species that the assumptions are based on paint a realistic image of all plant species. The default species consist of 37 plant species from a 25km² area in Sussex, United Kingdom. (Becher, et al., 2017) Sussex has a varied soil type, including clay soils (as in the trial locations relevant in this research) but also loamy and sandy soils. (Cranfield Soil and Agrifood Institute, n.d.) Climate is the same in Fryslân and Sussex. (Climate-data.org, n.d.) These facts (equal type of land-use, wide species palette, similar climate) make it plausible that the plant communities are similar in their ecology.

For the habitat input file, the amount of flowers per square meter was assumed to be 20 for every habitat. In chapter 2.5. (p. 21) comparisons between the estimated yields by Jacobs et.al. (2010) and the calculated yields of this research were made. From table 5 on that page, it becomes clear that the yields are not overall higher or lower than estimations by Jacobs et.al., which means that a value of 20 is reasonable. The range of flowers/m² found in the original, default plant species file is very large: from 0.5 to 180, with an average of almost 100 and a median of 6. 20 seems to be a reasonable number, being of middling order of magnitude.

Also in the habitat file, nature areas and residential areas were defined. These areas provided very important early season resources, at a low level. This was based on the fact that residential areas provide at least decent, and probably good, habitat for bumblebees (Theodorou, et al., 2020) (Gunnarson & Federsel, 2014) (Nakamura & Kudo, 2019) and the assumption that these areas provide flowers early in the season. This assumption is in turn based on the assumption and observation that humans like to have flowers in their garden for as much of the year as possible. Nature areas are assumed to be suitable places for endemic bumblebees to thrive. However, this is of course dependent on the management of the specific nature areas. Because nature areas are only a tiny fraction of the research areas and are largely outdone by residential areas, this was not further taken into account. As stated in paragraph 4.2, early season resources are likely still underestimated.

4.4. General conclusion

Stochastic modelling with the BEE-STEWARD model predicts 3 and 6 meter wide margins to be a more effective application structure for flower rich habitat than full fields. This is likely due to a more dispersed spread of resources throughout the area. Although not dispersion of resources directly, landscape complexity has been positively linked with bumblebee abundance. (Carrié, et al., 2017) (Morrison, et al., 2017) (Martin, et al., 2019) At the most beneficial application structure (6 meter margins) every hectare of BEESPOKE seed mixture was predicted to yield between 593 and 940 extra bumblebee queens after 5 years. This is a statistically significant effect ($W=75.138$, $df=1$, $p<.000$). Supplementation of floral resources with currently realistic amounts of beneficial seed mixture does not negate the effect of agricultural practises: Changes in crops rival the BEESPOKE seed mixture applications in effect size.

The predicted bumblebee species distribution is different from the real world observed distribution. The difference is roughly equal for all modelled areas, pointing in the direction of an underlying model based causation. Currently bumblebee species differ in only a fraction of the possible variable species specific traits implemented in the BEE-STEWARD model. This is due to a lack of exact data on these traits for each species. Furthermore, early season resources are likely underestimated. These are the hypothesised causes for the unexpected emergent species distribution. More data on the exact resources generated by the plant species as well as more data on bumblebee species specific traits could refine the outcomes of the BEE-STEWARD model.

5. Recommendations

For future research involving the BEE-STEWARD model

A great difficulty in this research has been defining the exact resource generation attributed to a specific plant species. These exact values are highly dependent on the surrounding biotic and a-biotic factors, and can therefore widely differ during the season. (Jacobs, et al., 2010) (Waser & Price, 2016) (Mu, et al., 2016) (Adgaba, et al., 2017) The method used in this research is an estimation based on the attractiveness and/or yield of a flower defined by observations of honeybees. This method could be improved upon by including field measurements of at least the major crops, perhaps following methodology as described by Fowler et.al. (2016). Although it would still be difficult to take surrounding a-biotic and biotic factors into account, it would provide a more rigid estimation of floral resources. Furthermore, detailed data on more bumblebee species specific traits would greatly improve the quality of (species distribution) predictions made by the BEE-STEWARD model. Disclosing this data, however, likely requires a completely separate study, as it would take considerable effort.

For bumblebee conservation

This research indicates that the addition of flower rich habitat is more efficient if it is dispersed over the area instead of centralized, at least at the order of magnitude of a single to a few individual farms. The floral availability through farmland crops also has a large influence on bumblebee abundance. The large effect of agricultural practises on pollinator populations are widely recognized in literature. (Carrié, et al., 2017) (Kosior, et al., 2007) (Nieto, et al., 2014) (Potts, et al., 2010) Therefore coordinating specific crop choices and rotations should also be kept into account as a tool for conservation. The BEE-STEWARD model can be used as a tool to predict where conservation measures would be most effective. This is especially true if more species specific data on flower plants and bumblebees becomes available, as this would reduce the amount of assumptions that are necessary.

For the BEESPOKE project

The expected results at the trial locations are wildly varied. Differences in crops or other environmental factors affect the results, possibly to a greater extent than the patches of seed mixture do. These possible effects should be taken into account when evaluating abundance numbers at the trial locations. However, for testing the practical applicability of the seed mixture and its development in the environmental situation at the trial locations this makes no difference. To get definitive, measurable positive effects at the trial locations a cover of at least 0.1 hectare per square kilometre seems needed. To not only get a measurable positive effect compared to the current situation, but to get close to the 4000 bumblebees that the runs were started with, a percentage cover of >4% seems to be needed (>4ha/km²).

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Appendix A: BEESPOKE seed mixture

The BEESPOKE seed-mixture details are shown in Table A1. These are the contents of BEESPOKE mixture 7, which is the mixture for perennial plants for region “west”. The species name and what percentage of the total mixture they contribute have been summarized.

Table A1: plant species that are in the modelled BEESPOKE mixture. The relative amount within the mixture is also given.

Dutch name	Latin name	Part of total
Wilde peen	Daucus carota	14 %
Duizendblad	Achillea millefolium	8 %
Korenbloem	Centaurea cyanus	18 %
Knoopkruid	Centaurea jacea	14 %
Echte kamille	Matricaria chamomilla	6 %
Rode klaver	Trifolium pratense	6 %
Witte klaver	Trifolium repens	6%
Gewone rolklaver	Lotus corniculatus	14 %
Boerenwormkruid	Tanacetum vulgare	8 %
Klein streepzaad	Crepis capillaris	6 %

Appendix B: Exponential plant production

In figure B1 and B2 the plant species that are initially embedded in the model are sorted from low to high production. On the y-axis are the grams of protein per day or the moles of sugar per day respectively. These data points roughly follow an exponential curve.

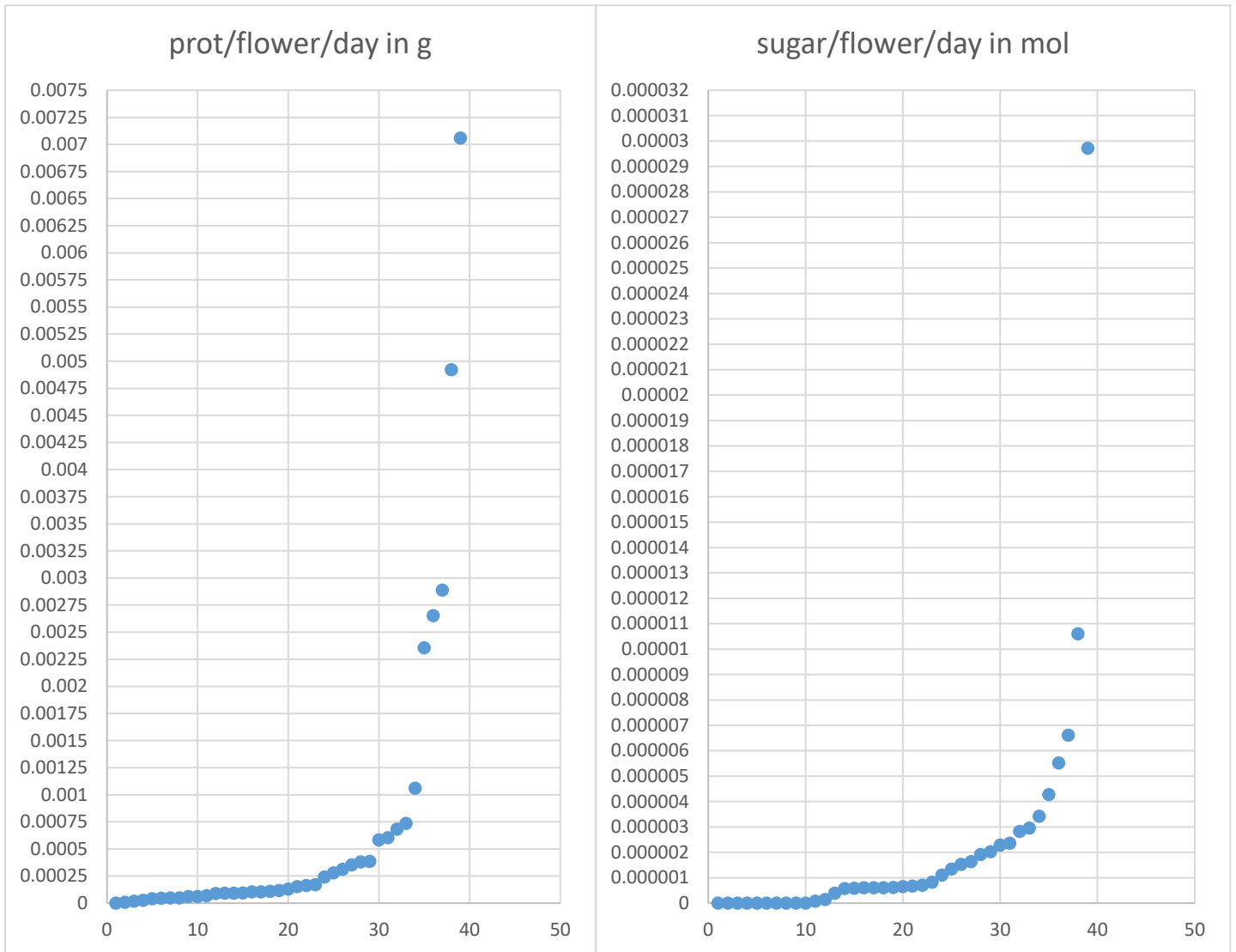


Figure B1: Protein per flower per day in grams for the 39 default model plant species, ordered from low to high production.

Figure B2: sugar production per flower per day in moles for all the 39 default plant species, ordered from low to high production.

Appendix C: BEE-STEWARD flower input data

In table C1 the English, Dutch and Latin species names can be found, together with the “attractiveness” of the plants to bees. This attractiveness is defined on a scale of 0 to 5 for both nectar and pollen separately. The flowering months and resulting start and stop day of the flowering period is also specified. This data is based on works from Jacobs et.al. (2010) and from Van der Steen & Cornelissen (2015). Missing (and assumed) data is shown in bold italics.

Table C1: Species names and resource values that were used to define the BEE-STEWARD model input regarding plant spp.

<i>English species name</i>	<i>Dutch species name</i>	<i>Latin species name</i>	<i>pollen</i>	<i>nectar</i>	<i>Flowering months</i>	<i>Flowering days</i>
Carrot	Wortel	<i>Daucus_carota</i>	1	2	jun-oct	152-304
Common yarrow	Duizendblad	<i>Achillea_millefolium</i>	1	1	Missing	150-250
Cornflower	Korenbloem	<i>Centaurea_cyanus</i>	4	5	jun-aug	152-243
Brown knapweed	Knoopkruid	<i>Centaurea_jacea</i>	2	3	jun-aug	152-243
Red clover	Rode klaver	<i>Trifolium_pratense</i>	3	3	may-oct	121-304
White clover	Witte klaver	<i>Trifolium_repens</i>	3	4	may-nov	121-334
Common bird's-foot-trefoil	Gewone rolklaver	<i>Lotus_corniculatus</i>	1	3	may-sep	121-273
Tansy	Boerenwormkruid	<i>Tanacetum_vulgare</i>	2	2	jun-sep	152-273
Potato	Aardappel	<i>Solanum_tuberosum</i>	1	0	Missing	150-250
Alfalfa/Lucern	Luzerne	<i>Medicago_sativa</i>	1	3	jun-sep	152-273
Smooth hawksbeard	Klein streepzaad	<i>Crepis_capillaris</i>	3	3	jun-oct	152-304
German chamomile	Echte kamille	<i>Matricaria_chamomilla</i>	2	2	Missing	150-250
<i>Nature (general)</i>	<i>Natuur (onspeciefiek)</i>	-	2	2	-	75-325
Flax	Vlas	<i>Linum_usitatissimum</i>	1	1	jun-aug	152-243
<i>Residential area</i>	<i>Bewoond gebied</i>	-	2	2	-	75-325
Broad bean	Tuinboon	<i>Vicia_faba</i>	2	2	may-jul	121-212
Maize	mais	<i>Zea_mays</i>	4	0	jun-aug	152-243
Rapeseed	Koolzaad	<i>Brassica_napus</i>	4	4	apr-may	91-151
Pumpkin	Pompoen	<i>Cucurbita_pepo</i>	1	2	jun-aug	152-243
Tulip	Tulp	<i>Tulipa (gesneriana)</i>	4	1	mar-apr	60-120
Bean spp.	Boon spp.	<i>Phaseolus_vulgaris</i>	2	2	jun-sep	152-273
Apple	Appel	<i>Malus_Domestica / Malus_sylvestris subsp. Mitis</i>	3	3	apr-may	91-151
Cherry	Kers	<i>Prunus_Avium</i>	4	4	apr-may	91-151

Appendix D: BEE-STEWARD Bumblebee species input data

In table D1 the default input for modelling of specific bumblebee species is shown. Reasoning for these settings can be found in Becher et.al. (2017) & (2016). Only the "nestHabitatsList" is not at the default setting; all the areas specified in the Habitats input file are added in this row for every species.

Table D1: Bumblebee species input file used by BEE-STEWARD. These are the default setting, except for the "nestHabitatsList" row.

species	B_terrestris	B_pascuorum	B_lapidarius	B_hortorum	B_pratorum	B_hypnorum	Psithyrus
name	B_terrestris	B_pascuorum	B_lapidarius	B_hortorum	B_pratorum	B_hypnorum	Psithyrus
emergingDay_mean	91	136	143	120	110	100	120
emergingDay_sd	28	14.5	20.5	8	30.5	10	15
nestHabitatsList	["Grassland"	["Grassland"	["Grassland"	["Grassland"	["Grassland"	["Grassland"	["Grasslan
proboscis_min_mm	6.9	7.3	7	11.3	6.5	6.2	6.5
proboscis_max_mm	11.1	11.6	11.9	15.6	10.3	10.2	10.3
growthFactor	1.88	1.88	1.88	1.88	1.88	1.88	1.88
seasonStop	305	305	305	305	305	305	305
maxLifespanWorkers	60	60	60	60	60	60	60
batchsize	12	7	12	12	10	12	12
flightVelocity_m/s	5	5	5	5	5	5	5
searchLength_m	2500	2500	2500	2500	2500	2500	2500
timeUnloading	165	165	165	165	165	165	165
specMax_cropVolume_myl	173	173	173	173	173	173	173
specMax_pollenPellets_g	0.15	0.15	0.15	0.15	0.15	0.15	0.15
minToMaxFactor	2	2	2	2	2	2	2
devAgeHatchingMin_d	5	5	5	5	5	5	5
devAgePupationMin_d	12.9	12.9	12.9	12.9	12.9	12.9	12.9
devAgeEmergingMin_d	23.8	23.8	23.8	23.8	23.8	19	23.8
devWeightEgg_mg	1.5	1.5	1.5	1.5	1.5	1.5	1.5
devWeightPupationMin_mg	62.4	48.5	90.7	71	51	112.4	140
devWeightPupationMax_mg	249.5	187.6	159.8	271	231	218	170
pollenToBodymassFactor	1	1	1	1	1	1	1
dev_Q_DeterminationWeight_mg	0	0	0	0	0	0	0
devAge_Q_PupationMin_d	17	17	17	17	17	17	17
devWeight_Q_PupationMin_mg	590	261	300	371	271	334	590
devWeight_Q_PupationMax_mg	980	461	850	751	491	410	980
devAge_Q_EmergingMin_d	32	32	32	32	32	32	32
dailyNestSiteChance	0.2	0.2	0.2	0.2	0.2	0.2	0.2

Appendix E: Input ratio bee species

The table E1 and graph E1 the ratio of bees as used to initiate the model is shown. The counts are the observations uploaded to Waarnemingen.nl in the province Fryslân, for the entirety of 2019.

Table E1: The 7 bee species that are modelled in BEE-STEWART, with the counts and resulting ratio as calculated from the Waarnemingen.nl Database.

ENGLISH NAME	DUTCH NAME	LATIN NAME	COUNT	RATIO
Buff-tailed bumblebee	Aardhommel	<i>Bombus terrestris</i>	1912	0.4054
Common carder bee	Akkerhommel	<i>Bombus pascuorum</i>	1313	0.2784
Small garden bumblebee	Tuinhommel	<i>Bombus hortorum</i>	301	0.0638
Early bumblebee	Weidehommel	<i>Bombus pratorum</i>	282	0.0598
Red-tailed bumblebee	Steenhommel	<i>Bombus lapidarius</i>	478	0.1014
Tree bumblebee	Boomhommel	<i>Bombus hypnorum</i>	255	0.0541
Cuckoo-bees (entire complex)	Koekoekshommels	<i>Bombus</i> subgenus <i>Psythirus</i> spp.	175	0.0371
Totals:			4716	1

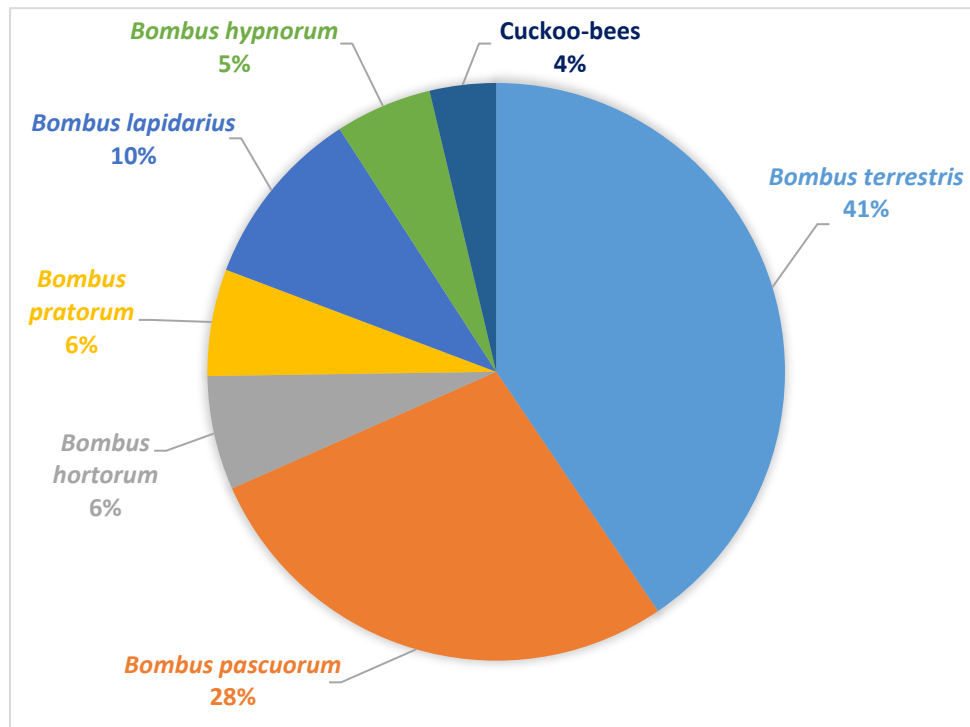


Figure E1: Graph of the different bees species and in what ratio the runs are initiated.

Appendix F: G*power sample size calculation

In figure F1 a screenshot of G*power is depicted. First the type of test needs to be specified. Following the rationale as outlined by Marusteri & Bacarea (2009) it is concluded that a one-way ANOVA is proper for the purpose of this research. This can be seen in red box nr. 1 in the screenshot.

Next the criteria need to be specified, as outlined in red box nr. 2. The α and β error probabilities are both set a 5% (which is standard by convention). There are 8 input maps with a total of 79 agricultural fields. This leads to 245 distinct runs (8*null situation + 79 incremental 3 m margins + 79 incremental 6 m margins + 79 incremental full flowering fields). This is the number of groups. A medium sized effect (F = .25 by convention) is assumed.

Having specified these 4 values in red box nr. 2, clicking “calculate” returns the values in red box nr. 3. Here it can be seen that a total sample size of 1715 data points is needed. This means $1715 / 245 = 7$ data points per group. It can also be seen that this results in a theoretical power of over 98% (meaning there is a >98% chance that H_0 will be rejected if H_1 is true).

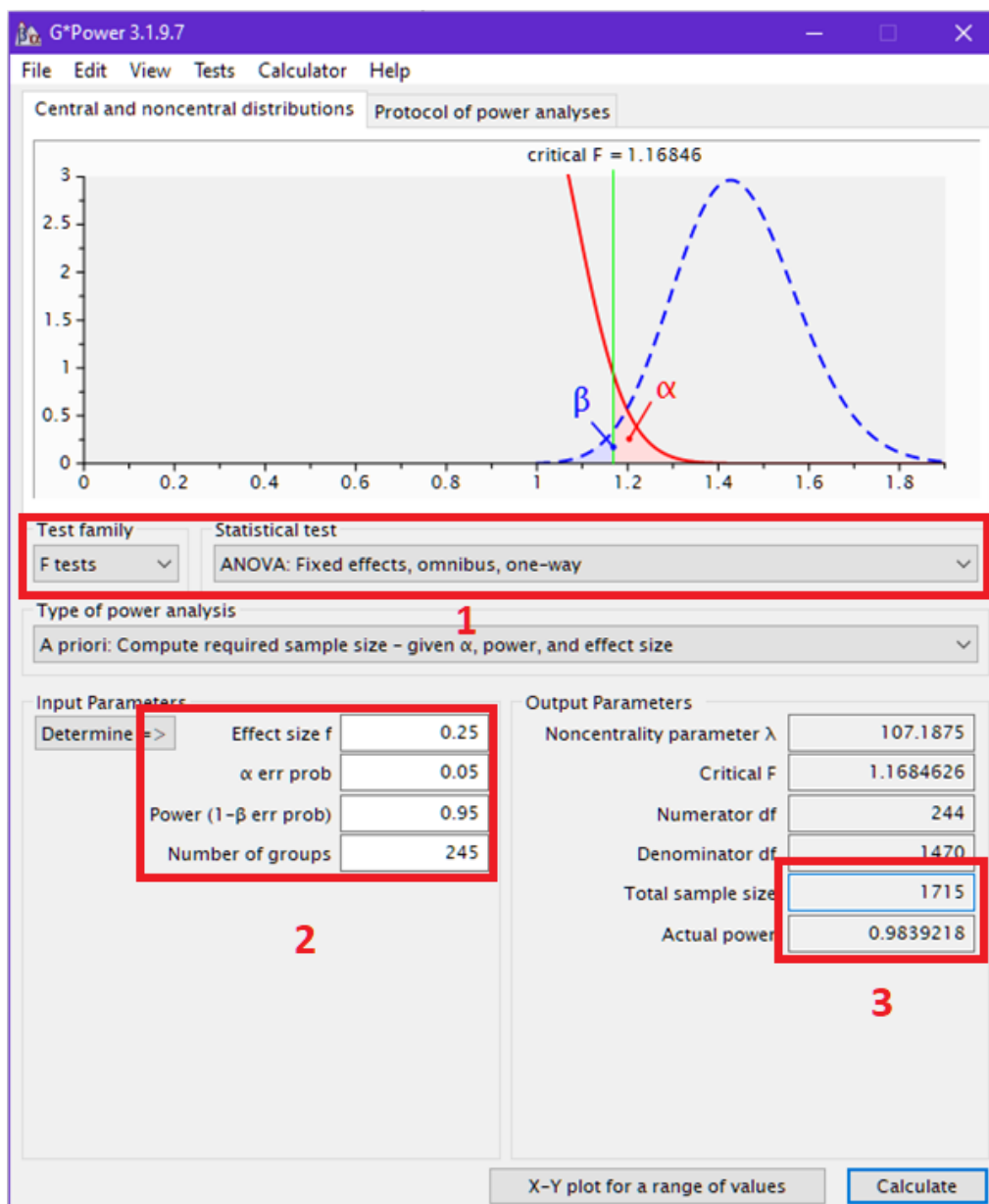


Figure F1: G*power screenshot after sample size calculations were done.