EXTERNAL SCIENTIFIC REPORT

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*Apis*RAM Formal Model Description

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Abstract

The *Apis*RAM model is an agent-based colony model for honey bees in which each bee is modelled as an individual agent. The behaviour of the colony emerges from the decisions and actions taken by individuals in the colony and the interactions between agents. The bees interact with, and react to, both other bees and the resources in the colony, the hive physical and chemical properties, and the environment outside the colony. A key feature of *Apis*RAM is the approach to representing bee health. This is a 'vitality' model which is used to integrate multiple stressors (unfavourable temperature, food shortage, infectious agents and pesticides) for each individual bee. The vitality of each model bee interacts with all the four stressors. The environment in which the colony is modelled is implemented as a dynamic landscape simulation within ALMaSS (the Animal Landscape and Man Simulation System). The ALMaSS landscape model is a spatially and temporally dynamic model which combines land use, detailed farm practices, weather, crop growth, semi-natural habitats, and flower resource models. With the combination of the colony and landscape models, the *Apis*RAM model provides a framework for in silico experiments, e.g., pesticides applications, designed to explore the effects of combined stressors on honey bee colonies under a variety of environmental and human (e.g. beekeeping management practices) factors.

Key words: Honey bee, agent-based model, multi-stressors, pesticide

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1. Introduction

1.1. Background and Terms of Reference as provided by the requestor

This contract was awarded by EFSA to:

Contractor: Aarhus University

Contract: Development of a mechanistic model to assess risks to honeybee colonies from exposure to pesticides under different scenarios of combined stressors and factors

Contract number: OC/EFSA/SCER/2016/03

2. Overview of *Apis*RAM

*Apis*RAM is a spatially explicit individual-based model, developed within ALMaSS (Animal Landscape and Man Simulation System) (Topping, Hansen et al. 2003). A spatially explicit individual-based approach is used both for honey bees as foragers in the landscape and for in-hive bees. The ALMaSS landscape model is a common core model for all ALMaSS species models and provides the environmental context for the bees and other species in ALMaSS. It is a complex simulation in its own right and hence only the details relevant to honey bees are covered here.

An individual-based model works by modelling each individual bee in the colony as an object within the code. ALMaSS species modelling is based on a state machine with transitions between states. In this case each individual bee, at any moment in time, is considered to be in a behavioural state. This behavioural state will cause the bee to carry out some actions, and depending on fulfilling certain conditions the bee will transition to a new state (e.g. when foraging, if sufficient resources are collected then, return to the colony). This means that, for each individual bee, we represent in code that individual, and its current physiological and behavioural properties, for example its age, temperature, state of hunger, and ongoing activity (e.g., foraging, scouting, guarding, etc.). It is spatially explicit because we model its position, both within the colony and in the landscape when it is foraging and/or scouting out of the hive. In-hive products are also accounted for in a spatially explicit model. For example, we track pollen and nectar within the hive to the spatial resolution of a cell within the honeycomb. This differs from a systems model, where we might store the number of bees at a particular life stage and pool the resources within the hive. But there are two exceptions of in-hive products/processes that are not modelled in a spatially explicit way. Honey bees usually deposit their waste outside the hive. However, when the weather is too cold for a bee to move out, waste is accumulated in the hive. Furthermore, when an adult bee dies in the hive, it can also result in waste in the hive. These two types of waste are pooled in the model, i.e., they are not tracked spatially to any cell in the hive. A single system variable defines the waste level. Bees tasked to remove waste reduce the value of this variable to represent waste removal and are assigned an appropriate metabolic rate. Thus, removal of these two types of wastes is different from cleaning a cell for a dead egg, larva and pupa. The act of removing waste is not modelled as a spatially explicit process, although the time and energy cost for this activity are calculated for each bee involved.

Externally (to the hive), the model is also spatially explicit. The simulation runs on top of a landscape model (ALMaSS) that defines the surrounding environment of the hive. The active simulation defines each habitat patch as a polygon within a GIS-like representation of the landscape structure. The state of each polygon changes according to land use, farm management, weather, and crop/plant growth phenology. The most important element in the landscape model for the *Apis*RAM simulation is the resource providing units which define, for each polygon in the GIS, the quantity and quality of pollen and nectar available to the foraging bees. The landscape input for the simulations to test and develop were created as part of another project (Dupont et al. 2021ab).

Another key feature of *Apis*RAM is the integration of multi-stressors including malnutrition, unfavourable body temperature, infectious agents and pesticides. This integration occurs are multiple levels, within the individual bee, within the colony, and within the landscape context. For the individual bee, no single stressor is isolated from others. The impact of each stressor is not constant, instead it varies depending on the bee's health status which is decided by the combination of all the stressors. To model this, we introduce a vitality model in which the vitality variable interacts with all the stressors. Through the vitality, all the stressors are connected and impact each other. The vitality component combines impacts on bee immune-response with feedbacks between stressors shown to be important in honey bees ((Di Prisco, Cavaliere et al. 2013) (Di Prisco, Annoscia et al. 2016) (Annoscia, Di Prisco et al. 2020)). The interactions in the colony occur via interactions between the bees, and those with the landscape relate to the conditions found by the bees. This means that events, e.g., farming practices, that might change resource availability will be integrated via foraging behaviour and resulting resource conditions within the colony, that will then determine the individuals' nutritional state. In addition, there is the potential for direct management of the bee colony by the beekeeper.

To implement all the features listed above, there are five inter-connected model modules in *Apis*RAM, namely individual bee development, individual bee activities, in-hive thermodynamics, infectious agents and beekeeping management practices. Each module will be detailed in the following sections.

*Apis*RAM is still under development and calibration with the aim of usage for environmental risk assessment with multiple stressors in 2025 (see LINK). More information about the *Apis*RAM development roadmap can be found in Section 12.

3. Notation, coordinate systems and movement of model bees

3.1. Notation

The size and complexity of the model inevitably leads to the inclusion of many variables and identifiers. The system described here is intended to make the naming of variables and constants as simple as possible and reduce the number of symbols to a minimum.

Variables and constants can have different values depending on the caste of the bee. In these situations, the caste is stated in superscript to the left of the variable. The symbol B is used in situations where the equation depends on the bee caste, but only the general equation is given. In this case, the equation represents multiple equations, each of which can be obtained by substituting a different caste attribute. As an example, we may refer to the general case of the metabolic rate of a bee as ${}^{B}q$, but would use ${}^{NN}q$ to represent the specific case of a non-nurse bee. The bee castes are shown in Table 1.

Table 1 Identifiers for the bee life stages, bee castes and worker categories. The life stages and castes can be combined. For example, DE represents 'drone egg'.

Category	Symbol	Type
Egg	*E*	Life stage
Larva	*L*	Life stage
Pupa	*P*	Life stage
Adult	*A*	Life stage
Any bee caste	*B*	
Worker	*W*	Caste

Drone	*D*	Caste
Queen	*Q*	Caste
In-hive bee	*IN*	Worker Category
Forager/Scouter	*FO*	Worker Category

If the stage of development is given for a bee, it is written to the right of the caste as an extra superscript. The notation ${}^{DE}q$ would be used for the metabolic rate of a drone egg. The tag A is used for adult stages, which is usually omitted unless needed for clarification. Bee classification can be constrained further by age classes. The age class is given after the caste identifier, either as a single day or a day range. As an example, the metabolic rate of worker bees in the range of 1 to 3 days after hatching would be given the notation ${}^{W\,1..3}q$.

Cell types follow a similar notation to bee castes, with the identifier placed in superscript to the left of the symbol. The types are given in Table 2. Age classes can be applied to the cell types as a subscript. For example, N_0 is freshly stored nectar and P_2 is two-day old pollen.

Table 2 Identifiers for cell types.

Cell types	Tasks	Meaning	Subcategories
Unbuilt	U	Not drawn out	
Empty	C	Empty cell	
Marked	M	Marked for future category	L (laying) P (pollen) N (nectar)
Occupied	O	Occupied by an immature stage	Bee type (Table 1)
Nectar	N	Nectar being converted to honey	Age in days
Honey	H	Nectar that has become honey and capped	
Uncapped honey	HU	Honey uncapped and in use	
Pollen	P	Pollen being packed	
Finished pollen	PF	Pollen that is under process, covered and stored	
Open pollen	PO	Pollen cell that is open and being consumed	

Other variables in the model use a common symbol for any quantity which can be annotated with cell or bee type specifiers. The symbols used are given in Table 3.

Table 3 Other symbols used in the model

Symbol	Quantity	Units
t	Time	S
T	Temperature	°C
Q	Heat	J
S	Stress	--
M	Spatial Map	--
N	Amount of nectar/honey	J
P	Amount of pollen/beebread	kg
q	Metabolic rate	J s^{-1}
F	Food consumed	kg s^{-1}
φ	Food demand	kg s^{-1}
r	Rate of progress	

3.2. Coordinate systems

Five coordinate systems are used in the model. Two coordinate systems are discrete indices mapping to individual cells in the hive. The other two coordinate systems are continuous, defining hive positions in Cartesian and polar coordinates, the final one represents landscape positions.

3.2.1. Five axis discrete coordinate system

When the in-hive information is displayed in the GUI interface, this coordinate system is used. An individual cell within the hive is referenced by five parameters; x, z, f, s and b. The coordinate system is defined with the front facing the frames and the entrance to the hive on the right-hand side.

- x: The horizontal axis along a frame (column). Column 1 is at the left-hand side.
- z: The vertical axis along an individual frame (row). Row 1 is located at the bottom of the frame. The rows in frames in different boxes are each indexed from 1.
- f: The frame index within a box. Frame 1 is at the front and subsequent frames positioned behind frame 1.
- s: The side of a frame. Side 1 refers to the front and side 2 refers to the back.
- b: The box index. The lowest box is box 1.

Example 1: Coordinates (x, z, f, s, b) = (5, 3, 6, 1, 2) refers to a cell in the box positioned directly above the lowest box. The coordinates refer to front side of the sixth frame from the front. The location of the cell in that frame is five cells from the left, third row up.

Note that the coordinate system maps the honeycomb shape on to a regular Cartesian grid. Each cell is indexed simply by row and column within a frame. On the hexagonal grid, even numbered rows are shifted to the right.

3.2.2. Three axis discrete coordinate system

When bees access the resource in the hive, move around and perform spatial explicitly activities in the hive, this coordinate system is used. An individual cell is indexed by three coordinates, x, y and z.

- x: The horizontal axis along a frame (column). Column 1 is at the left-hand side. This has the same meaning as the x axis in the five-axis system.
- y: An index to cells in the direction from front to back. The y index is represented by f and s in the five-axis system.
- z: Vertical index from the bottom row in the hive (row). Unlike z in the five-axis system, the z value will have unique values, rather than repeating for each box. The z value of the lowest row in any box will be 1 higher than the biggest z value in the box below. The z index is represented by z and b in the five-axis system.

This coordinate system also maps the honeycomb shape on to a regular Cartesian grid.

3.2.3. Cartesian continuous coordinate system

This coordinate system is used for calculating the usage of cells in the hive. Continuous coordinate systems represent positions within the hive, and the values are continuous (units of meters for example). The axes are x, y and z having the same alignment as the three-axis discrete coordinate system. Absolute values start at an origin positioned at the centre of the lower left cell in the front frame of the lowest box. Coordinates can also be relative.

3.2.4. Polar continuous coordinate system

This coordinate system is used to calculate the relative distance between two cells in the hive and the distance and angle between the hive and resource patches in the landscape. Polar coordinates are represented by the axes r, θ and φ. These have the following meanings,

r: Range. The distance from the origin.

θ: Azimuth. The angle anticlockwise viewed from above the hive. Angle $\theta=0$ is aligned along the frames from left to right.

φ: Elevation. The angle between the horizontal and the point. An elevation of zero is horizontal, and positive values lie above the horizon.

3.2.5. Discrete coordinates outside the regular honeycomb grid

This coordinate system is used in the landscape model in ALMaSS. Although honey bees are remarkable in the way they produce hexagonal honeycomb, some cells do not lie on the regular pattern. Examples are drone and queen cells. These will be represented within the model as lying in the grid coordinate system for computational efficiency. However, there is no requirement for the continuous positions of these cells to lie in positions defined by the grid. A queen cell would therefore be held in a cell within the five-axis coordinate system, and could be indexed that way, but its location within the hive is unconstrained and does not have to lie within regular grid positions.

3.2.6. Referencing individual bees

Individual bees within the hive are located spatially by grid cell using the coordinate system described in Section 3.2.2. There may be more than one bee located at a single grid cell. The number of bees per cell is limited in the model during normal bee activity to prevent too many bees working on the same cell, but a greater number of bees can be associated with a single grid cell if they try to pack close together for thermoregulation.

3.2.7. Movement of bees

Bees move from cell to cell within the colony. For example, a bee moving left by a single cell would change by x=x-1. Bees are also able to move in the vertical direction by moving up a single row for example. This will involve a shift in the horizontal direction, and the reverse of the horizontal shift if it moves another step in the upward direction. For the sake of simplicity, the index system ignores these horizontal shifts. However, the position of each cell or bee is accurate in terms of its continuous Cartesian coordinates. Any geometric calculations are made with one of the two continuous coordinates systems and will not be compromised by indexing cells on a regular Cartesian grid. In our model, a bee is associated to a cell. A cell has six immediate neighbours on a frame side (although edge cells have fewer), which of cell (x,y,z) are indexed by three axis discrete coordinate system as,

$$\{(x+1,z),(x+1,z+1),(x-1,z+1),(x-1,z),(x,z-1),(x-1,z-1)\} \quad (1)$$

We assume bees in the hive always move randomly from one cell to its neighbours until they find a task that they are able to manage or find the resource they need.

3.2.8. Algorithm for finding a resource

A bee is able to locate the nearest cell containing resource by its senses of smell and taste within one single frame side. When the bee cannot find any required resource in this area, it randomly chooses a direction in the frame to move out of this area. But we assume that the bee does not go back to visit the place it has been before in the same frame side. When it could not find anything in its current located frame side and reaches the edge of the current frame side, it will move to another frame side randomly (left or right). This will continue until it finds the resource, or it visits all the frame sides.

3.2.9. Spatial and temporal resolution of the model

The spatial resolution within the hive is the cell diameter. Within the landscape the resolution is 1 metre. The model time step is 10 minutes. We assume that each in-hive activity can be finished in one single time steps. In the current model, each bee can only perform one single in-hive activity in each time step. In other words, bees are not able to perform multiple activities in one single time step. For the foraging/scouting activity, it usually requires more than one time step. For this type of activity, it will be marked as uncompleted, to be continued in the following time step(s) until it is finished. Activities have their own energy cost in terms of sugar and pollen which will be recorded after bees finish the activities. The cost will be refilled when the bees consume resource. Usually, bees do not change to a different task within one day especially for the tasks with requirement of royal jelly and wax production. Therefore, in the model, we assume that a worker bee cannot produce both royal jelly and wax at the same day.

4. Hive thermodynamics

In order to model the influence of temperature, the calculation for the temperature of each cell in the honeycomb and the body temperature for each bee is required. This is implemented in the thermodynamics model.

Temperature influences the behaviour of individual bees and the decisions that they make (Heinrich 1980a,b, 1981; Fahrenholz et al., 1989). Physical processes, nectar evaporation for example, are temperature dependent (Park, 1925). Individual bees are not aware of the external temperature, only their own temperature and that of their immediate surroundings. In order for bees to make temperature dependent decisions it is crucial to model the temperature distribution inside the hive to control individual bee behaviour.

Unlike bumblebees (*Bombus* sp.), honey bees (*Apis mellifera* sp.) maintain a colony over winter. It can only do this because of the honey store that it builds during the summer. Over the winter months this honey store is metabolised to create heat to ensure survival of the bees and hence the colony. A model that considers in-hive resource use (mainly honey, but also pollen) must consider the thermal behaviour of the nest. The honey / heat budget is fundamental to the hive's operation and survival. Each bee generates heat according to its metabolic rate (Fahrenholz et al., 1989). We can consider each individual bee as a small heater that heats up part of the hive. The power (in Watts) of that heater is the heat generated per unit time. The amount of heat generated per unit time at any point within the hive will depend on the number of bees concentrated in that area and the metabolic rate of those bees. Heat will also be transferred from the hive to the environment and vice versa. Externally, the temperature that is considered is the ambient temperature (close to the hive?). Estimating the temperature distribution within the hive depends on a model that considers each individual heating element (bees with different activities at the same time) and the thermal path from each bee to the hive exterior. Convective cooling processes are present as well within the hive, and the amount of cooling can be increased by bees fanning at the entrance (Simpson, 1961).

Modelling the exact thermal processes within the hive would be an onerous task, involving sophisticated heat transfer equations through the composite hive structure, and the fluid dynamics of convection. Therefore, instead, we will produce a simpler model of the conductive processes that will approximate the in-hive temperature distribution using convolutional operations especially for wintertime.

To model the thermal distribution in the hive, we have a three-dimensional temperature map for the whole hive. Each bee will have a variable to track its own body temperature. In addition, each bee will contribute heat to the cell that it belongs to according to its activity at each time step (and eventually to the bees around). The temperature map will be firstly updated based on the generated heat from the bees. Then the temperature map will be further updated using convolutional operations in order to model the thermal flow within the hive. Here, we assume the environmental temperature could not be changed by the hive, which means the hive can only absorb or lose heat to its surrounding. Specifically, when the environmental temperature is higher than that within the hive, the hive will be warmed up by the environment. Otherwise, the hive would lose heat to the environment. When it is too hot in the hive, convective cooling will cool the adjacent sides between frames according to a cooling constant and the flow rate, which has a base rate and an additional flow rate associated with bees' fanning and evaporation. When the brood temperature is lower than the required one, bees will gather to the brood to warm it up. Similar movements will also happen during winter, bees will gather close to the queen to warm up each other in order to survive in the winter.

4.1. Temperature map

We have a temperature map T in three-dimension for the hive. In other words, T is a cube. Here, we use the three axis discrete coordinate system (Section 3.2.2) to index $T_{x,y,z}$, where $x = 0,1,\dots,N_{c,}N_c + 1$, $y = 0,1,\dots,N_{s,}N_s + 1$ and $z = 0,1,\dots,N_r, N_r + 1$. N_c, N_r and N_s is the number of columns in one frame, number of rows in one frame and number of frame side in the hive, respectively. When one of the indices equals to zero or the largest value (i.e. representing the outer edges), it is the same as the environmental temperature and will not be updated by the convolutional operations. We refer these as padding values since they are not updated by the convolutional operations.

4.2. Updating temperature map

At each time step, we first update the padding values in the temperature map using the environmental temperature. Afterwards, the temperature of each cell is updated by the equation below

$$T_{x,y,z}(t + \Delta t) = T_{x,y,z}(t) + r \sum_{i=1}^{N_{x,y,z}} h_i \qquad (2)$$

where $N_{x,y,z}$ is the number of bees on the cell of (x, y, z), h_i is the temperature difference between bee i and the cell ($h_i = T_i - T_{x,y,z}$), and r is the parameter controlling the heating exchanging rate between bees and cell. r ranges from 0 to 1. After this, the bee's body temperature will be updated as below

$$T_i(t + \Delta t) = T_i(\mathrm{t}) + (1 - \mathrm{r})h_i \qquad (3)$$

To model the thermal flow between adjacent cells within the hive and between the hive and environment, we use a three-dimensional filter cube to apply convolution operation on each value of the temperature map except for the padding ones.

In order to update the temperature map using this filter cube, we first define neighbouring cells in 3-dimension for each cell. As shown in Figure 1, we have six neighbours in the same frame side. Besides, we also have two other neighbours on y-coordinate, i.e., across frame or on the other side of the frame, which are usually further away than the six on the same frame side. Therefore, we will put less weights on these two neighbours in the filter cube.

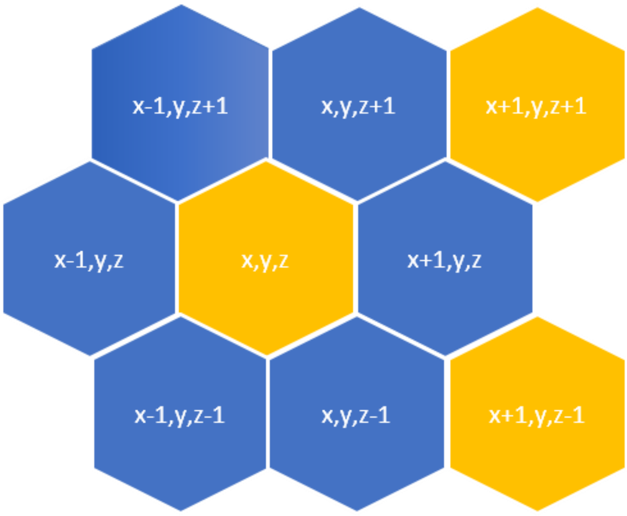

Figure 1: A patch of one frame side to show the six immediate neighbours (in blue) of the cell (x,y,z) in the same frame side.

Through the filter cube, the temperature map is updated again as below

$$
\begin{aligned}
&T'_{x,y,z}(t+\Delta t) = T_{x,y,z}(t+\Delta t)\\
&+(T_{x-1,y,z}(t+\Delta t) - T_{x,y,z}(t+\Delta t)\\
&+T_{x,y-1,z}(t+\Delta t) - T_{x,y,z}(t+\Delta t)\\
&+T_{x,y+1,z}(t+\Delta t) - T_{x,y,z}(t+\Delta t)\\
&+T_{x+1,y,z}(t+\Delta t) - T_{x,y,z}(t+\Delta t)\\
&+T_{x+1,y+1,z}(t+\Delta t) - T_{x,y,z}(t+\Delta t)\\
&+T_{x+1,y-1,z}(t+\Delta t) - T_{x,y,z}(t+\Delta t)\\
&+0.5\left(T_{x,y,z+1}(t+\Delta t) - T_{x,y,z}(t+\Delta t)\right)\\
&+0.5(T_{x+1,y,z-1}(t+\Delta t) - T_{x,y,z}(t+\Delta t)))/\beta
\end{aligned}
\tag{4}
$$

where β is for normalization. Through this equation, when the temperature of cell (x, y, z) is larger than its neighbours, it will transfer heat to its neighbours. Otherwise, it will absorb heat from its neighbours.

4.3. Movement of bees based on the temperature map

When the brood temperature is below the required target temperature (specifically 34-35°C ± 0.5°C) (Fahrenholz et al, 1989; Jones et al, 2004), the tasked bees will move towards the brood position, thus warming the brood until the brood temperature meets the requirement of about 35.0℃. To provide the temperature information to allow this behaviour, the temperature map will be updated using the method described in Section 4.2 during the movement in the end of each time step.

During winter and when there is no brood in the cell, bees gather together with the queen to warm up each other by forming a cluster (temperatures recorded in the centre of the cluster has been between 12.0℃ and 33.5℃ with an average value of 21.3℃ (Fahrenholz et al, 1989). During the movement, the temperature map is updated using the method described in Section 4.2 until bees reach their target temperature. When the bees successfully reach the required temperature, they can move as a group in order to reach food slowly (Fahrenholz et al, 1989). In *Apis*RAM this will be a function of the individual behaviour rather than modelled as a group phenomenon. This is realized through changing the bees' positions and corresponding change in the temperature map resulting from bee movement. Thus, bees which can move towards local food will 'drag' the cluster with them as other bees move to maintain the temperature targets. During the movement, we assume the queen always stays in the centre of the bees' cluster.

When the temperature outside the hive increases, e.g., spring comes, the bees can move freely around in the colony being able to perform all tasks including foraging.

4.4. Convective process

When the temperature is too high, and usually above 35.8℃, bees can carry out a convective process to cool the hive down (Lindauer 1954; Heinrich 1980a,b, 1981). This is done by fanning at the entrance. Modelling the flow dynamics using turbulent flow equations is beyond the scope of the project, and unnecessary. The effect of convective cooling is modelled by a simple flow rate that removes heat linearly, and the flow is a combination of a background flow rate and the sum of fanning bees. The change in heat between time t and t + Δt is given by,

$$
Q(t+\Delta t) = Q(t) + \gamma(\alpha + \beta N)\Delta t \tag{5}
$$

where α is the background flow, β is the extra flow generated by a single bee, N is the number of bees and γ is the change in heat caused by the given flow rate. The change in heat is applied to each side of each frame, and the change in the temperature map determined via the heat capacity of each cell and the distance between the cells to the hive entrance.

4.5. Summary

The methods described above are used to determine the body temperature of each bee within the hive through time, the time-dependent temperature of each cell, and the heat exchange between different cells and between bees and the cells at which they are located. Based on this, processes described elsewhere in this document that depend on temperature are defined in the sections below.

5. In-hive products

In the model, storage of pollen and nectar is spatially explicit. Each cell within the hive can be dedicated to storage of nectar or pollen. Activities regarding pollen and nectar storage for a worker bee are largely detailed in Section 7. Pollen is deposited in cells that have been marked for pollen storage (Section 7.3.9) and is packed and capped by workers (Section 7.3.10). Nectar is deposited in cells that are marked for nectar (section 7.3.6), and ripens (evaporates) at a rate that produces honey after a period of 3 days (Crane 1975, 1980) (section 7.3.7) after which, the cell is capped and marked for honey.

5.1. Food transport

Two processes are involved in food distribution. Honey/nectar is distributed via trophallaxis. Bees can also feed directly on resources stored within cells in the hive, usually to feed on pollen, but also for honey/nectar if they are unable to gain enough food via trophallaxis. Royal jelly is not explicitly modelled here since it is not stored but produced by a nurse bee and fed directly to the recipient. It is however, time and energy budgeted.

5.2. Trophallaxis for honey/nectar

Nectar and honey are dispersed throughout the nest by the bees transferring it to each other (Nixon & Ribbands, 1952). A nurse bee, for example, is not required to reach stores of nectar and honey within cells to eat. Instead, the food is passed between bees on the frame to reach the nurses. But we do not model this explicitly in the model for the sake of simplicity, i.e., the transferring procedure is omitted. When a bee eats honey/nectar, it does not go to the cell physically by itself, but it knows the index of the cell, and the consumed amount will be deducted from the cell. Furthermore, if the cell is contaminated by pesticide and/or infected by *Nosema*, there is a chance that the bee gets contaminated by pesticide and/or infected by *Nosema*.

5.3. Feeding from storage cells for pollen and/or beebread

Bees are required to feed directly from cells for their protein intake (pollen and/or beebread). They therefore need to navigate their way to the food stores. They are able to do this by smell and/or taste. The search algorithm is described in section 3.2.8. To discriminate this different pathway from trophallaxis, a different metabolic rate is used for feeding protein, i.e., more energy is needed for feeding on protein since it requires that a bee visits a cell physically by itself. In this case, the energy is only based on sugar.

6. Colony

6.1. Bee castes and life stages

Honey bees can be classified as belonging to one of the three castes: worker, drone or queen. Each caste follows the same basic stage progression, from egg to adult, as shown in Table 4. (Jay. 1963; Fukuda & Ohtani, 1977; Harbo et al, 1981). This is implemented in the development module.

The basic development rate for the progression through immature stages is known (Table 4). This basic rate is affected by temperature and the amount of food that it was provided with, or it could consume. At each life stage, the accumulated development time in days over the time step Δt is,

$$d^B(\mathrm{t}+\Delta\mathrm{t}) = d^B(\mathrm{t}) + \mathrm{r}\Delta\mathrm{t} \tag{6}$$

where r is the development rate for the accumulated development time which thus depends on the food received and temperature conditions.

Table 4 Development times through life stages

Caste	Progression	Duration (days)	References
Worker	$t_{egg\rightarrow larva}$	3	Harbo et al (1981)
Worker	$t_{larva\rightarrow pupa}$	6	Jay (1963)
Worker	$t_{pupa\rightarrow adult}$	12	Jay (1963)
Drone	$t_{egg\rightarrow larva}$	3	Harbo et al (1981)
Drone	$t_{larva\rightarrow pupa}$	6.5	Jay (1963)
Drone	$t_{pupa\rightarrow adult}$	14.5	Jay (1963)
Queen	$t_{egg\rightarrow larva}$	3	Harbo et al (1981)
Queen	$t_{larva\rightarrow pupa}$	5.5	Jay (1963)
Queen	$t_{pupa\rightarrow adult}$	7.5	Jay (1963)

When the accumulated development time of a bee reaches the duration in Table 4, it would move to the next life stage. Progress will be reduced if a larva is underfed (Newton & Michl, 1974; Herbert et al., 1977; Crailsheim, 1990; Schmickl & Crailsheim, 2001; 2002, 2004). This is modelled simply as the product of the ratios of food received *F* to food demand *D* of sugar, pollen and royal jelly. Demand is day dependent for each food type *P*. If the deficit between demand and supply exceeds a threshold U_P, the larva will be marked as being selected for cannibalism. It will then be removed from the model (the percentage of cannibalised underfed young larvae was found to be as high as 31% compared to the 7% cannibalised in normal conditions; Schmickl & Crailsheim, 2002). In this way the most underfed larvae are killed off, giving priority to the most well fed. Cannibalism may occur in eggs and larvae, going from earlier to older stages (1–4 days old for workers and 1-5 days for drone and queen). Also, eggs and young larvae (1–4 days old for workers and 1-5 days for drone and queen) are preferred for cannibalism to the older one (Woyke, 1977; Schmickl & Crailsheim, 2001, 2002). For the current model, the development of the queen is not included.

The development rate is modelled as a quadratic function of temperature where the rate drops as the temperature departs from the optimal 35.0ºC (Fahrenholz et al, 1989; Jones et al, 2004), proportionally with the coefficient R_T (a user-defined fitting parameter). Combining these two rules from food and temperature, the development rate can be calculated as,

$$\mathrm{r} = (1 - (R_T(\mathrm{T} - 35.0))^2) \prod_{p \in P} \frac{F_p}{\varphi_p} \tag{7}$$

where the first part is the quadratic function for temperature and the second part is the product of impact from different food resource. It is worth noting that development rate is zero when the temperature term is negative, but this will result in mortality (Medrzycki et al 2010).

6.2. Metabolic activity

Every bee consumes resources and generates heat according to its metabolic rate q, in units of kcal s^{-1}. Each class of bee has a metabolic rate determined by its activity. The temperature increase is defined as,

$$^{B}T(\mathrm{t} + \Delta\mathrm{t}) = {}^{B}T(\mathrm{t}) + {}^{B}Qs \tag{8}$$

where Q is the heat produced by burning $q\Delta t$ of nectar, and s is the heat capacity of the bee.

6.3. Resource consumption

Each bee has two "food stores"; ^{B}N, which is its current level of sugars (honey / nectar), and ^{B}P, which is the protein level from pollen and beebread. The sugar store drops according to the bee's metabolic rate.

$$^{B}N(\mathrm{t} + \Delta\mathrm{t}) = {}^{B}N(\mathrm{t}) + {}^{B}q\Delta\mathrm{t} \tag{9}$$

Replenishment of the sugar level is either via the bee network or by accessing honey or nectar cells directly.

Protein consumption depends on demand $^{B}\varphi$, governed by the bee's life stage and activity. The units of $^{B}\varphi$ are kg s^{-1}. At each time step the level of protein falls.

$$^{B}P(\mathrm{t} + \Delta\mathrm{t}) = {}^{B}P(\mathrm{t}) + {}^{B}\varphi\Delta\mathrm{t} \tag{10}$$

Replenishment of protein occurs when the bee visits a pollen or beebread cell and feeds.

7. Bees' activities

The bees' activities are modelled in the activity module. Bees carry out different activities based on the location and timing of the activities required by the colony as seen by the bee's local context. There exist two categories of activities that bees can perform:

1. In-hive activities
   This type of activities happens within the hive. Most of them are associated with a cell, e.g., cleaning cell, capping brood, capping nectar etc. But in the model, we also have two types of non-cell-related tasks, namely cleaning the hive and convection. In these two cases, a global variable is used to track the cleanness of the hive and convective process and activity time is assigned but the activity is carried out non-spatially.
2. External activities
   This type of activity is focused on foraging and scouting, which are detailed in section 7.6.2.

In the following subsections we introduce the method of selection of activities for worker bees. The activities to be modelled are described in the subsequent sections.

7.1. Beginning of model step

At the beginning of each model step, a check is made to see if the bee survived from the previous step. If the bee died, it will be removed from the model. Live bees will first check their body temperature. If it is below a user defined value, the bee will perform warming up activity. Otherwise, the bee will choose the activity as discussed in the next section.

7.2. Activity selection

When bees are active, they are always moving in a mostly random fashion in the hive in order to find a new activity for themselves. They are able to walk around the bottom and sides of frames and move between adjacent cells even from different boxes. A worker bee checks the attribute for the nearest cell to find out which types of activities are needed before selecting which activity it will do.

Spatially explicit activities depend on the cell that the worker bee is currently nearest to. Each cell within the hive has a property that the bee uses to decide what to do. The property holds a categorical value that defines either something that the cell needs (such as a larva that needs feeding) or something that it provides, such as an empty cell. The attributes for what a cell needs or provides are given in Table 5.

Table 5 Cell types, with attributes for what a cell needs and what it provides. A worker will satisfy a need if it is on that cell and is able to provide the cell with what is required.

ID	Cell Type	Symbol	Needs	Activity ID	Provides	Variables
1	Unbuilt	U	Building	10		Level of build
2	Empty, unclean	E_D	Cleaning	1		Level of cleanliness
3	Empty, clean	E_C			Available Cell	
4	Empty, marked for laying	E_L				
5	Empty, marked for pollen	E_P				
6	Unprocessed Pollen	P	Packing	9	Pollen	Mass of pollen

7	Processed Pollen (BB)	P			Pollen Store	
8	Open Pollen	P_U			Pollen	Mass of pollen
9	Nectar	N	Ripening	7	Nectar	Mass of nectar, concentration
10	Capped Honey	H			Honey Store	
11	Uncapped Honey	H_U			Honey	Mass of honey
12	Worker Egg	O_{WE}				
13	Worker Larva	O_{WL}	Feeding	3		Mass of Royal jelly, Honey**, BB**
14	Worker Pupa	O_{WP}	Capping, Warming	2		Level of capping
15	Drone Egg	O_{DE}				
16	Drone Larva	O_{DL}	Feeding	3		Mass of Royal jelly, Honey**, BB**
17	Drone Pupa	O_{DP}	Capping, Warming	2		
18	Queen Egg*	O_{QE}				
19	Queen Larva*	O_{QL}	Feeding	3		Mass of Royal jelly, Honey**, BB**
20	Queen Pupa*	O_{QP}	Capping, Warming	2		

*Not used yet

** Substitute Nectar / Pollen equivalent if not available.

Activity selection is one of the most sophisticated parts of the model. When choosing an activity, a bee considers all possible activities, which are weighted according to priorities. Priorities are defined according to the needs of the colony and the age of the bee (Seeley, 1982; Kolmes & Winston, 1988; Huang et al, 1994; Huang & Robinson, 1996; Fewell & Berthram, 1999; Johnson, 2008; Johnson, 2010). The genetics of the bees (e.g., patrilines) lead to different response thresholds for certain tasks as for example pollen collection (Pankiw & Page 2001) as well as resistance to diseases. However, data specifying the changes in attributes is scarce and hence this will not be taken into consideration in the current version of the model.

7.2.1. Age-dependent behaviour

Age-dependent behaviour is defined in the *activities_priorities.txt* file. Priorities are given for each activity according to the age of the bee in days (Seeley, 1982; Kolmes & Winston, 1988; Huang et al, 1994; Huang & Robinson, 1996; Johnson, 2008). The higher the value, the more likely the bee is to perform the task. Any positive integers can be used for task priorities, but the initial values chosen are either 0=Never, 3=Low, 6=Medium and 9=High. This allows for intermediate priorities to be used.

7.2.2. Colony priorities

At each time step, the numbers of all the required tasks in the hive are updated, which will be further changed by the colony states. For now, two colony states are used, FORAGING_ENABLED and FORAGING_DISABLED. The second will be turned on when it is too cold for foraging or during the night. When FORAGING_DISABLED is on, all the required tasks outside the hive are set to be zero.

7.2.3. HPG and wax flag

We assume that a bee cannot produce wax and royal jelly on the same day. In the model, there is a flag for each adult bee to indicate that it can generate either wax or royal jelly. This is reset at the beginning of each day. When the bee chooses to perform wax related task first, this flag will be set for wax for this day. Then, it cannot attend brood in the same day. But, if the bee chooses to attend brood first, this flag will be set as HPG, it can't perform activities that require wax for the rest of that day.

7.2.4. Activity Calculation

After using HPG flag to process the age-dependent behaviour priorities, the product of the age-dependent behaviour priorities and the colony priorities for each activity is calculated. This product represents the likelihood of a bee performing each activity. The bee will choose the activity with the largest multiplied result. When the product is zero for all the activities, the activity chosen will be based on the activity with the greatest priority from the colony. By doing this, we avoid the problem of the bees being idle while there is a request from the colony. The bee will choose an activity again following the normal procedure in the next timestep. If the result is still zero for all the activities, the bee will move randomly (see Walking Around, Section 7.3.16) during this time step.

The method presented in this section allows for flexibility in what the bees are able to do, compared to a model where bees have simple age-dependent behaviour, in the categories of nurse, non-nurse and forager. For example, if the weather is good and it is daytime, older bees will forage. If the weather is inadequate or it is night-time, however, foraging will be disabled and these bees will select an alternative task such as attending brood and capping brood, depending on hive priorities. This method also allows for the fact that at any point many bees may be 'inactive' in the walking around activity.

7.3. In-hive activities for worker bees

Each task is described in a separate section below, with the mathematical formulation of the variables that are changed by the activity. It is assumed that the worker bee will chose an activity also according to its age and HPG status (Seeley, 1982; Kolmes & Winston, 1988; Huang et al, 1994; Huang & Robinson, 1996; Pankiw & Page, 2001; Johnson, 2008), which is detailed in section 7.2.

7.3.1. Eating sugar/pollen

Bees require different amount of sugar and pollen according to their activities and needs. At each time step in a day, the required amount of sugar and pollen is recorded as an energy deficit as described in Section 6.3. When a day ends, the model bee tries to replenish the accumulated deficit (through honey and/or nectar) and pollen. According to DeGrandi-Hoffman & Hagler (2000) fresh nectar is distributed quickly to all bees and larvae in the hive, although foragers might prefer to consume honey (Gmeinbauer & Crailsheim, 1993; Harano et al, 2013). As for protein it has been recently demonstrated that bees prefer to consume freshly stored pollen than older stores (Anderson et al., 2014; Caroll et al, 2016). However, currently these preferences are not included, and the bees always choose the nearest resource source.

7.3.2. Cleaning cells

This is generally the first task that a bee performs when it hatches from the brood cell (Seeley, 1982; Johnson, 2008). In other words, before any other activities, the bee will first clean the hatched cell right after the hatching. It takes several minutes for a bee to clean a cell after hatching and for *Apis*RAM model this time frame has been set to 10 min. If the model bees encounter a cell with a dead egg, larva or pupa, then this cell will also contribute to the likelihood of a bee carrying out cleaning activity.

7.3.3. Capping brood

If a cell is classified as a brood cell and holds a larva that is 6 days old or higher, and is uncapped, the cell will switch on a *need* to be capped (Seeley, 1982; Johnson, 2008). When an available bee reaches such a cell, it will cap the brood cell. It takes about 10 min for a bee to fully cap one cell (Hepburn, 2012). We assume a bee always produces the required wax (Fergusson & Winston, 1987). When the worker bees produce wax or royal jelly, they need more energy as shown in Table 8.

7.3.4. Attending brood

If a cell with a larva presents a need for feeding, a worker bee will check the requirements of the cell, and then see if it is able to satisfy the need (Riessberger & Crailsheim, 1997; Johnson, 2008). Food requirements are given in Table 6. After an adult bee feeds a larva, the fed amount of sugar, pollen and royal jelly fed will be recorded. The amount of royal jelly will be deduced from the royal jelly that an adult bee can generate for one day (Table 7), defining the production rate as a function of age (Simpson et al, 1968; Winston 1987, page 95; Knecht & Kaatz 1990). The amounts of sugar and pollen consumed for attending brood will be recorded and, if possible, the bee we will be 'refuelled' as described in Section 6.3.

Table 6 Food requirements for larvae. Units are in mg per day except brood food. (Crailsheim, 1992; Harbo, 1993; Schmickl & Crailsheim 2004; Rortais et al, 2005)

	Worker			Drone		
Day	Brood food	Beebread / Pollen	Honey / Nectar	Brood food	Beebread / Pollen	Honey / Nectar
4	10 µl	0	0	20 µl	0	0
5	20 µl	0	0	30 µl	0	0
6	20 µl	0	0	30 µl	0	0
7	20 µl	2	20	25 µl	2.5	25
8	20 µl	2	20	25 µl	2.5	25

9	20 µl	2	20	25 µl	2.5	25
10				25 µl	2.5	25

Table 7 Relative gland production rates (unitless). To be multiplied by peak production rate. (Winston, p 95.) Values in *Apis*RAM states. (For HPGs Simpson et al, 1968; Knecht & Kaatz, 1990; For wax: Hepburn et al, 1984; Hepburn et al, 2014).

Day	Wax	HPG	Day	Wax	HPG
1	20	13.2	21	90	59.4
2	40	26.4	22	70	46.2
3	60	39.6	23	70	46.2
4	80	52.8	24	60	39.6
5	90	59.4	25	60	39.6
6	100	66	26	50	33
7	120	79.2	27	50	33
8	140	92.4	28	50	33
9	150	100	29	50	33
10	150	100	30	50	33
11	140	92.4	31	40	26.4
12	140	92.4	32	40	26.4
13	140	92.4	33	40	26.4
14	130	85.8	34	40	26.4
15	120	79.2	35	40	26.4
16	110	72.6	36	40	26.4
17	110	72.6	37	40	26.4
18	100	66	38	40	26.4
19	100	66	49	40	26.4
20	90	59.4	40	40	26.4

7.3.5. Receiving nectar

A foraging bee returning with nectar will increase the counter of requirement for nectar to be taken to an available cell. An in-hive worker, which is available for this, will decrease this counter by one to respond by taking the nectar resource from the forager (Seeley, 1982; Johnson, 2003; Johnson, 2008).

The forager is then free for further foraging flying, otherwise, if no workers are available the forager will deposit the foraged nectar by itself in the cell but using time to do so. In the case of trophallaxis, the receiver will record the amount of nectar and pesticide (if contaminated) received, and it will find an available cell to store the nectar.

7.3.6. Depositing nectar

When the nectar is received it will be deposited in a cell (Seeley, 1982; Johnson, 2003; Johnson, 2008). The cell must not be brood, marked for brood, pollen, or marked for pollen. Cells above the nest and nearest to the pollen store will be chosen preferentially (i.e., nearest to the nest. Workers won't start filling at the top of a new box if it is added – the food reserves will be put as close to the nest centre as possible). Cells nearest to the brood area will already be either pollen or marked for pollen. Nectar will be deposited in cells already containing nectar in preference to empty cells (Eyer et al, 2016). A bee will use an expanding circle search with an N cell radius for an open nectar cell. If it fails to find one it will use an unlimited expanding circle search to find either an open nectar cell or an empty cell.

Received nectar will have a sugar concentration determined by the foraging source. The sugar concentration in the cell will be recalculated, from the combined volume and concentration levels of the cell and received nectar (Eyer et al, 2016). It also contains pesticide residues if it is contaminated. In this case, the concentration of pesticide residues will also be recalculated. Further, there is a chance to pass *Nosema* to the stored nectar if the bee is infected by *Nosema*.

7.3.7. Ripening nectar

Each nectar cell has a volume of nectar (water + sugar), with a sugar concentration N_C. The volume will be reduced, and concentration of sugar will be increased by evaporation. The rate of evaporation would be very difficult to estimate from first principles. Theoretically, it would be possible to make an estimate from the temperature, surface area, relative humidity, and air velocity over the cell. There are many empirical formulae available to do this, but estimations can differ by orders of magnitude. When you also consider the effect that the worker has by manipulating droplets of nectar, it becomes an essentially impossible calculation. We therefore use a constant evaporation rate that ripens the nectar in 3 days (Park, 1925; Crane, 1975, 1980). The calculation will be made in each model step for each cell. The only effect for the worker bee performing this task is the change in metabolic rate.

7.3.8. Capping honey

When a cell is fully ripened the cell will flag a *need* to be capped. It takes several minutes for a bee to cap a honey cell, and in the model we set this time to 10 min, similar to brood capping. To perform a capping activity, a bee must have access to wax. As with capping brood, only fresh wax is used (Hepburn, 2012). A worker has to generate the required wax (Fergusson & Winston, 1997). The required energy is recorded and this energy needs to be replenished after the activity is concluded.

7.3.9. Storing pollen in cells

Pollen stores are located near to the brood nest, between the nest and the honey stores. How the bees choose which cells to use is unclear. In terms of model performance, what is important is that pollen is distributed on the frames in a realistic way, not without the goal of exactly mimicking the selection process. This method aims to do that.

The method initially used to specify which cells can be used for storing pollen is the following. For each frame side with brood, we firstly calculate the radius and centre for the brood (including the empty cells marked for eggs as can be found in section 0). Next, we draw a circle using 1.5 times of the brood radius from the brood centre. All the cells with this circle, which are not brood cells, can be used for storing pollen.

Cells marked for brood have preference over pollen. Brood is therefore able to expand outwards into areas previously used for pollen storage. As the brood size increases, the cells for pollen will also move outwards since we draw a circle using 1.5 times of the brood radius for the pollen cells. Whether the extension of the area for brood can include the super is determined by a parameter that describes whether a queen excluder is used or not. If not used brood can extend upwards as required by the above process if necessary.

Stored pollen may contain pesticide residues if it is contaminated. In this case, the concentration of pesticide residues in the stored pollen will be recalculated. If the bee is infected by *Nosema*, there is a chance to infect the stored pollen by *Nosema*.

7.3.10. Packing pollen

Pollen is brought into the hive by foragers and deposited into pollen cells. An unfinished pollen cell will present a *need* for packing. A worker will respond to this by checking the mass of the pollen in the cell and changing the cell to 'finished pollen' (bee bread) if it is above a threshold. This is done implicitly when a bee completes filling up of the pollen cell.

7.3.11. Comb building

Cells marked 'unbuilt' display a *need* for building. An unbuilt cell has a variable C_U that records the level of build. A worker can satisfy the building need if it has sufficient wax as described in Table 7. It will increment the variable C_U by proportion according to the wax deposited. (Fergusson & Winston, 1997). The builder worker bees altogether need about 2 hours to complete 3 cells (Nazzi, 2016). For now, this is not implemented in the model, since we assume all the frames are fully built and added by the beekeeper.

7.3.12. Ventilating at the entrance for Cooling the hive

This activity is described in section 4.4 (Egley & Breed, 2012).

7.3.13. Warming up activity

When the body temperature of a bee is below the threshold of 5℃, it will be in a chill coma, therefore, before the temperature drops below 12℃ the bee will move to the warmer place in the hive and the cluster will start to be formed (Heinrich, 1981; Fahrenholz et al, 1989).

7.3.14. Guarding

A proportion of available worker bees will be assigned for the task of guarding. In the model, this will change their metabolic rates (Table 8) and increase the chance of dying through a user defined value.

7.3.15. Removing debris

The hive has a cleanliness variable M_W (see the section on *Nosema*). A bee cleaning the hive will perform the action, $M_W=M_W-1$. This activity can only be triggered for the selection of activities as described in Section 7.2, when the external temperature is warm enough to fly and $M_W > 1$. A single event is set to 10 minutes.

7.3.16. Moving around

When the model bees cannot find a specific task in one time step, they will move randomly in the hive using the method described in Section 3.2.7.

7.4. In-hive activities for a queen

For the queen, we only model the activity of laying eggs. Furthermore, we use temperature and day-length as a trigger for the queen laying eggs. Specifically, when the environmental temperature is above T_E for several consecutive days (even just above freezing) and the day-length is more than 10 hours the queen will start laying eggs in the cells marked for laying (DeGrandi-Hoffman_et al, 1989). These two parameters (temperature and day-length) vary depending on the locality simulated.

The number of eggs laid (and therefore cells marked for laying) depends on the size of the pollen stores, number of nurse bees, day-length and temperature/season (Allen, 1963; Jay, 1974; Eischen et al, 1983; Harbo, 1986; Dustmann, 1988). This prevents the colony from producing more brood than it can support.

The first egg will be laid in the warmest cell in the nest. Subsequent cells will be laid next to the first cell, and the nest will grow outwards. In the beginning of simulation, a certain number of clean cells around the warmest cell will be marked for eggs. The queen therefore does not decide (in our model) when and where to lay eggs but will lay in cells that have been marked for her to use.

Afterwards, the number of new eggs that the colony can support is calculated as below,

$$N_L = KN_P - N_B \tag{11}$$

where N_L is the number of new eggs to lay, N_P is the number of pollen cells in the hive, N_B is the number of existing brood cells and K defines the number of pollen cells needed for each immature bee. The (night-time) warmest N_L empty cells in the hive will be marked for laying.

7.5. In-hive activities for drone bees

For drone bees, we model their life stages but without any other activity than consuming the required food to develop according to their development time.

7.6. External activities for worker bees

7.6.1. Resource providing unit (RPU) and environmental drivers (ED)

The ALMaSS landscape model (Topping et al. 2003) provides the basis of the *Apis*RAM. ALMaSS provides daily information for temperature, rainfall, wind speed and direction, sunrise, and sunset, for the location being modelled. Snow loading is derived from rainfall, temperature, and a snow decay function.

For each habitat patch, we define a daily production rate of both pollen and nectar, F_N, F_P. The calculation for crops patches is simpler than for semi-natural habitats because we consider only the crop species. The production rates are taken from empirical phenology curves which is generated by the parallel data collection project. However, it is worth noting that available data for nectar and pollen production rates are biased due to extraction by pollinating insects. So, production rates have been measured in the field, but not without the interaction with bees for example. More details about RPU and ED could be found in the GIS report. Further, the contamination of pesticide will be inferred from the vegetation pesticide concentration map as can be found in Section 9.

7.6.2. Foraging activity

Workers progress from in-hive duties to become foragers. The time when this happens depends mostly on the age of the worker (usually after the 15th day of age), but can also depend on environmental conditions (Riessberger & Crailsheim, 1997), the amount of resource in the landscape and current colony conditions and requirements (Winston & Fergusson, 1985; Huang et al, 1994; Huang & Robinson, 1996; Pankiw & Page, 2001). The lifetime of a forager is short, and most foraging bees will survive only a few days (Visscher & Dukas, 1997; Woyciechowski & Moron, 2009; Becerra-Guzman et al, 2005). However, the lifetime of a bee is also influenced by the time it becomes a forager because: a) mortality of foragers is higher than the mortality of in-hive bees (Dukas & Visscher 1994); b) the earlier the bee becomes a forager, the shorter its life span(Khoury et al., 2011; Hatjina et al., 2013). The colony supports an excess of workers that can be deployed as foragers when the need arises (Huang & Robinson, 1996; Riessberger & Crailsheim, 1997; Woyciechowski & Kozlowski, 1998). Workers will forage for nectar and pollen. Foraging activity depends on the ambient temperature T_A, and bees are only able to forage when $T_A > T_F$. (Witherelli, 1972; Southwick & Heldmair, 1987). Foraging also depends on wind speed, rainfall (Dukas 2008), sun light and light orientation (Crailsheim, Hrassnigg & Stabentheiner. 1996; Rossel & Wehner, 1984a,b). Further, we assume that honey bees will only forage during the daytime. Under shortages of pollen or in conditions of poor pollen quality, honey bee colonies usually increase the proportion of pollen foragers but without increasing foraging rate (Pernal and Currie 2001).

7.6.2.1. Age-related instinct to forage

There is no strict boundary between nurse bees and foragers and this flexible behaviour is implemented in the following way. A desire to forage depends on the age of a worker (Seeley, 1982; Huang et al.,1994). A bee will be physically capable of foraging at age t_{F1}. After that age, the instinct to forage will become stronger until it reaches an age t_{F2}, when it will become a forager regardless of colony conditions. This is modelled by the piecewise function,

$$F_I = \begin{cases} 0, & t_a \leq t_{F1} \\ (t_a - t_{F1})\dfrac{1}{t_{F2} - t_{F1}}, & t_a > t_{F1} \end{cases} \tag{12}$$

where t_a is the age of the bee. Before the age of t_{F1}, the bee has no instinct to forage and will not leave the colony under any conditions. Its instinct to forage F_I is zero. After the age t_{F1}, the desire to forage increases, until at age t_{F2}, F_I=1. A bee will be sure to become a forager when F_I>=1. This information is converted into the priority for different activities.

7.6.2.2. Colony drivers for foraging behaviour

Pollen

Brood size depends on pollen availability (Allen, 1963; Jay, 1974; Eischen et al, 1983; Harbo, 1986; Mattila & Otis, 2006a,b; Schmickl & Crailsheim, 2002). Suppose the numbers of young larvae (1-3 days) and old larvae (3-4 days for worker and 3-5 days for drone) in the hive are N_{BY} and N_{BO}, we use the method in (Schmickl & Crailsheim, 2002) to calculate the required number of pollen cells by a converting rate of K_P as below

$$N_P = \frac{N_{BY} + 20N_{BO}}{K_P} \tag{13}$$

(see also section 7.3.9). For the colony to expand, it needs more than N_P pollen cells. The colony will aim to maintain a percentage above the current requirement for colony growth. This percentage, P_G is set initially to 10%. The number of required pollen cells is therefore

$$N_G = N_P(1 + P_G) \tag{14}$$

The drive to forage for pollen depends on the age-related foraging instinct and the need for pollen. Assuming that the current cell number with pollen is N_{PC}, the number of cells marked/required for pollen is

$$N_{MP} = N_G - N_{PC} \tag{15}$$

N_{MP} will be used as a weight when the worker bees select activities.

Nectar

The instinct to forage for nectar differs from pollen. The decision is not based on immediate need because honey stores are built up over summer for later use in winter (when not all collected by beekeepers). The decision is therefore based on the amount of nectar available in the landscape and the storage capacity within the colony (Butler, 1945; Southwick et al, 1982; Seeley, 1986, 1989; Silva & Dean, 2000; Pirez & Farina, 2004; Sagili & Pankiw, 2007; Martinez & Farina, 2008). Therefore, the number of empty cells marked for nectar is used as the weight for worker bees selecting activities. In the model, all the empty cells that are not marked for eggs, pollens are made as marked for nectar. Foragers' default activity is to forage nectar when the need for pollen is not pressing.

7.6.2.3. Scouts and foragers

Foraging bees can be classified as either scouts or foragers and can alternate between these two roles. The distinction is somewhat blurred in nature, because both scouts and foragers perform dances on return, and both scouts and foragers collect nectar and pollen for the hive. Scouts, however, primarily explore the landscape to search for food and return with forage collected from new sources, while foragers collect resources from existing sources (Ai et al, 2017). The decision to forage is described above. Different rules are used, however, for scouts. A scout will assess the hive needs and make a decision to scout the landscape based on these decisions.

Decision rules for scouts

It will initialise scouting behaviour if the hive is running short of nectar or pollen, and there are workers available for this task (Seeley, 1994; Fernandez et al., 2003; Edwards & Myerscough, 2011). The colony will try and fill frames with honey when nectar/honeydew is available in the landscape, so the bees will try and fill the frames in a new hive box, if it is added. In our model, foraging for nectar and filling new frames with honey is the 'default' behaviour.

The number (N_N) of nectar cells required for a brood size N_B is calculated as below

$$N_N = \frac{N_B}{K_N} \tag{16}$$

where K_N is a user defined parameter. A colony typically has an excess of nectar, because the honey bee strategy is to store honey for the winter months. If, however, honey stores do run low when the colony has brood, it will respond by initiating increased scouting behaviour to increase incoming nectar. This scouting behaviour is constrained in the autumn and winter because the brood size is low or zero.

Like pollen, a colony would like to maintain more than N_N nectar cells, again with a percentage P_G over (this can be different from nectar if required).

$$N_{GN} = N_N(1 + P_G) \tag{17}$$

And the foraging instinct will be

$$F_{IN} = 1 - \frac{N_C - N_N}{N_{GN} - N_N} \tag{18}$$

where N_C is the current number of nectar cell in the hive. Scouting behaviour will be triggered when $F_{IN}>1$ or the known place for nectar is below a user defined threshold.

Scouting behaviour

Scouts will first choose a direction at random and then fly between 45 m and 6 km (Hagler et al.,2011) to find available resource but they can even fly to a distance of 10 Km (Steffan-Dewenter & Kuhn, 2003; Pahl et al, 2011). If a bee fails to find resource when it reaches this distance it will return. If the bee enters a habitat patch that is defined as an RPU, it will forage from that patch, return with the resources foraged, and perform a dance in the hive to communicate the direction, distance and quality of the resource.

Dance communication

In reality, scouts (and foragers) will communicate the location of resources on return to the colony. The dance will be observed/noticed by several workers on the frame that the bee is dancing on. The dance will communicate direction, distance and food quality. The dance can initiate foraging activity for the available foragers in the hive. In the model, the dance communications are implemented by using a known resource locations list, which is used to record all the known resource locations which have been scouted and/or foraged by the bees in the hive. The list is sorted based on the available amount of resource. When there are enough locations, the bee will choose one location in the list to forage, which means locations with more resource will be visited by more bees (Fernandez et al, 2003; Beekman & Lew, 2008; Ai et al, 2017). When a bee comes back from foraging and/or scouting, it will check this list. If the forage location is not in this list, the place will be inserted to the list. Otherwise, the available resource amount for the location will be updated. If the available amount of resource is below a threshold value, the location will be deleted from the list.

7.6.2.4. Flying to a resource patch

Foragers will fly at a speed of V_F ms^{-1} directly towards the forage patch. While in flight a forager will have a metabolic rate q_F. (Higginson & Gilbert, 2004). Usually they fly at about 15km /hour (Pahl et al, 2011), but this speed can be altered due to different conditions of weather, wind etc. When they fly back, the speed is usually lower due to the extra weight from the foraged nectar or pollen. The time and energy required will be calculated and deduced for the foragers.

7.6.2.5. Collecting a resource

Foragers will collect a resource until either the resource is depleted, or the bee has reached its carrying capacity. The mass of forage is F_M. The rate at which the forage is collected depends on the quantity of forage in the patch. Foraging will become more difficult as the resource is depleted. The rate also depends on the resource. The rate of accumulation is given by

$$F_M = F_{RC} F_A \tag{19}$$

where F_{RC} is the foraging rate for the crop or semi-natural habitat (this varies because a resource can be gathered more quickly from some flowers, and different flower densities for different plant species). F_A is the amount of forage still available at the habitat patch. F_A will be reduced by F_m as a result of a bee foraging.

The metabolic rate while collecting resource (and flying back to the colony) increases to

$$q_{FL} = q_f \frac{B_m + F_m}{B_m} \quad (20)$$

where B_m is the mass of the bee, to account for the weight of the forage.

7.6.2.6. Returning from a resource

Foragers will fly at a speed V_B ms^{-1} back to the hive, with a metabolic rate determined by equation (20). To cover long distances, higher than 7km, the bees would have to drink nectar to refuel on the way, since a crop load of 20 µl 1.3 M sugar solution will keep a bee flying for just about 25 min, or 7 km (Hanauer-Thieser & Nachtigall, 1995). For pollen, the bee will first update the known location list for pollen (dance) and store it by itself. For nectar, the bee will first update the known location list for nectar (dance) and then try to find an available bee to receive the nectar. If there is one available to receive the foraged nectar, the nectar will be passed to this available bee. Otherwise, the forager will store the nectar by itself.

7.7. Finishing activities

When a bee finishes an activity, the required energy in term of sugar and pollen will be accumulated as shown in Table 8. In addition, the corresponding heat generated by the in-hive activity will be calculated and further converted into the bee's body temperature followed by the heating exchange between the bees and hive.

Table 8 Food required for activities for in-hive and foraging bees. Units mg per day. Food demand will also depend on gland and wax activity and temperature.

ID	Activities	Age	Nectar	Pollen
0	Move to random neighbour cells	Any day	10	4 (on average)
1	Cleaning cells	1-4	20	6
2	Ventilating entrance	3-12	20	6
3	Capping brood	3-12	35	6
4	Attending brood	2-12	35	6
5	Attending queen	2-12	35	6
6	Polishing the cells	5-22	20	4
7	Packing pollen	8-18	20	4
8	Guarding	8-26	20	4
9	Removing debris / dead bees	8-26	20	4

10	Test flights- orientation	8-18	20	1
11	Comb building	8-20	20	4
12	Capping honey	10-24	30	1
13	Receiving nectar	10-24	30	1
14	Ripening nectar	10-24	30	1
15	Foraging nectar	10- 45	10 mg /hour of flight= 25 Km	1
16	Foraging pollen	10-45	10 mg /hour of flight= 25 Km	1
17	Foraging propolis	10-45	10 mg /hour of flight= 25 Km	1
18	Foraging water (not modelled)	10-45	10 mg /hour of flight= 25 Km	1
20	Resting	Any day	10	1
21	Shivering- thermoregulation (winter bees no brood)		10	1
	Shivering- thermoregulation (winter bees WITH brood)		35	6

8. The *Apis*RAM vitality approach

*Apis*RAM includes a unique approach to integrate the various stressors and factors modulating them (pesticides, infectious agents, nutrition, and temperature) on individual bees. We do this by incorporating a variable (v_b) per bee that indicates its vitality rate which ranges from 0 to 1. A vitality rate of zero will indicate a dead bee. In other words, it is a likelihood of survival and can be used as the bee's health indicator.

In addition to direct effects, e.g. mortality probability with pesticide exposure, we assume that a reduction in vitality occurs based on the size and intensity of any stressor. To implement this, we make both the pesticide and infectious agents stressors interact with the bee's immune system strength, which is linked to its vitality, as shown in Figure 2. The details about the linkage between the vitality and pesticide and infectious agents through immune system strength can be found in Sections 9 and 10, respectively. Besides the pesticide and biological impacts, the bee's nutrition and body temperature also change its vitality value. Good nutrition (a bee has enough food) will increase and/or help to recover vitality, whereas poor nutrition will contribute to a decreasing vitality, which is detailed in Section 8.1. Comfortable body temperature range helps the bee to recover from stress caused by temperature (see Section 8.2). At each time step, the rate of change in vitality is calculated using the equation below.

$$\frac{d_{v_b}}{d_t} = (r_a + c_a(\sigma_F + \sigma_T + i_b - 1.5))v_b \qquad (21)$$

where r_a is the recovery rate of the vitality where σ_F is the food stressors and i_b is the immune system strength and σ_T is the effect of temperature (i.e., temperature stressor), and c_a is a user defined weight. Through this equation, when the immune system is strong and the bee has good nutrition and body temperature, the bee's vitality could be strengthened. Otherwise, the vitality will decrease until the bee dies. By combining these stressors through the vitality rate, we can mechanistically model the feedback between stressors which is a characteristic of bee colonies. We can expect that the model will create non-linear feedback linking different stressors, e.g., the impact of pesticides will be enlarged on weakened bees which are suffering from infectious agents and/or nutrition stressors.

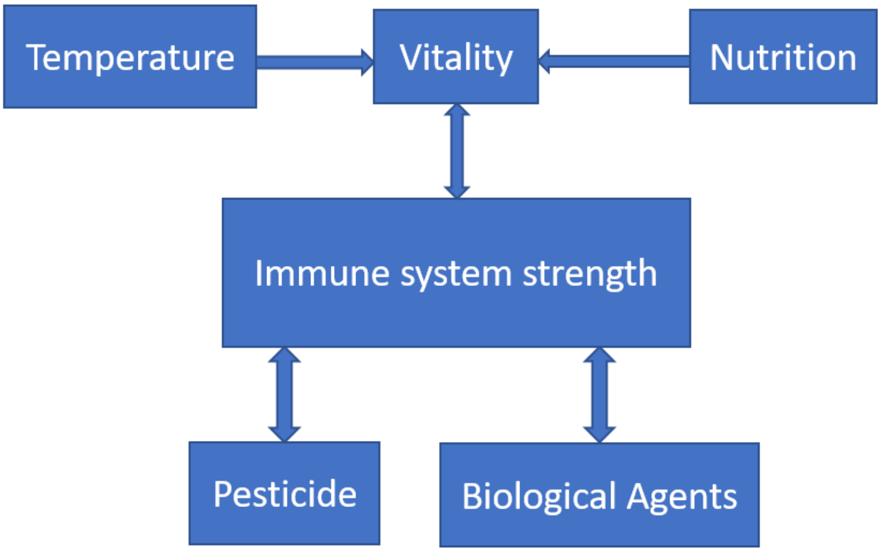

Figure 2 Linkage between vitality and stressors.

8.1. Nutrition

Nutritional stress is modelled based on the quantity of food required. The quality of the food is not modelled. Individual bees suffer nutritional stress when they need food but are not able to obtain the required food at that moment in time. Food stress σ_F is calculated as the product of the ratio of food deficit $(\varphi_p - F_p)$ to food demand (φ_p) for each food type. Specifically, when the bees can obtain a certain proportion (user defined) of the required food, there will be no additional stress added to the bees. Above this, they will recover from the nutrition stress at a constant rate (user defined). When the bees are not able to obtain enough food (below the user defined proportion), the stress from nutrition is updated by the equation below

$$\sigma_F(\mathrm{t} + \Delta\mathrm{t}) = \sigma_F(\mathrm{t}) - \prod_{p \in P} \frac{\varphi_p - F_p(t \to \Delta\mathrm{t})}{\varphi_p} \tag{22}$$

where *p* represents all the required food types, F_p is the food the bee has eaten or been fed. For *larvae*, they need sugar, pollen and royal jelly. For adult bees, they need sugar and pollen. When σ_F is equal to 1, it means that the bee has no food stress and is under good nutrition condition. When σ_F is close to 1, it will contribute positively to the rate of change in vitality, see equation (**21**).

When the bees can have enough food (larger than the user defined proportion), the stress from nutrition is updated by the equation below

$$\sigma_F(\mathrm{t} + \Delta\mathrm{t}) = \sigma_F(\mathrm{t}) + r_F \tag{23}$$

where r_F is the recovery rate when the bees can obtain enough food.

8.2. Temperature

We assume that the bees suffer from temperature stress when their body temperature is below a certain lower value T_C (cold) or above a certain higher value T_H (heat). The range between the user defined lower and higher value is the bee's comfortable body temperature range. Stress from heat or cold is measured in degree minutes. With the assumption that the amount of cold stress that a bee can endure is S_C, also measured in degree minutes, each bee calculates its cold stress σ_F by,

$$\sigma_T(\mathrm{t}+\Delta\mathrm{t}) = \sigma_T(\mathrm{t}) + \frac{(T - T_C)\Delta t}{S_C} \quad (24)$$

when its body temperature is below T_C.

Similarly, when the bee's body temperature is too high ($T > T_H$) the heat stress in degree minutes is given by,

$$\sigma_T(\mathrm{t}+\Delta\mathrm{t}) = \sigma_T(\mathrm{t}) + \frac{(T_H - T)\Delta t}{S_H} \quad (25)$$

where S_H is the amount of heat stress that a bee can endure when it is too hot.

When the bee's temperature is between T_C and T_H which is the bee's comfortable body temperature range, it will recover from its cold stress at a constant rate (user defined) as the equation below.

$$\sigma_T(\mathrm{t}+\Delta\mathrm{t}) = \sigma_T(\mathrm{t}) + r_T \quad (26)$$

where r_T is the recovery rate when the bee's body temperature belongs to the comfortable range.

For temperature stress, to ensure the temperature stress lies in the interval [0, 1], we set to σ be 0 when it is smaller than 0 and 1 when it is larger than 1. The temperature stress is linked to vitality the same way as nutrition (see equation (**21**)).

8.3. Mortality

At each time step, a bee has a probability of death, which is re-computed in every 10-minutes time-step. The modelled bees will be killed and removed from the model randomly according to the mortality probability.

The mortality rate depends on several factors. The most basic factor is the age of the bee. The mortality rate is close to 1 when the bee reaches its maximum age. The exception to this is that the maximum age can be prolonged when overwintering. In addition to the basic mortality rate, different stressors and their modulators (food shortages, diseases, pesticides and low and/or high temperature through vitality) and special activities (e.g., foraging, scouting and guarding) change the mortality rate as described in the equation below.

$$m_p = \max\left\{\frac{a}{a_{max}}, \quad 1 - v_b\right\} + g_g m_g + g_o m_o \quad (27)$$

where m_p is the mortality rate, a is the bee's developed age, a_{max} is the maximum age of the bee. v_b is the bee's vitality value. When the bee's vitality value is bigger, it has lower probability of dying. m_g is the mortality increment rate for guarding task. g_g is 1 when the bee is guarding and 0 when it is in-hive. Similarly, g_o is 1 when the bee is out of the hive for foraging or scouting and 0 when it is in-hive. m_o is the mortality increment for foraging and scouting tasks. When m_p is larger than 1, we set it to 1. Mortality is implemented as a probability test against m_p which is evaluated at each time step.

9. Pesticides

The treatment of pesticides in ApisRAM closely follows section 9 in the EFSA (2016) but is adapted to the approach of an individual based model (IBM) in order to simulate multiple types of pesticide. With an IBM, it is possible to track the pesticide body burden for each individual bee after it is exposed to pesticide through overspray, contact with contaminated vegetation, and via eating contaminated honey, nectar and pollen (for now, water is not modelled as an exposure route for pesticides due to lack of knowledge and data). A cell (wax) can also be contaminated when it stores resources with pesticide contamination.

Two types of pesticide application, spraying and seed coating, are included. When a pesticide is applied by spraying to a field (drift is included in this case), bees flying there for foraging can be contaminated by contact with the vegetation and potentially by overspray if they are there at the actual time of spraying. Further, nectar and pollen can be contaminated by the pesticide application and be available to the foraging bees. In addition to this, nectar and pollen can also be contaminated when the seeds are treated by pesticide (seed-coating). The pesticide in the nectar and pollen will be brought back to the hive when bees forage on these.

In order to include drift for pesticide spraying application which requires heavy computation power, at maximum two types of pesticide (2 a.s. in a tank mix or a compound and its metabolite, or one seed treatment and one spray application of one product) can be supported. More than two types of pesticide can be potentially included without the consideration of drift; however, this requires another different implementation method of the pesticide module, which is not part of this version of *Apis*RAM (i.e. version 1), see section12 for the projected development timeline

9.1. Pesticide in the landscape

To model all these aforementioned exposure paths with supporting of two types of pesticide in ALMaSS, we model different environmental compartments for pesticide in the landscape as shown in Figure 3. In total, there are five compartments, namely, in-soil, in-plant body, plant surface, pollen and nectar.

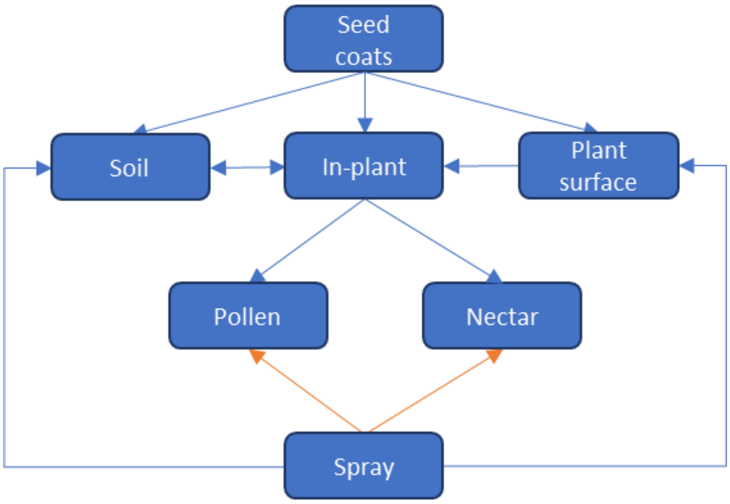

Figure 3 Pesticide compartments and transferring paths in the landscape considered in ApisRAM

To track the pesticide concentration in the different compartments, we create a 4D array, $\boldsymbol{P}$, which can be indexed by (x, y, j, k). x and y are used to index the location in the landscape and the resolution is one meter for both directions. j ranges from 1 to 6 (i.e. the number of pesticide compartments) while k ranges from 1 to N_{pest} (i.e. the number of pesticide types; with drift included in the simulation, this value is two). Specifically, j indicates soil (1), plant surface (2), in-plant (3), nectar (4), pollen (5), seed coats (6) and k represents pesticide type. At the beginning of the simulation, $\boldsymbol{P}$ is set to be zero, afterwards, it is updated once per day. If the historical pesticide usages are needed to be modelled, we can set P(x,y,1,k) with non-zero values from the beginning of the simulations. As shown in Figure 4, it is an example of the 4D array with four locations in the landscape with two types of pesticide.

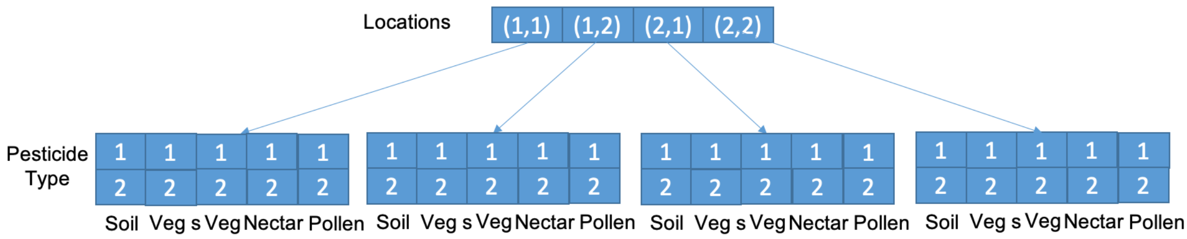

Figure 4 An example of the 4D array for pesticide with four locations and two types of pesticide. Veg S means vegetation surface while veg means vegetation..

9.2. Pesticide in the hive

Within the hive, nectar and pollen are stored in individual cells. In other words, the storage units are spatially and temporally explicit. The level of contamination in individual storage cells depends on the level of contamination of the stored resources foraged. The level of contamination of each cell itself and the resource in the cell is updated when new foraged pollen or nectar is stored in the cell. Therefore, the pesticide in the hive is tracked in cell level every 10 minutes.

9.3. Pesticide spray application

Pesticide spray application is controlled by the management scheme for individual crops. The pesticide needs to be specifically added to a crop management program before it can be used by *Apis*RAM. The pesticide spray application model checks the weather before application. If the weather is unsuitable, e.g., raining, the application will be delayed until the next opportunity.

Pesticide spray application is applied at the spatial scale of individual landscape elements (defined as polygons on a GIS map). The model will take as inputs the polygon ID (i), pesticide type (k), application time, and application rate (r: mg per square meter). In ALMaSS, we can get the area of a polygon in square meters, which are represented by s_i, in the meantime, the vegetation cover area as v_i and biomass weight as b_i are also available for the given polygon. A 2D array $\boldsymbol{R}$ is formed and initialized to be zero, which is indexed by x and y as the first two dimensions of $\boldsymbol{P}$. Afterwards, for each location (x, y) belonging to polygon i, $\boldsymbol{R}(x, y)$ is set to be r. Drift is modelled by convolving $\boldsymbol{R}$ with a two-dimensional drift pattern array $\boldsymbol{D}$. Firstly, all the element of $\boldsymbol{D}$ will be set to 1. Afterwards, it will be skewed using the wind direction and speed. Then, we use this drift pattern array to do convolutional operations on all the elements of $\boldsymbol{R}$. The drift pattern array size is user-defined.

After the drift calculation, $\boldsymbol{P}$ could be updated for all the locations (x, y) using the four equations ((28)-(**33**)) below. The pesticide is firstly apportioned between the soil and vegetation surface linearly. When the spray happens during flowering period, partial of the pesticide will go to the pollen and nectar directly. This is controlled by two user defined values (f_p and f_n).

$$\mathrm{P(x, y, 1, k) = P(x, y, 1, k) + R(x, y)} \times \frac{s_{i(x,y)} - v_{i(x,y)}}{s_{i(x,y)}} \tag{28}$$

$$\mathrm{P(x, y, 2, k) = P(x, y, 2, k) + R(x, y)} \times \frac{v_{i(x,y)}}{s_{i(x,y)}} \times (1 - f_n - f_p) \tag{29}$$

$$\mathrm{P(x, y, 4, k) = P(x, y, 4, k) + R(x, y)} \times \frac{v_{i(x,y)}}{s_{i(x,y)}} \times f_n \tag{30}$$

$$\mathrm{P(x, y, 5, k) = P(x, y, 5, k) + R(x, y)} \times \frac{v_{i(x,y)}}{s_{i(x,y)}} \times f_p \tag{31}$$

9.4. Pesticide seed-coating

Pesticide seed-coating is also controlled by the individual crops. In ALMaSS, we can define which crop is used for seed-coating. Then, when the crop is sown $\boldsymbol{P}$ will be updated for the locations with seed-coated crops. The model will take the polygon ID (i), pesticide type (k), planting time, and application rate (r: mg per square meter) as inputs. When the seed is sown, $\boldsymbol{P}$ is updated by the two equations below for the locations (x, y) belonging to polygon i.

$$\mathrm{P(x, y, 1, k) = P(x, y, 1, k) + r \times w} \tag{32}$$

$$\mathrm{P(x, y, 3, k) = P(x, y, 3, k) + r \times (1 - w)r} \tag{33}$$

where w is a user-defined value from 0 to 1 that distributes the seed coating pesticide into the soil and vegetation compartments.

9.5. Pesticide transferring from soil into vegetation

Each day, a user defined value $t_{s \to v}$ (from 0 to 1) is used to transfer the pesticide concentration in the soil to the vegetation in the same location. The transferred amount is deduced from the pesticide concentration in the soil afterwards. These are done by the equations below.

$$\mathrm{P(x, y, 3, k) = P(x, y, 3, k)} + t_{s \to v}\mathrm{P(x, y, 1, k)} \tag{34}$$

$$P(x, y, 1, k) = (1 - t_{s \to v})P(x, y, 1, k) \quad (35)$$

9.6. Pesticide transferring from vegetation surface into vegetation

The pesticide residue on the vegetation surface could be absorbed by the vegetation as well, which is implemented by another user defined value $t_{vs \to v}$ ranging from 0 to 1. Through this value, a certain amount of pesticide on the vegetation surface is transferred into the vegetation. This is implemented through the two equations below.

$$P(x, y, 3, k) = P(x, y, 3, k) + \frac{P(x, y, 2, k)v_{x,y}t_{vs \to v}}{b_{x,y}} \quad (36)$$

$$P(x, y, 2, k) = P(x, y, 2, k)(1 - t_{s \to v}) \quad (37)$$

9.7. Pesticide transferring from vegetation into nectar and pollen

With the growing of the vegetation, the nectar and pollen are contaminated through the pesticide residual within the vegetation. These are controlled by two user defined values $t_{v \to n}$ and $t_{v \to p}$, which both range between 0 and 1.

$$P(x, y, 4, k) = P(x, y, 3, k)t_{v \to n} \quad (38)$$

$$P(x, y, 5, k) = P(x, y, 3, k)t_{v \to p} \quad (39)$$

$$P(x, y, 3, k) = P(x, y, 3, k)(1 - t_{v \to p} - t_{v \to n}) \quad (40)$$

9.8. Pesticide in the hive

When the nectar and pollen being foraged contain a pesticide residue, the cell for storing the foraged resource will be updated for pesticide concentration. We use one vector $\boldsymbol{p}_c$ to track the total pesticide concentration (in mg) in the cell itself and the resource in the cell. Here, we use one cell c as an example to explain how the pesticide concentration vector is updated. And we only give the equations for nectar. For pollen, we only need to replace $P(x, y, 4, k)$ with $P(x, y, 5, k)$, where k is used to indicate the pesticide type.

$$p_c(k) = p_c(k) + P(x, y, 4, k)w_{fr} \quad (41)$$

where w_{fr} is the weight of the foraged resource that are stored in the cell.

9.9. Exposure routes for bees

In the model, bees can be exposed to pesticide through contacting the vegetation surface with pesticide, when flying in a field with ongoing pesticide spraying, and by eating contaminated food. There is a vector $\boldsymbol{p}_b$ for each bee to track multiple pesticide body burden. The length of this vector is the same as the number of pesticide types. This vector is updated by different exposure paths and degraded according to pesticide-specific DT50s.

9.9.1. Oral exposure

When a bee eats honey, nectar and pollen stored in cells containing pesticide residues, the bee will ultimately absorb those residues. Its pesticide body burden is updated according to the pesticide concentration in the food as below.

$$p_b = p_b + \frac{p_c w_e}{w_r + w_c} \tag{42}$$

$$p_c = \frac{p_c(1 - w_e)}{w_r + w_c} \tag{43}$$

where w_e is the weight of the food eaten by the bee, w_r is the weight of the resource stored in the cell and w_c is the weight of the cell itself. Through this updating method, there will still be pesticide residues in the wax, even after the cell is empty, which can be transferred between cell and future resources stored there is also modelled.

9.9.2. Contact exposure

When a bee forages on the vegetation which has pesticide residue on its surface, it will be contaminated by contacting the vegetation. Suppose one bee flies to a location (x,y) for foraging, its pesticide body burden for type k is updated by the equation below.

$$p_b(\mathrm{k}) = p_b(\mathrm{k}) + \mathrm{P}(\mathrm{x}, \mathrm{y}, 2, \mathrm{k})t_{vs \to b} \tag{44}$$

where $t_{vs \to b}$ is a parameter used to transfer the pesticide on the vegetation surface into the bee. The unit for $t_{vs \to b}$ is m^2.

9.9.3. Overspray exposure

Individual bees foraging in landscape patches that are being sprayed at the same time could potentially be over sprayed. If it happens, its pesticide body burden vector is updated by the equation bellow. The mass of pesticide deposited on the bee for type k is given by,

$$p_b(\mathrm{k}) = p_b(\mathrm{k}) + r_k s_b t_{o \to b} \tag{45}$$

where r_k is the application rate for the used pesticide type k, s_b is the average surface area of a honey bee (Poquet et al. 2014), and $t_{o \to b}$ is the absorbing rate (0 to 1) for a bee absorbing the over sprayed pesticide into its body.

9.10. Residue decline

Every day, $\boldsymbol{P}$ reduces according to half-life parameters, DT_{50}, for pesticide in the soil, on the vegetation surface, in the vegetation, in the pollen and nectar and in the hive and the bees. All of these are controlled by user defined values. The degradation of the pesticide concentration is updated using the equations below based on the degradation rates.

$$\mathrm{P}(:, :, \mathrm{j}, \mathrm{k}) = P^{-1}(:, :, \mathrm{j}, \mathrm{k})(1 - d_{j,k}) \tag{46}$$

$$p_c(\mathrm{k}) = p_c^{-1}(1 - d_k^c) \tag{47}$$

$$p_b(\mathrm{k}) = p_b^{-1}(1 - d_k^b) \tag{48}$$

where -1 as superscript means the value from previous day, $d_{j,k}$ is degradation rate for pesticide type k in host j in the landscape, d_k^c is the degradation rate for pesticide type k in the cell where d_k^b is the degradation rate for pesticide type k in the bee body.

9.11. Pesticide effect

Following the exposure calculations above the model is able to create a time-variant body burden per individual bee. This body burden must be translated into effects. Further, we assume the effect of multiple pesticides is additive unless specified otherwise. The pesticide burden will cause pesticide stress to the bee and have an impact on the bee vitality rate through immune system strength and may have sub-lethal effects.

In all cases below we assume that detailed dose-response relationships are not available and therefore default to a threshold and probability response. However, in some case e.g., homing ability loss, it would be easy to replace with a dose response should that information be widely available.

9.11.1. Pesticide stress

Chronic stress: Currently, we add all the body burden from different pesticide types to calculate a chronic pesticide stress. A user defined value $\boldsymbol{p_{max}}$ as a threshold is used. When the summation of all pesticide body burden is above this threshold, the bee will die immediately. The pesticide stress is calculated as below

$$\sigma_p(\mathrm{t}) = \sigma_p(\mathrm{t}-1) - \frac{\sum_k p_b(k)}{p_{max}} + y_p i_b \tag{49}$$

where i_b is used to indicate the bee's immune system strength and will be illustrated in Section 10. y_p is a parameter used to control how a bee could recover from pesticide stress based on its immune system strength. The pesticide stress ranges from 0 to 1, where 1 means no stress from pesticide at all and 0 means fully stressed from pesticide. This means that the threshold is fixed but the interpretation of whether a bee dies will depend on its own current health.

Acute lethality: We also model the direct pesticide lethal effect. For each type of pesticide modelled, a single threshold is used for all the bees. The death of the bee will occur randomly, but based on a probability distribution, at the time when the threshold is triggered. This method allows the direct use of data such as LD_{50} if measured over a time period, as it gives the probability of death per day. A more detailed Toxico-Kinetic Toxico-Dynamic (TKTD) model (Ashauer et al, 2010, 2015) could be implemented for each type of pesticide if the necessary parameterisation is available.

9.11.2. Reproductive performance of queens

The exposure to pesticides is calculated for each individual in the hive, including the queen. A reduction in reproductive performance will be calculated from the dose that the queen has been exposed to. The reduction in fecundity will be calculated from the effect threshold and a slope (Dai et al, 2010; Chaimanee et al, 2016; Martin et al, 2018).

9.11.3. Hypopharyngeal gland development

Jelly production for individual bees is day dependent and read from a lookup table (Table 6). A reduction of 15% in HPG size will be applied when the pesticides body burden is reached to a user defined threshold (Hatjina et al, 2013: Zaluski et al, 2017).

9.11.4. Homing ability

When a bee is contaminated by pesticide, its homing ability may be decreased. To implement this, the bee will take a mortality test related directly to user input regarding the level of pesticide needed to trigger loss of homing ability using the same concept as the acute lethality. This will be applied when the bee is foraging. This requires user input on a threshold body burden and associated probability of triggering loss of homing function to the extent that we assume the bee dies.

10. Infectious agents

In infectious agents' module, *Nosema*, *Varroa* and Deformed Wing Virus (DWV) and Acute Bee Paralysis Virus (ABP) are modelled. From the beginning of the simulation, a certain proportion of bees carrying *Nosema*, *Varroa* and Deformed Wing Virus (DWV) and Acute Bee Paralysis Virus (ABP) are randomly assigned. In other words, it is assumed that hives are infected by infectious agents from the beginning of the simulation. The level of infection can be controlled by the users.

10.1. Nosema

Nosema is a unicellular parasite that infects the guts of honey bees. Infection alters the behaviour of bees. It can cause an increase in food demand and hasten to transition to forage. However, higher levels of infection can also be fatal to individual bees. Bees become infected by ingesting *Nosema* spores. Within the hive, *Nosema* can be transferred by ingesting faeces from infected bees, and from ingesting stored pollen and honey. Survivability of *Nosema* in stored resources is temperature and species dependent, with *N. apis* tolerating lower temperatures than *N. ceranae* (Fries, 2010). It is worth noting that *Nosema* is not transmitted by contact between bees; only by ingestion (Goblirsch, 2014; Goblirsch 2018; Traver, 2011; Graystock et al 2015).

Both *N. ceranae* and *N. apis* were modelled. For each adult bee, there is one variable for each type of *Nosema* to record the number of *Nosema*. Bees can be infected by *Nosema* through; 1) ingestion of nectar/honey and pollen; 2) cleaning the hive.

When an infected bee forages and/or stores pollen or nectar to a cell, *Nosema* can be transferred into the pollen or nectar with the probability P_C. We do not track the number of *Nosema* in the cell, instead there is a flag variable for each cell to indicate whether the cell is contaminated by *Nosema* or not. When a bee ingests resource from a contaminated cell, it can be infected by *Nosema* with the probability of P_I.

Bees prefer to leave their faeces outside the hive, but when the weather is too cold for them to fly out, they must excrete within the hive. They generally do this away from the comb to avoid contaminating brood and food stores, usually near the hive entrance. In winter months, however, waste build up will cause an increased risk of contamination within the hive. Bee waste is pooled within the model, rather than it being spatially explicit.

For the sake of simplicity, we assume that bees only leave their droppings when the temperature is lower than 5°C for at least one week (and they cannot fly out of the hive) (Fahrenholz et al, 1989). Furthermore, the model uses counts rather than units of mass. Three variables, W_H, C_H and A_H, are used to track the counts of waste in the hive, the number of *Nosema ceranae* and the number of *Nosema Apis* in the waste, respectively. Each bee contributes 1-unit count to the waste W_H at each model step only when they leave their droppings within the hive (Forsgren & Fries, 2010). If the bee is infected with *Nosema*, M_C and M_A counts of *Nosema ceranae* and *Apis* will transfer to the waste. Then, W_H, C_H and A_H will be updated by $W_H = W_H + 1$, $C_H = C_H + M_c$ and $A_H = A_H + M_A$. When a bee is trying to clean the hive and take out amount of M_B unit counts waste, it could be infected by $C_H M_B / W_H$ number of *Nosema ceranae* and $A_H M_B / W_H$ number of *Nosema Apis* with the probability of P_W.

Nosema is vulnerable to temperature. Upper and lower limits are given in Table 9. The temperature of the waste pool is calculated at the start of each model step, as the average between the honeycomb cell nearest to the entrance hole and the ambient temperature. This average temperature value is used to check if the spores have been exposed to the upper and lower extremes for spore survival (Gisder et al 2010).

Table 9 Constants and variables for *Nosema* modelling.

Symbol	Units	Value	Meaning
M_H	Counts	--	Count of waste in hive.
C_H	Counts	--	Count of *Nosema ceranae* in the waste in hive.
C_A	Counts	--	Count of *Nosema Apis* in the waste in hive.
M_C	Counts	5×10^6	Count (no of spores) of *Nosema ceranae* in 1 unit count of bee dropping (Forsgren & Fries, 2010).
M_A	Counts	5×10^6	Count (no of spores) of *Nosema Apis* in 1 unit count of bee dropping (Forsgren & Fries, 2010).
M_B	Counts	1	Unit count of waste for a bee to take out with one-time cleaning.
P_W	Percentage	100%	Probability of infection from cleaning.
T_{HC}	°C	60	Upper survival temperature for *Nosema ceranae* (Fenoy et al, 2009).
T_{LC}	°C	0	Lower survival temperature for *Nosema ceranae* (Gisder et al, 2010).
T_{HA}	°C	40	Upper survival temperature for *Nosema Apis* (Martín-Hernández et al, 2009; Higes et al 2010).
T_{LA}	°C	-20	Lower survival temperature for *Nosema Apis* (Fries, 2010).

10.1.1. Behavioural effects of *Nosema*

When a bee is infected by *Nosema*, its life span will be shortened by a constant number, which means it will transfer to the next stage faster. The bee will also need to digest more pollen and sugar (nectar or honey), which is controlled by another user defined parameter.

The *Nosema* infection will also affect the bee's immune system strength as can be found in Section 10.3.

10.2. Varroa

The *Varroa* mite (*Varroa destructor*) is an ecto-parasite that infests honey bees. Most hives have some level of infection. If left untreated the colony is likely to die in 2-3 years. The *Varroa* mite has two life stages, a non-reproductive stage where the mites stay on the adult bees usually it lasts about 5 to 11 days and reproductive stages in capped brood. Transmission within the colony occurs between adult bees when bees are in close contact, and between adult bees and brood when bees are attending brood. Transmission between hives can be from mites dropped on to flowers at shared foraging sites or by drifting workers (Rosenkranz et al 2010; Becher et al, 2014; Martin 1998), however, this is not modelled for now.

The reproductive stage of Varroa occurs within the hive. Adult female mites invade brood cells just before capping. The female attaches itself to the bee pupa and begins to lay eggs. Like honey bees, the *Varroa* mite has haploid / diploid sex determination. The first egg that the female lays is unfertilised (haploid) and will develop into a male. Subsequent eggs are fertilised, and therefore female. Mating occurs within the brood cell. Mature, mated females emerge from the brood cell with the adult bee. Immature females and the males die (Rosenkranz et al 2010; Becher et al, 2014; Martin 1998).

The full reproductive behaviour of the reproductive stage is not modelled, i.e., the egg stage and male are not modelled. Instead, the model produces a certain number of mated female mites emerging with the hatched adult bee dependent on the development time (and therefore time between capping and emerging) of the bee pupa. The model also accounts for mortality of the mated female mites in the brood cell. A probability of the emerging female mites not being mated is considered, and the individual removed from the model (effectively dying) if this is the case The number of emerged Varroa is generated from a Poisson distribution. The expect value of the Posisson distribution is equal to the number of capped days of the cell. Mites in drone (V_d) cells therefore, will produce more offspring than mites in worker (V_w) cells. Average numbers to emerge are given in Table 10.

Table 10 Constants and variable used for *Varroa* modelling.

Symbol	Value	Units	Meaning
V_w	1.45	-	Average offspring, worker cell (Fries et al., 1994; Martin, 1998; Boot et al., 1995a,b; Donzé et al., 1998)
V_d	3.9	-	Average offspring, drone cell (Fries et al., 1994; Martin, 1998 1995; Boot et al., 1995a,b; Donzé et al., 1998)
V_u	0.3	-	Probability that female is unfertile (Martin , 1998)
V_m	0.006	Per day	Probability that female dies (Martin , 1998)
V_h		Per day	Probability that mite hops to another host (Bowen-Walker & Gunn 1998)
V_f	0.03	Per day	Probability that mite falls from host (Martin , 1998)
V_b	?	Per visit	Probability that a mite will infect a worker brood cell
V_o	?	Per visit	Probability that a mite will infect a drone brood cell
	0.9	Per day	Probability that a larva/pupa will be infected by DWV if *Varroa* carries the virus (Martin 2001)

	1	Per day	Probability that a larva/pupa will be infected by APV if *Varroa* carries the virus (Martin 2001)
	0.02	Per day	Probability that a larva/pupa will die from DWV (Martin 2001)
	1	Per day	Probability that a larva/pupa will die from APV (Martin 2001)

In-hive *Varroa* epidemiology is modelled. The non-reproductive stage is modelled as a simple individual based model piggybacking on the honey bee ABM. Each adult bee holds a flag to indicate *Varroa* infection and an integer number of parasitic mites. Mites can hop to other bees if the bees have the same cell coordinates. The frequency of hopping is controlled by the V_h. Mites will initially infect the first bee(s) that enter the cell coordinates that the bee hatched from. Mites can also fall off adult bees, with a frequency V_f. Mortality is not age dependent. This would require the model to track the age of each individual mite, in effect requiring a full ABM for the parasites. Instead, mortality at each time step is a constant V_m that is not age dependent. Mites leave their host and enter a brood cell when the larva is between 5 and 5.5 days, with a probability of V_b for worker cells and V_o for drone cells.

10.2.1. Behavioural effects of *Varroa*

Varroa is a vector for various virus. Here, we model two different viruses, Deformed Wing Virus (DWV) and Acute Bee Paralysis Virus (ABP), which could be found in Section 10.3. The probabilities of a larva/pupa infected by DWV and ABP through *Varroa* can be found in Table 10.

Varroa feeds from the fat body of both adults and larvae, which could weaken the bees. Therefore, infected bees will be less efficient. This is modelled by a user defined number to prolong the required time for different activities. The probabilities of a larva/pupa dying from DWV and ABP infection can be found in Table 10. As with *Nosema*, *Varroa* will also affect the bee's immune system strength as described in Section 10.3.

10.3. Virus and bee immune system strength

Varroa mites vectoring virus directly inject virus particles from adult bees to adult bees during the non-reproductive phase where it feeds on the bees' blood and fat; and from adult bees to brood during the reproductive phase (Martin 2001, Rosenkranz et al 2010; Becher et al, 2014; Sumpter and Martin, 2004; Ratti et al 2015). When a *Varroa* mite jumps from a virus infected bee to another healthy bee, the new host bee could be infected by a used defined probability of P_V.

After a bee is infected by a virus, the virus will start to develop based on the host bee's health status. In order to implement this, each bee in the colony holds two variables (V_D and V_A) representing the numbers of DWV and ABPV, respectively. Besides, there is another variable (i_b) for each bee to indicate its immune system strength, i.e., immune ability. The development rate (Nazzi et al, 2012) of virus depends on the bee's current number of carrying virus particles and the current immune system strength which is given by

$$\frac{dV}{dt} = (\mathrm{r} - \mathrm{c}i_b)\mathrm{V} \tag{50}$$

where t stands for time in seconds, r is the rate of pathogen replication virus and c is a rate of immunological control. We use the same equation for two viruses, therefore, we omitted the subscript of V. For each time step (ג), the number of virus will be increased by $\frac{dV}{dt}$ג. From equation (**50**) we can find that the replication of virus is suppressed by the immune system. On the contrary, the bee's immune system (health indicator) can be suppressed by the number of virus particles, which is given by

$$\frac{di_b}{dt} = \mathrm{a} - \mu i_b + (\mathrm{b} - \mathrm{sV})\mathrm{V} \tag{51}$$

$$\mathrm{a} = a_b v_b + a_p \sigma_p \tag{52}$$

$$\mu = \begin{cases} 1, & \text{if the bee has Nosema or Varroa above a threshold} \\ 0, & \text{else} \end{cases} \tag{53}$$

where a is the increment rate of the immune system strength which depends on the pesticide stressor and the vitality, u is the immune decreasing factor which is controlled by the fact that whether a bee carries *Varroa* and/or *Nosema* since that they can destroy the bee's immune system. b and s are the parameters to control how the immune system reacts to virus. When the number of virus particles is below a certain value, assuming the nutritional status of the bee is good, the immune system will be enhanced, otherwise, it will be weakened by the virus infection. Like the virus particle number, the immune system strength will be updated by $\frac{di_b}{dt}$ at each time step in addition to any changes caused by other factors (*Nosema*, pesticides, nutrition). The overall effect of virus infection on the vitality will therefore depend on the level of vitality, the relative rates of viral impact on the immune system response and the recovery of the response dependent upon nutritional state.

11. Beekeeping management practices

For beekeeping management practices (BMP), we have defined several events, for example, treatment for *Varroa*, replacing/removing/ frames (Sperandio, et al., 2019). This is done by reading from an external events file by an event control module within ALMaSS. The event control module (Section 11.5) will apply the events in this file at the specified time.

To date, the following functions have been implemented for BMP in the model.

11.1. Chemical treatments

Chemical control of *Varroa* considers organic and conventional treatments. The immediate effect is to kill off a proportion of the mites. The proportion killed will depend on a user supplied variable. In addition to this an input variable will control a reduction in the laying rate of the queen and a variable for killing a proportion of bees randomly (Birnie, 1997; Van Engelsdorp et al, 2008; Johnson et al, 2009; Dahlgren, 2014; Dahlgren et al, 2012; Gashout, 2017).

11.2. Replacing of frame

It will be possible in the model to dynamically change the properties of any frame within the hive at any time. This includes removal of a frame or adding a new frame configured with the desired properties. All the properties of a frame can be configured; brood cell types immature stages, resources, pesticide contamination, parasite load etc.

Adding or removing brood combs and adding a number of workers will affect the demography of the colony on both donor and receiver colony (Huang & Robinson, 1996), additionally, might increase/ remove pathogen loads. Adding or removing feed combs will also affect both donor and receiver colony, in terms of food stores, as well as chemical residues in them (Akyol, et al, 2006).

For now, it is possible to remove a frame and replace it with an empty frame or with a full honey frame which will be detailed in the next subsection.

11.3. Supplementary feeding

Supplementary feeding is modelled by adding a special food resource for the eating sugar activity (see Section 7.3.1). When this practice is trigged, the model bees can access the supplementary sugar resource.

Supplementary feeding will affect colony development and will up the development or help a weak colony to recover (Mărghitaş et al, 2010). In the model this will occur as a result of improved nutrition for the bees and the subsequent effect on individual vitality.

11.4. Beekeeper experience

Beekeeper management practices is defined in the model by the actions described in this section (chemical treatments, replacing frame and supplementary feeding). For now, there is a user defined variable to show whether we model an experienced beekeeper or not. If it is an experienced beekeeper, the scheduled actions will be applied at the recommended time. Otherwise, it will be delayed. Currently, it will be postponed by one month, but this is user defined and could be varied within a range.

11.5. Event control module

The ALMaSS include a module for implementing events by reading external event control file. The event control module is used to implement BMP.

Events consist of a time and a task list. These events happen at the beginning of the given day for the event.

When an event is triggered a list of tasks is performed. The implemented tasks for now can be found in Section 11.

Events are defined in an external json file that can optionally be defined by the user. Currently, we only support time specified events. Some example events are shown in the figure below.

```json
{
    "Jobs":
    [
        {
            "task": "KillVarroa",
            "type": "Timed",
            "day": "1",
            "month": "1",
            "frame": "-1"
        },

        {
            "task": "AddHoneyFrame",
            "type": "Timed",
            "day": "1",
            "month": "1",
            "frame": "2"
        },

        {
            "task": "ReplaceOneFrame",
            "type": "Timed",
            "day": "1",
            "month": "1",
            "frame": "2"
        }
    ]

}
```

Figure 5 An example of jason file for beekeeping management practice.

12. Roadmap and timeline for the development of ApisRAM for its use in risk assessment

As can be seen in Figure 6, the first version of *Apis*RAM will be launched by the end of January 2022, where the colony and in-hive products will be calibrated using the data from the EFSA field data project (Dupont et al. 2021a, b). By the summer of 2022, comparison between the simulated data and the EFSA field data will be done after including the flower resource model which is developed in H2020 B-GOOD project. In the end of 2022, the foraging, infectious agents, and thermal modules will be calibrated using the data collected under H2020 B-GOOD project. By May 2023, the vitality module will be calibrated for the purpose of modelling multiple stressor interactions. *Apis*RAM is expected to be ready for environmental risk assessment with the capability of addressing multi-stressors by 2025.

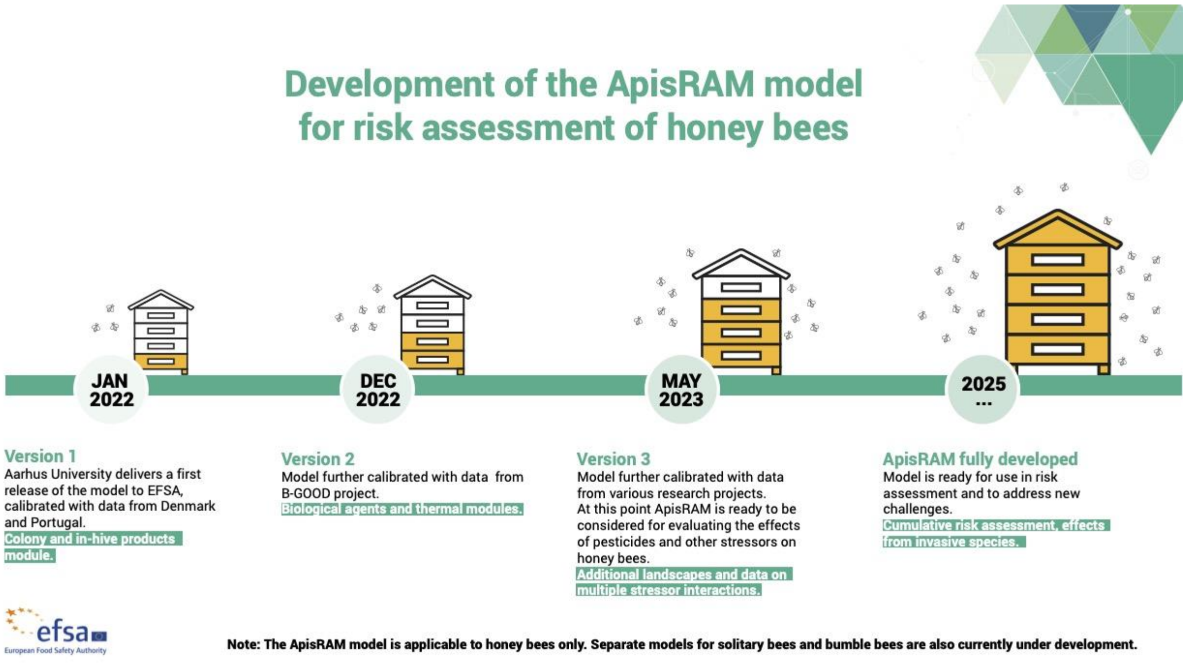

Figure 6 Development roadmap of *Apis*RAM suggested by EFSA in 2021

13. References

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14. Annex A - Variable selection and literature review

Annex A can be found in the online version of this output (‘Supporting information’ section):

https://doi.org/10.2903/sp.efsa.2022.EN-7184

15. Annex B - ApisRAM Computer Program Report

Annex B can be found in the online version of this output ('Supporting information' section):

https://doi.org/10.2903/sp.efsa.2022.EN-7184

16. Annex C - ApisRAM User Manual

Annex C can be found in the online version of this output ('Supporting information' section):

https://doi.org/10.2903/sp.efsa.2022.EN-7184

17. Annex D - Bee conceptual model

Annex D can be found in the online version of this output ('Supporting information' section):

https://doi.org/10.2903/sp.efsa.2022.EN-7184

18. Annex E - Literature search and assessment

Annex E can be found in the online version of this output ('Supporting information' section):

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