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# Price structure of traded honey, pollen and wax linked to winter survival of a honey bee colony

Mathieu Kohli

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## Abstract

We consider the contribution of both honey and pollen to winter survival of a bee colony in order to assess how valuable both these commodities are from the bees' perspective. In turn, this leads us to a method to help beekeepers evaluate the marketprice of honey and pollen.

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## Introduction

The interaction between *Apis mellifera* honeybees and beekeepers raises the issue of how they can mutually beneficially cooperate. While bees

struggle to be resilient through tough weather conditions, beekeepers need to sell honey at a reasonable price. Here we investigate from a mathematical perspective how a resilient bee colony would price its own honey depending on its internal state and on environmental factors. The underlying structure of price that we develop throughout this paper is presented in Figure 1.

It is in the best interest of both a bee colony and the beekeeper tending to it that the honey harvest happens in a geographic and seasonal setting where the price the colony pays for loosing its honey is minimal.

## 1 Long term prosperity of a population of colonies

A beekeeper may want to understand if a bee colony population will thrive several years after having settled in a apiary.

In order to answer such a question, we compare the number of colonies at the beginning of winter of a given year to the number of colonies at the same point in time the next year.

Colonies are not all equal when they enter the cold winter season, some are strong and others are weaker. The two main variables that account for the strenght of a healthy colony are its population size ( $N$ ) and the weight of honey it has stockpiled ( $H$ ) (to which we can add the age of its queen). When describing the "demographics" of a population of colonies, it is necessary to take

that information into account. The mathematical structure that encodes such information is a distribution over the plane  $(H, N)$ .

To come back to the original question : how does the population of colonies tend to evolve on a yearly basis ? The answer to this question can be summarized by an endomorphism  $\tilde{\mathcal{Y}}$  that maps a quantitative distribution of colonies on the plane  $(H, N)$  to the average implied distribution of colonies the following year.

The framework introduced in the present paper consists in a mathematical model that describes the underlying structure behind the endomorphism  $\tilde{\mathcal{Y}}$  in a given environment. This model allows us to compute this endomorphism and extract relevant environmental indicators from it.

Endomorphism  $\tilde{\mathcal{Y}}$  contains a major piece of information : its spectral radius which corresponds to the asymptotic growth rate of the population of colonies. Indeed, it follows from the Perron-Frobenius Theorem that there exists an eigenvector  $\tilde{D}$  with positive coefficients representing a quantitative distribution of colonies on the plane  $(H, N)$  which grows at a steady rate  $\rho(\tilde{\mathcal{Y}})$  year after year. We choose  $\tilde{D}$  to be normalized as a probability distribution.

Note that the idea that year-long stable cycles can be used to describe honey bee colonies and to study them through an economic lense can be found in [Champetier et al. 2015].

Now that we understand the relevance of studying  $\tilde{\mathcal{Y}}$  let us divide the year into four periods:

- *during winter*, the bee colony stays inside its hive and forms a bee cluster. Each bee uses its body as a radiator to keep the cluster warm by using the honey stockpiled by the colony as an energy source,
- *during the foraging season*, the bee colony explores the surroundings of its hive by sending scouts to find resources that foragers then exploit,
- *between both seasons*, we also consider two transition steps :

one at the beginning of winter when "summer bees" are replaced by "winter bees" that live longer than their summer counterparts, all of which have essentially the same work : heating the hive.

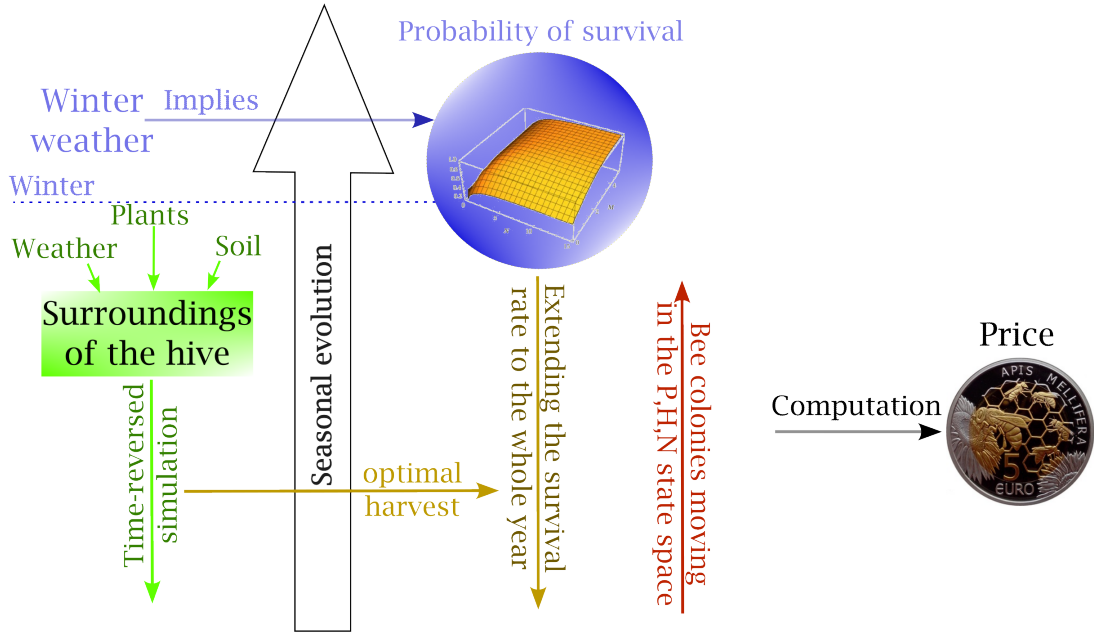
The other transition phase happens at the beginning of spring when "summer bees" replace "winter bees". These summer bees have shorter lives than winter bees and are highly age-structured as their occupation is a function of their age.

If we are able to describe how bee colonies navigate these four periods of a year, in particular how they reproduce (see Section 6) and how their reserves and population fluctuate, then we can reconstruct  $\tilde{\mathcal{Y}}$ .

## 2 Value of honey resources

The starting point of our study is the knowledge that a specific flower field, or bush, or tree in the vicinity of a hive has a limited potential to feed the hive. Inasmuch as the flowers only provide nectar to bees (as opposed to pollen), this potential can be defined as the *net* energy intake gained by the colony *per time unit* as it sends *one* forager bee back and forth between the hive and that resource. We call it the potential efficiency of a forager bee on this nectar resource. It depends on parameters that are identified in [Kohli and Anstett]:

- the greater the distance  $d$  separating the hive and the floral resource, the more energy is spent to transport nectar [Ausseuil et al. 2018] and the longer it takes to travel between these two points. To this, we must add the effect of wind, which is equivalent to a distortion of distances on the geographic map [Kohli and Anstett]. Distances can be compared to the maximal distance from the hive  $d_{max}$  at which bees can be found foraging [Beekman and Ratnieks 2000, Greenleaf et al. 2007, Ratnieks and Shackelton 2015].
- The flowers can be highly or scarcely rewarding for bees. We measure this quality through a coefficient  $q_f$  that is defined as the energy contained in the stomach of a forager that is full with nectar from flower  $f$ , to which we subtract the energy needed to transform this quantity of nectar into honey through evaporation of superfluous water [Mitchell 2019]. Quantum  $q_f$  can be compared to  $q_0$  that corresponds to a reference flower which is the most rewarding flower possible. The flower species also influences the average number of flowers  $m_f$  a forager must visit to fill its stomach with nectar, as well as the average time  $\beta_f$  a bee spends on a flower to forage.
- The higher the density  $\rho_f$  of flowers, the less energy and time is lost collecting nectar within a small range. Density  $\rho_f$  should be compared to a critical density  $\rho_{f,crit}$  below which flowers are too scattered to form a resource.



**Figure 1:** Visualization of the different steps that lead to price computation. Sections 2 and 3 focus on the *optimal harvesting* process. Section 4.1 as well as Appendices A and B correspond to an investigation of the link between *winter weather conditions* and the *probability of survival* of a colony at the beginning of winter. Sections 4.3, 5.1 and Appendix C are devoted to *extending the probability of survival to the whole year*, provided that we possess a model describing the *growth of the plants* surrounding the hive (see Section 5.2). Section 7 defines the *price* of honey from the perspective of bees.

- Some parameters do not depend on the floral resource but must be deduced from experiment. Namely  $V$ , the speed at which foragers travel between the hive and the flowers [Nachtigall et al. 1995], as well as  $v_{hop}$ , the average speed at which bees hop from one flower to another. The last relevant parameter that is included in the model we consider is the average time  $t_{hive}$  a forager spends inside the hive between two trips to a floral resource [Fewell et al. 1991, Colin et al. 2022]. The time a pollen forager spends inside the hive is far greater than the time a nectar forager spends in the hive. Indeed, pollen foragers deposit their pollen load directly in the cells around the brood, while nectar foragers quickly transmit the nectar they collected upon arrival at the hive [Chabert et al. 2024].

Once the parameters that affect the potential efficiency  $\eta_f$  of a forager bee on a nectar resource have been stated, we can express it through the following formula [Kohli and Anstett]:

$$\eta_f = \frac{q_0 \left( \frac{q_f}{q_0} - \frac{d}{d_{max}} - \frac{q_f}{q_0} \sqrt{\frac{\rho_{crit,f}}{\rho_f}} \right)}{t_{hive} + 2\frac{d}{V} + m_f \left( \beta_f + \frac{1}{2v_{hop}\sqrt{\rho_f}} \right)}. \quad (2.1)$$

If we assume the bee colony optimizes the use of its foragers on nectar resources, it should send as much foragers as possible to the resource where the foragers have the maximal forager efficiency. If some foragers remain unemployed, they should be affected to the second best resource in terms of efficiency for the bees, and so on until no forager is left idle.

To implement the previous process, the knowledge of how many foragers  $\phi_f$  a floral resource can constantly feed is required. That can be derived from the same parameters that were used to express the efficiency of foragers [Kohli and Anstett]:

$$\phi_f = \frac{S\rho_f\lambda_f}{q_f} \left( t_h + \frac{2d}{V} + m_f \left( \beta_f + \frac{1}{2v_{hop}\sqrt{\rho_f}} \right) \right), \quad (2.2)$$

where  $S$  is the surface of the floral resource and  $\lambda_f$  represents the power offered to foragers by one individual flower [Baude et al. 2016].

### 3 Relative price of pollen compared to honey

Unlike honey, pollen does not provide the energy the hive needs. It provides the matter (amino acids, essential fatty acids, vitamins,...) necessary to form bees [Di Pasquale et al. 2013]. Therefore, the *net gain* for the bee colony brought back by a forager bee is a quantity of matter minus an energy, which can not be directly reduced to one unity. To overcome this challenge, we admit that each day during the foraging season, bees are able to assign a value to both nectar and pollen based on their current needs. The ratio between the value of high quality pollen and the value of honey is the *relative price* of pollen in honey.

To implement this in practice, we replace  $q_f$  in Formula (2.1) by

$$price \times \tilde{q}_0 \frac{\tilde{q}_f}{\tilde{q}_0} \quad (3.1)$$

where

- $\tilde{q}_0$  is the maximal mass of pollen that a forager can transport on its legs,
- *price* is the energetic equivalent of the maximal mass of pollen  $\tilde{q}_0$  *provided this pollen is of the highest quality possible pollinic flower*, in the sense that bees that eat this pollen live the longest (see [Di Pasquale et al. 2013])
- $\frac{\tilde{q}_f}{\tilde{q}_0}$  is the ratio between the average lifespan of a bee fed with pollen of flower  $f$  and the average lifespan of a bee fed with the reference flower [Di Pasquale et al. 2013].

To summarize, a relative price of pollen in honey corresponds to the distribution of foragers on the local floral resources, which in turn corresponds to a certain inflow of nectar and pollen in the hive.

Notice that the allocation of forager bees to *either* nectar collection *or* pollen collection is done once and for all when a bee starts foraging. The relative price of pollen in honey influences the behavior of bees that just started foraging and can also deter pollen foragers from collecting pollen [Chabert et al. 2024].

To compute the variation of the reserves of both nectar and pollen, we subtract the losses to the inflows. We write the balance sheet for energy as stated in [Kohli and Anstett]:

$$\frac{dE}{dt} = \mu \frac{\delta M_{forag}}{dt} - \alpha \frac{\delta N_{death}}{dt} - \pi N - h(T, N). \quad (3.2)$$

Each term in the previous equation has a specific meaning:

- $\frac{\delta M_{forag}}{dt}$  stands for the *net* quantity of honey produced with the nectar inflow entering the hive through foraging. This term can be computed as

$$\mu \frac{\delta M_{forag}}{dt} = \sum_{\substack{f \text{ exploited} \\ \text{nectar} \\ \text{resource}}} \eta_f \phi_f, \quad (3.3)$$

where  $\phi_f$  is computed through Equation (2.2) except for the resource where the foragers are the least efficient, where  $\phi_f$  simply is the number of remaining foragers that are not working on a better resource.

- $\frac{\delta N_{death}}{dt}$  is the death rate in the bee colony. See [Di Pasquale et al. 2013] for a study of this death rate related to the pollen the colony feeds on.
- $\pi N$  represents the "basis metabolism" inside the hive, where  $\pi$  stands for the average metabolic rate of a bee that is neither flying nor taking part in the thermoregulation of the hive [Kovac et al. 2007] and  $N$  is the number of bees.
- $h$  represents the energy used to thermoregulate the hive [Stabentheiner 2021]. It is a function of the outside temperature and the number of worker bees, but also of the number of males, the number of nurses and the size of the brood.

A similar equation holds for pollen and the number of bees this pollen is transformed into. It has terms equivalent to those in Equation (3.2) except for term  $h$  in Equation (3.2) that has no pollinic equivalent.

### 4 Winter survival rate and quantitative state of the colony

At the start of winter, there are two major factors that depend on the bees' work during the previous months and that account for the colony's ability to successfully reach the next spring. Those factors are the quantity of honey enclosed in the hive and the number of bees surrounding the queen.

Through a thermodynamic simulation of energy consumption as a function of probable winter conditions outside the hive [Omholt and Lonvik 1986, Myerscough 1993, Ocko and Mahadevan 2014, Kohli and Anstett] (see Appendix 4.1) combined with experimental data collection [Free and Racey 1968, Döcke et al. 2019], one can establish the probability  $\mathbb{P}(t = \text{fall} \rightarrow \text{winter}, N, H)$  of surviving through winter if at the time of transition between fall and winter, there are  $N$  bees and  $H$  kilograms of honey inside the hive.

#### 4.1 Probability of survival at the beginning of winter

We investigate how the winter heating mechanism shapes the probability of surviving winter at the transition period between fall and winter. Thanks to the heat equation we prove in Appendix A that:

$$H_{\text{consumption}} \propto N^{\frac{1}{3}} \int_{\text{Start winter}}^{\text{End winter}} T_{\text{center}} - T_{\text{out}}, \quad (4.1)$$

where the left hand side of the previous identity is the total honey consumption during winter,  $N$  is the number of winter bees, and  $T_{\text{center}} - T_{\text{out}}$  stands for the temperature gap between the outside of the bee cluster and the core of the cluster where the queen is hidden.

Notice that the beginning and the end of winter in the previous formula depends on when the bees choose to stay inside their hive.

Let  $\phi$  stand for the cumulative distribution function (see Appendix B) of the random variable:

$$\begin{aligned} \{\text{winters}\} &\longrightarrow \mathbb{R} \\ \text{winter} &\longmapsto \int_{\text{Start winter}}^{\text{End winter}} T_{\text{center}} - T_{\text{out}}. \end{aligned} \quad (4.2)$$

In order to survive winter, the honey stock must exceed its consumption, which, by definition of the cumulative distribution function happens with probability:

$$\phi\left(\nu \frac{H}{N^{\frac{1}{3}}}\right), \quad (4.3)$$

where  $\nu$  is a constant that should be derived from measures such as those described in [Free and Racey 1968] combined with the corresponding winter weather data [<https://digital.nmla.metoffice.gov.uk/>]

The previous Expression (4.3) may be considered as a first attempt to express  $\mathbb{P}(t = \text{fall} \rightarrow \text{winter}, N, H)$ . However, it falls

short of that expectation because it predicts that very small clusters with  $N \rightarrow 0$  can easily survive winter. This fails because in small colonies, individual bees would have to deliver a heat power far greater than they are able to. To capture this missing barrier to survival, we notice that according to Appendix A, a rescaling of the heat equation implies that the heat power emitted by each bee inside the bee cluster is proportional to:

$$\frac{T_{\text{center}} - T_{\text{out}}}{N^{\frac{2}{3}}}. \quad (4.4)$$

The previous quantity has a fixed upper bound  $\theta_0$  since bees have a maximal individual heating power. Moreover, since the bee cluster needs to "extract" the oxygen to breathe from its surface, the heating power used by the entire colony is limited by its surface, which implies that for some constant  $\theta_1$ ,

$$\frac{T_{\text{center}} - T_{\text{out}}}{N^{\frac{2}{3}}} \times N \leq \theta_1 N^{\frac{2}{3}}. \quad (4.5)$$

In the rest of this section, we assume that the breathing constraint prevails over the constraint resulting from the heating limit for individual bees.

We set  $\psi$  the cumulative distribution function of the random variable:

$$\begin{aligned} \{\text{winters}\} &\longrightarrow \mathbb{R} \\ \text{winter} &\longmapsto T_{\text{center}} - T_{\text{out},\text{min}}, \end{aligned} \quad (4.6)$$

where  $T_{\text{out},\text{min}}$  is the coldest temperature reached during a specific winter. The Fisher–Tippett–Gnedenko theorem suggests that  $T_{\text{center}} - T_{\text{out},\text{min}}$  follows a Gumbel distribution (see Figure 2).

The probability that the bees will be able to breathe during winter is therefore given as  $\psi\left(\theta_1 N^{\frac{1}{3}}\right)$ . To estimate  $\theta_1$ , data on the size of surviving winter clusters is necessary (such data is collected in [Döcke et al. 2019] for instance).

Let us now suggest an expression for the probability to survive winter.

$$\mathbb{P}(\text{fall} \rightarrow \text{winter}, N, H) = \phi\left(\nu \frac{H}{N^{\frac{1}{3}}}\right) \psi\left(\theta_1 N^{\frac{1}{3}}\right). \quad (4.7)$$

Although the previous formula does not take into account the non-independence of the two random variables that are involved, it is a first step towards understanding the probability we are focusing on.

From (4.7), we deduce a remarkable subset of the state space. Indeed, honey is slowly accumulated all year long by bee colonies and on a short period of time, it is easier for a colony to regulate its population rather than its honey reserves. In particular, just before winter, the bee colony should optimize its winter survival by adjusting its population with fixed honey reserves. This means that at the beginning of winter, a bee colony should be on  $\zeta$ , the subset of the  $(H, N)$ -states space such that:

$$\frac{\partial \mathbb{P}}{\partial N} = 0. \quad (4.8)$$

The set  $\zeta$  is a 1-dimensional curve along which:

$$\frac{d}{dH} \left( \frac{\partial \mathbb{P}}{\partial N} (H, N_\zeta(H)) \right) = 0. \quad (4.9)$$

Still along  $\zeta$ ,

$$\left( \frac{\partial}{\partial H} + N'_\zeta(H) \frac{\partial}{\partial N} \right) \frac{\partial \mathbb{P}}{\partial N} = 0. \quad (4.10)$$

The differential equation satisfied by  $N_\zeta$  reads

$$N'_\zeta(H) = - \frac{\frac{\partial}{\partial N} \frac{\partial \mathbb{P}}{\partial H}}{\frac{\partial^2 \mathbb{P}}{\partial N^2}}. \quad (4.11)$$

## 4.2 Restricting the $\tilde{\mathcal{Y}}$ endomorphism to $\zeta$

Now that we noticed that bee colonies should start overwintering close to the  $\zeta$  curve, we choose to restrict  $\tilde{\mathcal{Y}}$  to  $\zeta$ . More precisely, if  $\Pi$  matches any point  $(H, N)$  to the intersection point of  $\zeta$  with the level set of  $\mathbb{P}$  (*fall*  $\rightarrow$  *winter*) that contains  $(H, N)$ , we define

$$\mathcal{Y} = \Pi \circ \tilde{\mathcal{Y}}|_\zeta : \zeta \longrightarrow \zeta. \quad (4.12)$$

From a computational perspective,  $\mathcal{Y}$  compresses information from  $\tilde{\mathcal{Y}}$ .

From now on, we assume that the growth rate of a population of colonies is  $\rho(\mathcal{Y})$  (the spectral radius of  $\mathcal{Y}$ ) and we consider  $D$  a probability distribution along  $\zeta$  that is an eigenvector linked to the eigenvalue  $\rho(\mathcal{Y})$  of  $\mathcal{Y}$ .

Let us notice that in order to implement  $\mathcal{Y}$  in a computer, the curve  $\zeta$  is divided into several intervals.  $\mathcal{Y}$  is then encoded so as to act on discrete distributions over the subintervals of  $\zeta$ . The set of

discrete distributions over the subintervals of  $\zeta$  is a finite dimensional vector space.

If we assume that  $\mathcal{Y}$  can be diagonalized as an endomorphism over a finite dimensional vector space, its matrix in an adapted basis is

$$\begin{pmatrix} |\lambda_1| e^{i\theta_{1,1}} & & & & \\ & |\lambda_1| e^{i\theta_{1,2}} & & & \\ & & \ddots & & \\ & & & |\lambda_2| e^{i\theta_{2,1}} & \\ & & & & |\lambda_2| e^{i\theta_{2,2}} \\ & & & & & \ddots \end{pmatrix} \quad (4.13)$$

If the distribution of colonies is initially set to  $D_0$  the first year, then after  $n$  years the distribution of colonies is  $D_n = \mathcal{Y}^n D_0$ . Let us assume that the eigenvectors linked to eigenvalues whose modulus is  $|\lambda_{k(n)}|$  prevail in the decomposition of  $D_n$ . The prevailing  $|\lambda_{k(n)}|$  increases as years pass by and ultimately reaches  $\rho(\mathcal{Y})$ . When  $|\lambda_k|$  prevails,

$$\frac{D_{n+1}}{|\lambda_k|^{n+1}} = P^{-1} \begin{pmatrix} e^{i\theta_{k,1}} & & & \\ & e^{i\theta_{k,2}} & & \\ & & \ddots & \\ & & & \ddots \end{pmatrix} P \frac{D_n}{|\lambda_k|^n}. \quad (4.14)$$

## 4.3 Probability of surviving the next winter during the foraging season

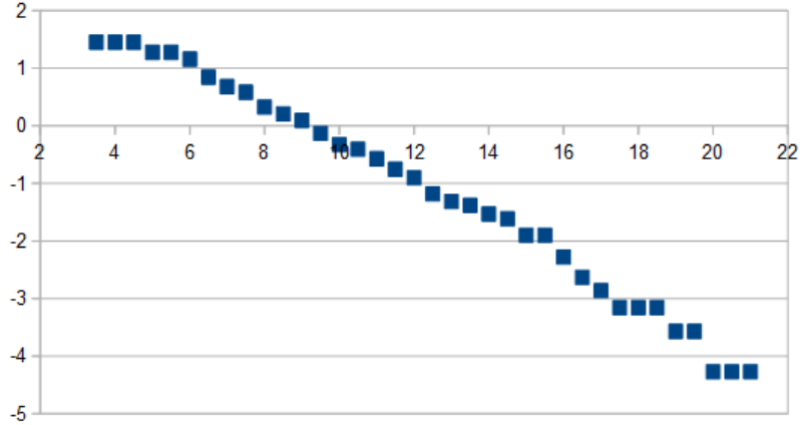
At times during the foraging season, in order to describe the quantitative state of the bee colony, it is relevant to decompose the number of bees  $N$  into several components that list the number of bees of different age groups:  $N_i$  denotes the bees that are  $i$  days old.

We now endeavour to compute, at any time  $t$  between the beginning of spring and the end of fall,  $\mathbb{P}(t, N, H, \text{Envir})$ . The previous quantity  $\mathbb{P}(t, N, H, \text{Envir})$  is defined as the probability to survive the following winter if on day  $t$ , there are  $H$  kilograms of honey and  $N$  bees in the hive, if the bees know the environmental parameters *Envir* from spring to fall in advance.

The function

$$\begin{aligned} \text{Envir} : \\ [ \text{spring} ; \text{fall} ] \longrightarrow \{ \text{weather} \} \times \{ \text{floral maps} \} \end{aligned} \quad (4.15)$$

contains all environmental information during the foraging season *including future times* after  $t$ .



**Figure 2:** Graph of  $T \mapsto \ln \left( \frac{1}{\psi(T+T_{center})} \right)$  in Dijon (France) between 1945 and 2022, where temperatures are stated in  $^{\circ}C$ , [<https://meteo.data.gouv.fr/datasets/>] It is a straight line when  $T_{center} - T_{out,min}$  behaves according to a Gumbel distribution.

The complete knowledge of the environment between time  $t$  and the beginning of winter implies determinism in the optimal choices of the colony between time  $t$  and the beginning of winter, so that all the randomness comes from winter. And at any time before winter, we can write

$$\frac{d}{dt} \mathbb{P}(t, N(t), H(t), Envir) = 0. \quad (4.16)$$

This translates into

$$N'(t) \frac{\partial \mathbb{P}}{\partial N} + H'(t) \frac{\partial \mathbb{P}}{\partial H} = - \frac{\partial \mathbb{P}}{\partial t}. \quad (4.17)$$

In the previous equation, term  $\frac{\partial \mathbb{P}}{\partial t}$  corresponds to the loss in probability of winter survival that would arise if the hive was somehow "put onto pause mode" between time  $t$  and time  $t + dt$ . Optimizing the survival rate in winter requires to maximize  $-\frac{\partial \mathbb{P}}{\partial t}$  through an optimal choice of foraged resource, which is equivalent to an optimal choice of price of pollen in honey (see Section 3):

$$\frac{\partial}{\partial \text{price}} \frac{\partial \mathbb{P}}{\partial t} = 0, \quad (4.18)$$

Equation (4.18), however, is implicit and therefore computationally expensive and impractical to solve. To approximate the optimal exchange rate, we suggest a demand-driven explicit expression that takes into account the relative contribution of honey and pollen to the survival of a colony, but that does not depend on the

available resources around the hive :

$$\text{price} = \frac{\frac{\partial \mathbb{P}}{\partial N_1}}{\frac{\partial \mathbb{P}}{\partial H}}. \quad (4.19)$$

The problem of computing  $\mathbb{P}$  for any time  $t$  during the foraging season can now be solved. Since we assumed that  $\mathbb{P}$  is known at the beginning of winter, we only need to deduce  $\mathbb{P}(t - dt)$  from  $\mathbb{P}(t)$ . We start by finding out which price satisfies Equation (4.19), which allows us to discover  $H'(t)$  and  $N'(t)$ . Then we use Equation (4.17) that leads us to an expression for  $\mathbb{P}(t - dt)$ .

As regards the transition phases -when bees from one season are replaced by bees adapted to the following season- the foraging process is similar to the one that takes place during the foraging season except that the allocation of foragers towards floral resources isn't regulated freely by the exchange rate between pollen and nectar (Formula (4.19)). Instead, since all the bees must be replaced, we assume a minimal number of foragers are assigned to nectar collection to maintain honey reserves and the rest collects as much pollen as possible.

## 5 Randomness in the environment

Of course, the future is not fixed and there are different scenarios  $Envir$  that can play out with different probabilities. We denote by  $\mathbb{S}$  the probability on the set of environmental conditions.

## 5.1 Combining several environmental pathways towards winter, bubble algorithm

### 5.1.1 Building the foam structure

If there are several environments  $Envir_i$ , we write  $\mathbb{P}_i(N, H)$  as a short notation for  $\mathbb{P}(t, N(t), H(t), Envir_i)$ .

The union of graphs

$$\bigcup_{i \text{ envir.}} \left\{ \begin{pmatrix} N \\ H \\ \mathbb{P}_i(N, H) \end{pmatrix} \right\} \quad (5.1)$$

forms a foam-like structure where each graph linked to an environmental path is one of its bubbles.

Each bubble in the foam structure can be constructed all the way from winter to spring by applying the time-reversed algorithm described in Section 4.3.

To simplify memory usage, one may choose to only consider some typical scenarios to which a bee colony must be prepared.

Notice that since the foam structure was built going backwards through time, it is more complex at the beginning of spring, and reduced to one bubble at the beginning of winter. The environmental scenarios linked to these bubbles therefore form a tree rooted at the beginning of winter and whose leaves represent, at the beginning of spring, all the potential environmental paths leading to winter.

After the foam structure has been computed in a time-reversed manner, we switch back to the natural orientation of time.

### 5.1.2 Starting from one colony

To describe the path of a specific colony in the natural orientation of time, instead of *knowing* the future, the colony has to *bet* on the future. When it has bet on one environmental scenario, it stays on the bubble linked to this scenario and follows the trajectory imposed by the movement of this bubble (described by Equation 4.16). This goes on until

- *either* the environmental scenario has been proven wrong by the actual environment that unfolds in reality. When a scenario collapses, colonies that had bet on it fall on a remaining scenario that is one of the closest to the collapsed one ("close to" with respect to the tree representing the potential environmental scenarios for the remaining time until winter)

- *or* the colony chooses to form a swarm (see Section 6)
- *or* the colony reaches the intersection of two bubbles and it has a choice. According to Appendix C, the ratio of the probability of staying on bubble 1 to the probability of switching to bubble 2 is equal to

$$\frac{(v_2 - v_1) \mathbb{P}_2}{(v_1 - v_2) \mathbb{P}_1}. \quad (5.2)$$

To take into account the probability of both choices, one may represent a single colony as a Dirac distribution. As a colony hits the intersection between two bubbles, it splits into two Diracs that follow their own separate paths on both bubbles. The mass of the initial Dirac is shared between the two Dirac distributions that emanate from it proportionally to the probability of following each path.

We have almost entirely described how a colony goes from the beginning of spring to winter in a *real* environment that it discovers as time passes. The remaining question is : on which bubble does the colony start when it is in a state  $(N, H)$  at the beginning of spring ? One solution is to start by preparing for the worst case scenario and to choose to put the colony on the lowest bubble for this state  $(N, H)$ .

### 5.1.3 Starting from a distribution of colonies

More generally, we start not from *one* colony at the beginning of winter, but from a weighted distribution of colonies on a finite number of points along  $\zeta$ . In order to push forward a distribution through winter, we assume that each colony that survives has a constant population  $N$  all winter long and then splits into several states that represent different possible winter honey depletions computed thanks to Relation (4.1) (depending on the random harshness of winter encoded in  $\phi$ ).

During an actual year with real time environmental measures, the weighted distribution of colonies on the probability foam is pushed forward in time through the foraging season by pushing forward each of its colonies according to the previously described method.

### 5.1.4 Combining all potential environmental realities

The last step is to run the previous algorithm that pushes forward in time a distribution of colonies

along  $\zeta$  not just once, but as many times as there are environmental scenarios. Each time we run the algorithm, we assume a new environment  $Envir_i$  is actually taking place during the year and we multiply the weight of each colony linked to "this reality" by the corresponding factor  $\mathbb{S}(Envir_i)$ .

## 5.2 Environmental scenarios data for generative models

In order to take into account the different possible environmental scenarios that might play out during the months between the current day and the beginning of winter, we resort to simulation. The parameters that play a key role in the thriving of a bee colony are weather, local vegetation (species, abundance and phenology), and soil that influences the vegetal growth. We may want to find equations that describe the evolution of those environmental parameters and solve them. In practice, this would involve tremendous amounts of computational power. Moreover, solving weather equations requires more than just local weather data, and since we are adopting the perspective of the bee colony that only has access to local information, this approach is irrelevant.

Instead, it is more appropriate to use generative models. This requires data :

- As regards weather in France, data can be obtained at [<https://meteo.data.gouv.fr/datasets/>].
- A map that presents the nature of the soil on which vegetation grows in France is made available by INRIA [INRIA 2018].
- To assess vegetal growth, one can rely on satellite data from the Copernicus program that is available at [<https://www.wekeo.eu/>]. For some crops species such as sunflower crops, phenology has been studied [Desfonds and Garcia De Cortazar Atauri 2020].
- To know which plants grow on a geographic spot, or at least which plants are cultivated for agricultural purposes, data from France can be found at [<https://geoservices.ign.fr/rpg>]. In Europe, euro crop maps (2018 and 2022) are available [d'Andrimont et al. 2021, ECJRC 2022].

More precisely, the information flow for the current model is described in Figure 3. Both the hive and environment models are currently being written in Python language in order to carry out simulations [Kohli 2025].

### 5.2.1 Temperatures

#### State space

Let us start by explaining how one can encode temperature measures. The first obvious solution is to write the temperature on day  $d$  expressed in Celsius degrees or Kelvins or in Fahrenheit as a real number. If we write  $\mathcal{T}_d$  the space of temperatures on day  $d$ , it is merely a copy of  $\mathbb{R}$  and a sequence of temperatures measures for  $N$  consecutive days would be an element of  $\mathcal{T}_d \times \mathcal{T}_{d+1} \times \dots \times \mathcal{T}_{d+N-1}$  which can be seen as  $\mathbb{R}^N$ .

A drawback to this easy approach is that this representation depends on a chosen unit of measurement, and projects the additive structure of  $\mathbb{R}$  on temperatures while we are primarily interested in the order structure on temperatures (colder/hotter). To extract the order structure from temperature, we focus on quantiles.

By means of the cumulative distribution function of temperatures in a geographic spot, and depending on the level of precision that we assign to our measures, we cut  $\mathcal{T}_d$  into  $n$  quantiles. We now consider  $T_d$  as the complex vector space generated by the *orthonormal basis* made of the quantiles of  $\mathcal{T}_d$  (the quantiles are now seen as vectors). If a measurement falls in a certain quantile inside  $\mathcal{T}_d$  its associated state inside  $T_d$  is this same quantile.

The natural generalization of this process to describe a  $N$ -days long sequence of temperature in  $\mathcal{T}_d \times \mathcal{T}_{d+1} \times \dots \times \mathcal{T}_{d+N-1}$  is to match to a sequence of temperatures the basis vector of  $\bigotimes_{i=d}^{d+N-1} T_i$  whose component on  $T_i$  represents the temperature quantile in which the temperature in  $\mathcal{T}_i$  falls. This idea is valid and will indeed be used to mix non homogeneous measurements (temperature, sun irradiance, rain levels, wind speeds) in Section 5.2.2. However, it is possible to considerably reduce the dimension of the space that represents a  $N$ -days long temperature sequence due to the fact that the temperatures on different days share the same quantiles *by definition*. So we can replace  $\bigotimes_{i=d}^{d+N-1} T_i$  with  $\bigoplus_{i=d}^{\perp, d+N-1} T_i$  without having to compare the norm of different quantiles on different days : the norm of all the quantiles are equal to one *by definition*.

Notice that the representation in  $T_d$  of a temperature on day  $d$  and of a sequence of temperatures in  $\bigotimes_{i=d}^{d+N-1} T_i$  both actually fall in the unit spheres  $\mathcal{S}(T_d)$  and  $\mathcal{S}\left(\bigotimes_{i=d}^{d+N-1} T_i\right)$ . We would like the same to happen for the representation in  $\bigoplus_{i=d}^{\perp, d+N-1} T_i$ . In order to ensure this, we require the

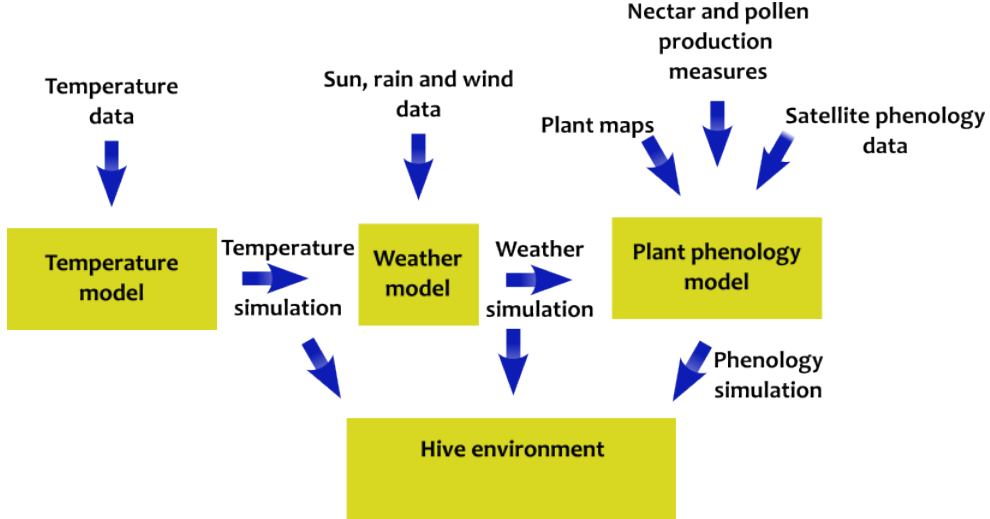


Figure 3

orthogonal projection of the state in  $\bigoplus_{i=d}^{\perp d+N-1} T_i$  on  $T_i$  to be the representation of  $\mathcal{T}_i$  in  $T_i$  divided by  $\sqrt{N}$ .

In the following, we denote by  $\Pi_1$  the orthogonal projection  $\bigoplus_{i=d}^{\perp d+N-1} T_i \rightarrow T_d$ .

To build the state space  $T_i$  we have only considered *pure states* that are reached from points in  $\mathcal{T}_i$ . Any *mixed state*  $\Psi$  in  $\mathcal{S}(T_i)$  represents a state in which there is a probability  $|\langle \Psi, \Theta \rangle|^2$  to be measured on the pure state  $\Theta$ . Parseval's identity guarantees that the total probability is indeed 1.

We have now built the temperature state space  $\mathcal{S}\left(\bigoplus_{i=d}^{\perp d+N-1} T_i\right)$ . We proceed similarly to define the space of temperature variations  $\mathcal{S}\left(\bigoplus_{i=d}^{\perp d+N-1} V_i\right)$ , where the temperature variation on day  $d$  is the difference between the temperature on day  $d+1$  and the temperature on day  $d$ .

### Time

Since the temperature states are now encoded as elements of a sphere, it is natural to see time as the action of a rotation on the state space. This rotation has complex eigenvalues whose modulus are all equal to one and whose arguments are  $\pm \frac{2ik\pi}{\Lambda}$  where  $\Lambda$  is a characteristic time period of the temperature and where  $k \in \mathbb{N}$ .

For computational purposes, one may choose to restrict  $k$  to 1, 2, 3 and  $\Lambda$  to an adapted finite set. As a consequence, there only remains  $6 \times \#\{\Lambda\}$  eigenvalues representing the action of time. This leads us to also restrict the state space

to its core component  $\Omega$  that evolves by following the reduced time action. We therefore introduce an orthogonal projection

$$\rho : \bigoplus_{i=d}^{\perp d+N-1} T_i \rightarrow \Omega \quad (5.3)$$

as well as

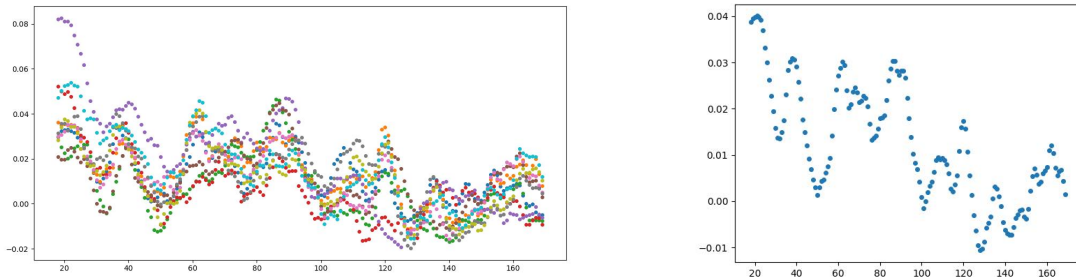
$$\Delta : \Omega \rightarrow \Omega \quad (5.4)$$

where  $\Delta$  is the time-action endomorphism whose  $6 \times \#\{\Lambda\}$  eigenvalues have just been described, and where  $\Omega$  is a  $6 \times \#\{\Lambda\}$ -dimensional space included in  $\{(1 \ 1 \ \dots \ 1)\}^{\perp}$  (we exclude the state that gives equal weights to all quantiles because that is the time-independent weight of quantiles and we are focusing on the time factor).

Here  $\Delta$  will describe how temperatures evolve going *backwards* in time but the same method can be implemented to simulate *future* weather.

Before we go any further and ask how to build  $\rho$  and  $\Delta$ , we should explain how it is possible to find  $\Lambda$  values that correspond to relevant temperature cycles. To do this, as described in Appendix B.2, we plot the correlation between the temperature on a given day and the temperature  $n$  days later. We notice that there are correlation peaks that are shared by several cities in France (see Figure 4). We choose these peaks to constitute to set  $\{\Lambda\}$ .

In order to evaluate if a couple  $(\rho, \Delta)$  is relevant to explain temperature dynamics we define



**Figure 4:** Left : Correlation between the temperature on day  $d$  and day  $d + n$  as a function of  $n$  in different towns in France. Right : Average value of all these correlation functions as a function of  $n$ .

Predict  $(\rho, \Delta)$  as the following quantity

$$\sum_{d=2}^{D-N+1} \left| \left\langle \Pi_1 \left( L_\rho \left( \frac{\Delta \circ \rho(v_d)}{\|\rho(v_d)\|}, v_{d-1} \right) \right), \Pi_1(v_{d-1}) \right\rangle \right|^2, \quad (5.5)$$

where

$$L_\rho(w, v) = \|\rho(v)\| * w + v - \rho(v) \quad (5.6)$$

lifts  $w$  through  $\rho$  to bring it as close as possible to  $v$ .

By design, Predict  $(\rho, \Delta)$  is maximal when the empirical frequencies of quantiles are best aligned with the theoretical probability to obtain these quantiles. We should therefore maximize Predict to find  $\rho$  and  $\Delta$ , which can be done by gradient descent.

Once  $\rho$  and  $\Delta$  have been optimized, it is possible from knowing an  $N$ -day long sequence of temperatures to randomly generate a plausible temperature the day before, and incrementally generate a sequence of temperatures backwards in time. However, this falls short because the process fails to take into account the continuity of temperatures : indeed, no structure has been added that explains which quantiles are close or far from each other. This is the reason why we introduced the temperature variation state space  $\mathcal{S} \left( \bigoplus_{i=d}^{\perp d+N-1} V_i \right)$  in the first place, along with the temperature state space. Similarly to what we did with the temperatures, we build  $\rho_V, \Delta_V$  as well as Predict $_V$ .

The probability to obtain a certain temperature quantile  $\Theta$  one day before an  $N$ -day long sequence, that used to be expressed as  $|\langle \Psi, \Theta \rangle|^2$  can now integrate variation information (whose value relative to the temperature information can be quantified through the Predict function) and

$|\langle \Psi, \Theta \rangle|^2$  is now replaced by

$$|\langle \Psi, \Theta \rangle|^{\frac{2\text{Predict}}{\text{Predict} + \text{Predict}_V}} * |\langle \Psi_V, \Theta \rangle|^{\frac{2\text{Predict}_V}{\text{Predict} + \text{Predict}_V}}. \quad (5.7)$$

This method yields valuable results as can be seen in Figure 5.

## 5.2.2 Other weather measures

Apart from temperature, weather is also characterized by solar irradiance, rain levels and wind.

Sun and rain directly influence both plant growth and foraging behavior (by encouraging or prohibiting foragers from leaving the hive and therefore acting on the daily foraging time) while wind affects foraging flight aerodynamics (see Appendix D).

From a technical perspective, everything is done as in Section 5.2.1, except:

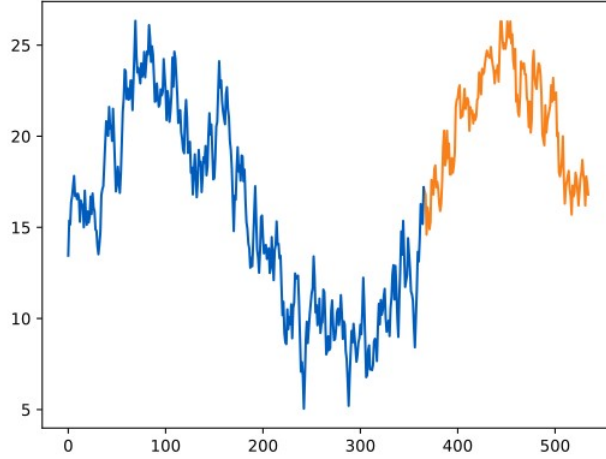
- $\bigoplus_{i=d}^{\perp d+N-1} T_i$  is replaced by  $\Omega_{d-1} \otimes S_d \otimes R_d \otimes W_d$  where  $\Omega_{d-1}$  is the reduced temperature state space described in Section 5.2.1 and  $S_d, R_d$  and  $W_d$  represent the sun, rain and wind states on day  $d$ ,
- $\Pi_1$  is replaced by the marginal projection  $\Pi : \mathcal{S}(\Omega_{d-1} \otimes S_d \otimes R_d \otimes W_d) \rightarrow \mathcal{S}(S_d \otimes R_d \otimes W_d)$  whose expression on the quantile basis is :

$$\Pi \left( \sum_{o,s,r,w} \alpha_{o,s,r,w} e_{o,s,r,w} \right) = \sum_{s,r,w} \sqrt{\sum_o \alpha_{o,s,r,w}^2} \tilde{e}_{s,r,w}. \quad (5.8)$$

## 5.2.3 Plant phenology

In this section, we assume we are focusing on a certain plant species.

By using the same technique that enabled us to add other weather parameters to the temperature, we can add satellite phenology data to the



**Figure 5:** Orange : actual temperatures measured in Nice, France. Blue : temperatures generated with the method explained in Section 5.2.1

weather data. Here if we want a reduced weather state space that represents the last *past* days rather than the next *future* days we must re-run the entire process described in sections 5.2.1 and 5.2.2 to switch back to the natural orientation of time.

The operation of combining weather data and plant growth data *is not* intended to increase information (indeed, if the soil doesn't vary, plant growth is a function of weather so it does not bring more information) *on the contrary* the goal is to compress the plant phenology information to turn it into an annual biological clock. It would be superfluous for a biological clock to focus on all the timescales relevant to explain weather phenomena. We choose to merely focus on the  $3 \times 2 = 6$  eigenvalues that represent the timescales 365, 365/2 and 365/3 days.

Now that we have built a 6-dimensional biological clock for a plant species, it is possible to measure each day if the flower is blooming or not and attach this measure to the 6-dimensional clock-space to "color" this space and therefore delimit and describe when the flowers bloom. Once this has been done, the more precise blooming dynamic is studied in the following Section 5.2.4.

### 5.2.4 Blooming flowers' wave

Here we investigate how flowers can regulate their nectar production to adapt to pollinators' presence or absence and what this entails at a flower field scale. By default, a flower should minimize its nectar output as long as this does not deter pollinators from transporting its pollen to another

flower. Since a blooming flower field cannot measure its distance from the closest bee colony, it can gradually, day after day, increase the nectar it provides as an incentive for pollinators to visit until :

- *either* enough pollinators have visited it,
- *or* it cannot extract enough energy from the soil to keep on rising nectar production.

The remaining question is : how fast must a flower field increase its nectar output? If we choose a perspective not focused on a flower field *but instead* centered around the closest bee colony from this flower field, the "goal" of a flower field is to "convince" this colony that it is a better option to visit it than any other field closer to the colony. As has been noticed, scout bees judge which flower field is the best for their colony to forage on by selecting flower fields where the net power output is maximized :

$$\eta_f = \frac{q_0 \left( \frac{q_f}{q_0} - \frac{r}{r_{max}} - \frac{q_f}{q_0} \sqrt{\frac{\rho_{crit,f}}{\rho_f}} \right)}{t_{hive} + 2\frac{r}{V} + m_f \left( \beta_f + \frac{1}{2v_{hop}\sqrt{\rho_f}} \right)}. \quad (5.9)$$

A scout bee that is currently exploring its hive's vicinity has two choices at every point in time.

- Follow the direction  $r \frac{\partial}{\partial \theta}$  and therefore stay at the same distance from the hive .
- Follow  $\frac{\partial}{\partial r}$  and go further away from the hive.

If the bee were to follow  $r \frac{\partial}{\partial \theta}$  all the way around the hive, it would encounter flower fields with

nearly the same  $\eta$  by circular symmetry. However, there remain small variations and along the  $r$ -radius circle around the hive,  $\eta(\theta)$  is similar to a symmetric random walk. This means that a scout bee can estimate the maximum of  $\eta$  on the  $r$ -radius circle where it currently is (at point  $x$ ) to be  $\eta(x) + \tilde{\alpha}\sqrt{r}$ . In order for the bee scout to go towards the  $\frac{\partial}{\partial r}$  direction, the following condition must be satisfied :

$$\frac{\partial \eta}{\partial r} \geq \alpha' \sqrt{r}. \quad (5.10)$$

If we assume that flowers minimize their nectar expenditure,

$$\eta(r) = \alpha r^{\frac{3}{2}}, \quad (5.11)$$

for  $r$  large enough (while for  $r$  small enough, the randomness prevails and  $\eta(r) \propto \sqrt{r}$ ).

By combining 2.1 and 5.11, we see that  $\sqrt{r}$  satisfies a quintic equation. When the plant maximizes  $q_f$ , the highest solution to this equation indicates the furthest distance the plants are able to attract the bees to, and again through 5.11, one can deduce the highest efficiency  $\eta_{\max,f}$  a plant species can offer to honeybees. We refer to [Baude et al. 2016, Baude et al. 2025] for quantitative data regarding the maximal value of  $q_f$ .

Now that we described the spatial aspect of flower patches' reaction to the presence of a bee colony, let us explain how this reaction can arise even though flowers can not directly measure their distance from this bee colony. Let us assume that the first day a flower species starts to bloom, all the flower fields of this same species produce nectar as if they were as close as possible to a bee colony. Only the flowers that are just next to the hive get pollinated and as time flows, the other flower fields start improving  $\eta$  until they hit the threshold described in 5.11 that ensures pollination. There remains the question of how fast a flower field should increase  $\eta$ . If we consider flower fields of the same species, they should *cooperate* in order to all receive the same pollination service from the bees regardless of their spatial position. Since individual honey bee foragers consistently visit the same flower species, one can think of it as the flower fields transmitting the foragers to one another. So that all flower fields benefit from the same pollination time, if at time  $t$ ,  $r_{forag,f}(t)$  is the current distance between a bee colony and its foraging spot on a flower species  $f$  and if the flowers are fully cooperating with each other they can

enforce

$$\frac{d}{dt} r_{forag,f} \propto \frac{1}{r_{forag,f}}, \quad (5.12)$$

which entails

$$r_{forag,f}(t) \propto \sqrt{t}.$$

In turn, *from the bees' perspective*, by reformulating 5.11 we obtain

$$\eta(t, r_{forag,f}(t)) = \eta_{\max,f} \left( \frac{t}{t_{\max}} \right)^{\frac{3}{4}} \quad (5.13)$$

*From the standpoint of the plant*, before it has been reached by pollinators, it should, as long as it can, adjust  $q_f$  (and  $m_f$ ,  $\beta_f$  and  $\rho_f$ ) so that

$$\frac{q_0 \left( \frac{q_f}{q_0} - \frac{\gamma\sqrt{t}}{r_{\max}} - \frac{q_f}{q_0} \sqrt{\frac{\rho_{crit,f}}{\rho_f}} \right)}{t_{hive} + 2\frac{\gamma\sqrt{t}}{V} + m_f \left( \beta_f + \frac{1}{2v_{hop}\sqrt{\rho_f}} \right)} = \alpha\sqrt{\gamma}t^{\frac{3}{4}}. \quad (5.14)$$

This leads to writing

$$q_f(t) = \alpha_{\frac{5}{4}}t^{\frac{5}{4}} + \alpha_{\frac{3}{4}}t^{\frac{3}{4}} + \alpha_{\frac{1}{2}}t^{\frac{1}{2}}. \quad (5.15)$$

As we have already noticed, at some point in time, it becomes impossible for flowers to maintain these high  $q_f$  levels and the blooming ends. Simultaneously, the foragers which have been attached to one flower species are gradually replaced with younger foragers who visit other flower species.

At the landscape scale, if at time  $t$  we divide the plants into two categories : those that have already been pollinated and those that await pollination, the average value for  $q_f$  is proportional to the remaining surface to be pollinated

$$q_{f,average} = \left( 1 - \frac{t}{t_{\max}} \right) \left( \alpha_{\frac{5}{4}}t^{\frac{5}{4}} + \alpha_{\frac{3}{4}}t^{\frac{3}{4}} + \alpha_{\frac{1}{2}}t^{\frac{1}{2}} \right). \quad (5.16)$$

At a regional scale, if we only take into account honey bees as pollinators, we can start answering the question : are there enough honey bee colonies in a given region to support a particular flower species on the long run ? Indeed, so that a species can maintain its *unity*, its individuals must be *connected*. In the case of flower species, this means that the disk around a bee colony that covers the area that these bees can pollinize must

not be isolated and must overlap with other such disks linked to other bee colonies.

*Random geometric graph theory* accounts for the connectedness (or absence thereof) of such a network [Appel and Russo 2002]. Let us define  $\mathcal{A}$  as the total expansion area of a flower species and  $\rho$  as the bee colony density. The threshold value for how far the blooming flower wave around bee colonies must reach in order to guarantee connectedness and unity of the flower species is

$$R_{\text{thres}} = \sqrt{\frac{\ln(\mathcal{A}\rho)}{\pi\rho}}. \quad (5.17)$$

## 6 Swarming conditions

For a hive to form a swarm, the probability that both halves of the initial colony die before the beginning of the next spring should be inferior to the probability that the initial colony dies before that same moment. This translates into

$$\left(1 - \mathbb{P}\left(t, \frac{N}{2}, \frac{H}{2}\right)\right)^2 \leq 1 - \mathbb{P}(t, N, H). \quad (6.1)$$

Here, we did not take into account the dissymmetry between the old queen that leaves with the danger of wandering and the new queen that stays inside the hive with all the wax structure already built.

Notice that Inequality (6.1) contains  $\mathbb{P}$  with no *Envir* argument. Indeed, in this setting,  $\mathbb{P}$  stands for the weighted average of survival probabilities at every point of the foam above the specified  $(H, N)$ -state (on any bubble), each point being weighted by the total sum of the weights of colonies on this particular bubble.

Let us notice that the beekeeper has one major advantage over the bee colony when it comes to estimating  $\mathbb{P}$ : he has access to meteorological predictions for the next few days. At a pivotal moment of the year such as swarming period, that means that he can anticipate swarming behavior and manage it accordingly.

## 7 Absolute prices

Harvesting honey on a colony decreases its probability of surviving. If  $\alpha$  is the market price of one bee colony, harvesting a certain quantity of honey directly costs a beekeeper  $\alpha \frac{\partial \mathbb{P}}{\partial H}$ . We elaborate on what we mean by the previous partial differential: at any given date,  $\alpha \frac{\partial \mathbb{P}}{\partial H}$  stands for the weighted average of the partial differentials of the probability of survival in the direction of  $H$  at each

point representing a colony computed in Section 5.1 on their respective bubbles. The weight of each colony in the average is the one computed in Section 5.1.

## Discussion

Our inquiry into the value of honey has led us to notice that honey represents a survival potential that can be quantified as such. While analyzing the underlying structure of the price of honey, several practical results spawn as a consequence: *When* should a beekeeper harvest honey or pollen? *When* those resources are cheap. *When* should a beekeeper feed the bees sugar or pollen? *When* those resources are most valuable. *When* should a beekeeper divide a bee colony? *When* it is about to swarm.

While our model can help answer those timing issues, it can also address the question of the geographic distribution of hives. *Where* is the most favorable location for an apiary situated? It depends on the goal. On the one hand, if the beekeeper intends to sell honey, the present model allows to sort out spots where the price of harvesting honey is low. On the other hand, a beekeeper that considers selling bee colonies can rely on the growth rate of bee colonies introduced in the present model as a more relevant metric. Another reason to choose to set up hives in a specific place is to aim at one specific flower, either for pollination purposes or to produce monofloral honey. Our study allows us to glimpse into the distribution of bees on floral resources and to confirm that the foragers do reach the target.

At larger space and time scales, the state in which a colony begins winter not only indicates if it is likely to survive winter but also suggests if it is strong enough to be used for breeding queens. Breeding new queens is a challenging matter, especially if a new queen is transported to a different region. The present model does separate the environment a colony is adapted to (that is represented by the probability foam) from the actual environment it faces so it could be applied to understanding how transporting a bee colony to a different region might affect it.

The algorithms we introduce here are currently being implemented in Python language.

## A Rescaling the heat equation

When bees are heating their winter cluster, the heat equation applies. If we assume that this

cluster is spherical and that it has reached thermal stability, we can write this equation in a dimensionless manner as:

$$\frac{1}{r^2} \frac{\partial}{\partial r} \left( r^2 \frac{\partial T}{\partial r} \right) + Q(r) = \overbrace{\frac{\partial T}{\partial t}}^{\text{stationarity}} = 0. \quad (\text{A.1})$$

Now if we change variables and replace  $r \in ]0, R]$  where  $R$  is the radius of the cluster by  $x \in ]0, 1]$ , we find:

$$Q(Rx) = -\frac{1}{R^2} \frac{\partial}{\partial x} \left( x^2 \frac{\partial T}{\partial x} \right). \quad (\text{A.2})$$

And the heat power emitted by a single bee is:

$$q_{bee} = \frac{V_{bee}}{R^2} \frac{\partial}{\partial x} \left( x^2 \frac{\partial T}{\partial x} \right), \quad (\text{A.3})$$

where  $V_{bee}$  is the volume of a bee. If the bee density is constant within the cluster,  $R$  is proportional to  $N^{\frac{1}{3}}$  and:

$$q_{bee} \propto \frac{T_{\text{center}} - T_{\text{out}}}{N^{\frac{2}{3}}}. \quad (\text{A.4})$$

As a consequence, the heat power emitted by the whole cluster is proportional to:

$$N^{\frac{1}{3}} (T_{\text{center}} - T_{\text{out}}). \quad (\text{A.5})$$

## B $\phi$ accounts for daily temperature variability as well as randomness on the boundary of winter

The parameters that influence  $\int_{\text{Start winter}}^{\text{End winter}} T_{\text{center}} - T_{\text{out}}$  during a specific winter are the beginning of winter, the end of winter and the daily temperature variation during winter.

### B.1 Variability on the boundary of winter

As regards the time when winter ends, let us first notice that the average temperature  $T$  follows a pattern

$$T(d) = (T_{\text{sum}} - T_{\text{win}}) \frac{1 - \cos\left(\frac{2\pi(d-d_0)}{365}\right)}{2} + T_{\text{win}}, \quad (\text{B.1})$$

where  $d$  is the day of the year (see Figure 6), to which a random variable is added that also

depends on the day and whose distribution is Gaussian with standard deviation  $\sigma$ .

During a given year, if  $\tau$  is a temperature reached on day  $d$ , we know that  $d$  is near  $T^{-1}(\tau)$  with a random Gaussian error with standard deviation  $\sigma \left| (T^{-1})'(\tau) \right|$ . We can compare the maximal temperature during a day to  $12^\circ\text{C}$  to decide whether this day is a winter day or not.

The beginning of winter is triggered similarly. In Dijon, the maximal daily temperature revolves around

$$T_{\text{max}}(d) = 22.5 \frac{1 - \cos\left(\frac{2\pi(d-d_0)}{365}\right)}{2} + 4.5, \quad (\text{B.2})$$

In particular, in Dijon  $\left| (T_{\text{max}}^{-1})'(12) \right| = 6.9 \text{ days } K^{-1}$  at the beginning and the end of winter and in that town the average winter is 98 days long.

To the length of actual winter, it is necessary to add the time it takes for the queen bee to rear the winter bees that will replace the summer bees.

### B.2 Daily temperature variation

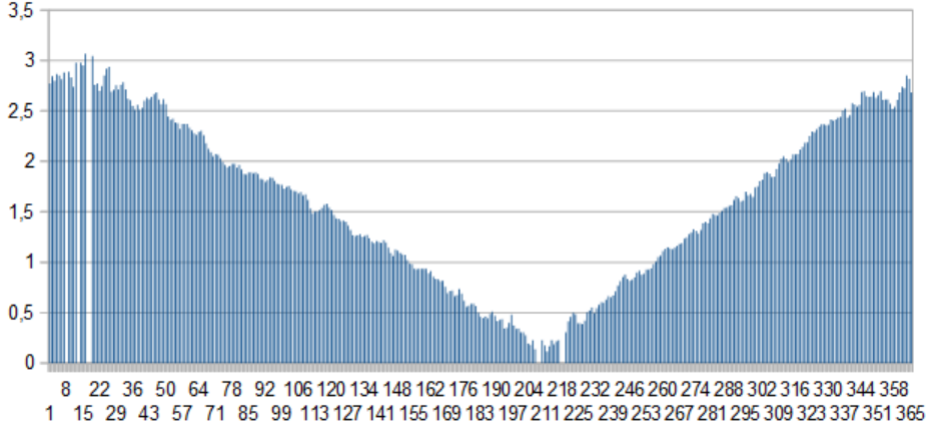
On a fixed day the randomness in temperature around the average for this day of the year can be described by a normal distribution. The question is : for how many days does a variation around the average temperature persist ?

To answer this, we compute  $Cor(n)$  the correlation between vectors  $V_0$  and  $V_n$  where  $V_0$  is the vector whose  $d$ -th coordinate (on a period lasting at least several years) records the temperature on day  $d$  from which we subtract the average temperature on that calendar day of the year, and where  $V_n$  is the vector whose  $d$ -th coordinate contains the temperature on day  $d+n$  from which we subtract the average temperature on that calendar day of the year.

The average persistence (in days) of a temperature variation around the average is then computed as

$$\int_0^1 Cor^{-1}(x) dx \quad (\text{B.3})$$

In other words, every  $\int_0^1 Cor^{-1}(x) dx$  days, one might consider that the temperature is a new independant random variable. As a consequence, if winter lasts  $W$  days, and the standard deviation of temperatures on a fixed day is  $\sigma$  then the standard deviation of the integral of temperatures during



**Figure 6:** For each day  $D$  of the year (except the 29<sup>th</sup> of february), we plot  $\arccos\left(2 * \frac{T(D)-1.5}{19.5} - 1\right)$ , where  $T(D)$  is the average temperature on day  $D$  in Dijon (between 1950 and 2022). Minimal temperatures occur around the 17<sup>th</sup> of January and maximal temperatures are to be found around the 26<sup>th</sup> of July. If there were an exact symmetry between the increasing temperature period and the decreasing temperature period, the maximum would happen on the 19<sup>th</sup> of July, which is only one week apart from the actual peak of summer.

winter is:

$$\underbrace{\sigma \int_0^1 Cor^{-1}(x)dx}_{\text{standard deviation of one block of days}} \underbrace{\sqrt{\frac{W}{\int_0^1 Cor^{-1}(x)dx}}}_{\text{square root of the number of blocks}} \quad (\text{B.4})$$

$$= \sigma \sqrt{W \int_0^1 Cor^{-1}(x)dx}. \quad (\text{B.5})$$

In the specific case study of Dijon between 1950 and 2022 that we develop throughout this paper,  $\int_0^1 Cor^{-1}(x)dx = 3.2$  days.

### B.3 Total standard deviation

Since the randomness on the quantity  $\int_{\text{Start winter}}^{\text{End winter}} T_{\text{center}} - T_{\text{out}}$  is the sum of three independent normal random variables (the first of which is the integral we consider with *fixed* winter boundaries, the second being the contribution to this integral of the uncertainty on the starting point of winter and the last one corresponding to the variability of the end of winter), the total is a Gaussian random variable whose standard deviation comes from adding up that of the three random variables as follows:

$$\mathcal{S} = \sqrt{\sigma^2 W \int_0^1 Cor^{-1}(x)dx + 2 \left( \sigma_M (T^{-1})'(\tau) (T_{\text{center}} - \tau) \right)^2}, \quad (\text{B.6})$$

where  $\sigma$  is the standard deviation of the *average* daily temperature,  $\sigma_M$  is the standard deviation of the *maximum* daily temperature and  $\tau$  is the temperature above which winter ends. If we use data from Dijon, France between 1950 and 2022, in this town,  $\sigma = 3,4K$  and if we consider that  $\sigma_M = \sigma$ , it follows that  $\mathcal{S} = 315K$  day.

## C Betting on two opposite teams simultaneously

Let us assume a player is given the choice to bet between two outcomes.

	Gain if Team 1 wins	Gain if Team 2 wins
Player bets on Team 1	a	c
Team 2	b	d

To be consistent, we impose  $b < a, c < d$ . If instead of betting all on one team, the player decides to bet  $\frac{d-b}{(a-c)+(d-b)}$  on Team 1 and  $\frac{a-c}{(a-c)+(d-b)}$  on Team 2 then the player knows he will always win  $\frac{ad-bc}{(a-c)+(d-b)}$ . This strategy is the most resilient one, as it brings at its maximum the amount that is won with certainty.

If it so happens that the amount that should be bet on one team is negative, which is the case if and only if  $a < c$  or  $d < b$ , this leads to betting

entirely on the opposite team. This corresponds to the "preparing for the worst, hoping for the best" strategy.

In the case we are studying, we translate this using the dictionary

$a$	$\mathbb{P}(t, N, H, Envir1)$
$d$	$\mathbb{P}(t, N, H, Envir2)$
$\frac{a-b}{dt}$	$(v_{Envir1} - v_{Envir2}) \mathbb{P}(t, N, H, Envir1)$
$\frac{d-c}{dt}$	$(v_{Envir2} - v_{Envir1}) \mathbb{P}(t, N, H, Envir2)$

Here,  $dt$  denotes the time it takes for the hive to realize which of the two environmental scenarios actually is taking place.

The ratio of hives that choose to bet on *Envir1* relatively to those who bet on *Envir2* is the translation of  $\frac{a-c}{d-b}$

$$\frac{\mathbb{P}_1 - \mathbb{P}_2 + dt(v_2 - v_1)\mathbb{P}_2}{\mathbb{P}_2 - \mathbb{P}_1 + dt(v_1 - v_2)\mathbb{P}_1}. \quad (C.1)$$

The previous allocation formula only makes sense (otherwise it is negative) on the codimension 1 set of points in  $(N, H)$  such that  $\mathbb{P}_1(N, H) = \mathbb{P}_2(N, H)$ , where the ratio  $\frac{a-c}{d-b}$  becomes :

$$\frac{(v_2 - v_1)\mathbb{P}_2}{(v_1 - v_2)\mathbb{P}_1}. \quad (C.2)$$

## D Wind

In Formula 2.1 it is implied that the time and the energy spent by a bee to go to a resource is proportional to the physical distance between the hive and the resource. However, wind changes the referential in which the bees actually fly. If  $\vec{V}$  represents the speed at which bees travel relatively to air and if  $\vec{w}$  is the wind speed then we can decompose the movement between the hive and the floral resource into a sum

$$\overrightarrow{HF} = t_{H \rightarrow F} (\vec{V} + \vec{w}), \quad (D.1)$$

where  $H$  is the hive and  $F$  is the floral resource (see Figure 7). In order to find the intermediate point  $I_1$  such that

$$\overrightarrow{HI_1} = t_{H \rightarrow F} \vec{V} \quad \text{and} \quad \overrightarrow{I_1F} = t_{H \rightarrow F} \vec{w} \quad (D.2)$$

we may find the intersection between the straight line that goes through  $F$  and is parallel to  $\vec{w}$ , and the circle defined as

$$\mathcal{C} = \left\{ M \in \mathbb{R}^2 \mid HM = \frac{\|\vec{V}\|}{\|\vec{w}\|} MF \right\}.$$

We proceed to introduce  $I_2$  similarly to  $I_1$  on the way back from the flowers to the hive. We then define

$$t_{flight} = t_{H \rightarrow F} + t_{F \rightarrow H} = \frac{I_1 I_2}{\|\vec{w}\|} = \frac{2}{\|\vec{w}\|} I_1 P, \quad (D.3)$$

where  $P$  is the middle of  $[I_1, I_2]$ . So that:

$$\begin{aligned} t_{flight} &= \frac{2}{\|\vec{w}\|} \sqrt{I_1 O^2 - O P^2} \\ &= \frac{2OA}{\|\vec{w}\|} \sqrt{1 - \left(\frac{OP}{OA}\right)^2} \\ &= \frac{2OA}{\|\vec{w}\|} \sqrt{1 - \left\langle \vec{u}_{HF^\perp}, \frac{\vec{w}}{\|\vec{w}\|} \right\rangle^2} \left(\frac{OF}{OA}\right)^2, \end{aligned} \quad (D.4)$$

where  $O$  is the center of  $\mathcal{C}$ ,  $\vec{u}_{HF^\perp}$  is a unitary vector that is orthogonal to  $\overrightarrow{HF}$  and  $A$  is the intersection between  $[HF]$  and  $\mathcal{C}$ . If  $B$  is the point of  $\mathcal{C}$  diametrically opposed to  $A$  as shown in Figure 7, we then have

$$\frac{FA}{AH} = \frac{\|\vec{w}\|}{\|\vec{V}\|} \quad \text{and} \quad \frac{FB}{BH} = \frac{\|\vec{w}\|}{\|\vec{V}\|}, \quad (D.5)$$

so

$$\begin{aligned} 2OA = AB = BH - AH &= \frac{\|\vec{V}\|}{\|\vec{w}\|} (FB - FA) \\ &= 2OF \frac{\|\vec{V}\|}{\|\vec{w}\|}. \end{aligned} \quad (D.6)$$

And

$$\begin{aligned} 2OA = AB = AF + FB &= \frac{\|\vec{w}\|}{\|\vec{V}\|} (AH + BH) \\ &= 2OH \frac{\|\vec{w}\|}{\|\vec{V}\|} = 2(OF + FH) \frac{\|\vec{w}\|}{\|\vec{V}\|} \end{aligned}$$

$$= 2OA \left( \frac{\|\vec{w}\|}{\|\vec{V}\|} \right)^2 + 2FH \frac{\|\vec{w}\|}{\|\vec{V}\|} \quad (\text{D.7})$$

which implies that

$$2OA = \frac{2FH \frac{\|\vec{w}\|}{\|\vec{V}\|}}{1 - \left( \frac{\|\vec{w}\|}{\|\vec{V}\|} \right)^2}. \quad (\text{D.8})$$

Finally,

$$t_{flight} = \frac{2FH \sqrt{1 - \left\langle \vec{u}_{HF^\perp}, \frac{\vec{w}}{\|\vec{V}\|} \right\rangle^2}}{\|\vec{V}\| \left( 1 - \left( \frac{\|\vec{w}\|}{\|\vec{V}\|} \right)^2 \right)}. \quad (\text{D.9})$$

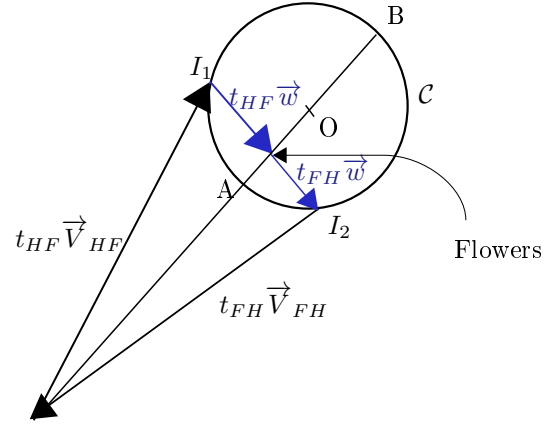
We obtained a formula giving the flight time to go back and forth between the hive and a floral resource. If  $\|\vec{w}\|$  and  $\|\vec{V}\|$  are constant, we deduce that the set of points that are at a fixed temporal distance of the hive satisfy the polar equation of an ellipse.

More generally, if  $\|\vec{V}\|$  is the speed at which foragers prefer traveling and if  $\vec{w}$  is a vector field bounded by  $\|\vec{V}\|$ , the temporal back-and-forth metric depends on  $\vec{w}$  which means that the distance between two points is Riemannian.

Notice that an other factor than wind that might contribute to the dilation of perceived distances from the foragers' perspective is the presence of pesticides in the environment that can disorient the bees.

## References

- [d'Andrimont et al. 2021] d'Andrimont, R., Verhegghen, A., Lemoine, G., Kempeneers, P., Meroni, M., van der Velde, M. (2021) *EUCROPMAP 2018*. European Commission, Joint Research Centre [Dataset] PID: <http://data.europa.eu/89h/15f86c84-eae1-4723-8e00-c1b35c8f56b9>
- [Appel and Russo 2002] Appel, M. J., Russo, R. P. (2002). *The connectivity of a graph on uniform points on  $[0, 1]^d$* . Statistics and Probability Letters, 60(4), 351-357.
- [Ausseuil et al. 2018] Ausseuil, A. G. E., Dymond, J. R., Newstrom, L. (2018). *Mapping*



Hive

**Figure 7:** Decomposition of the movement between the flowers and the hive in its part due to the wind and its part due to the effort of the bee

*floral resources for honey bees in New Zealand at the catchment scale*. Ecological applications, 28(5), 1182-1196. <https://doi.org/10.1002/eap.1717>

- [Baude et al. 2016] Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A., Morton, R.D., Smart, S.M., Memmott, J. (2016). *Historical nectar assessment reveals the fall and rise of floral resources in Britain*. Nature, 530(7588), 85-88. <https://doi.org/10.1038/nature16532>
- [Baude et al. 2025] Baude, M., Kunin, W., Davies, N., Wright, E., Memmott, J. (2025). *A dataset of pollen production for 168 common flowering plants in the United Kingdom*. Ecological Solutions and Evidence, 6(2).
- [Beekman and Ratnieks 2000] Beekman, M., Ratnieks, F. L. W. (2000). *Long-range foraging by the honey-bee, Apis mellifera L.* Functional Ecology, 14(4), 490-496. <https://doi.org/10.1046/j.1365-2435.2000.00443.x>
- [Chabert et al. 2024] Chabert, S., Morison, N., Buffière, M-J., Guilbaud, L., Pleindoux, C., de Premorel, G., Royer, P., Harruis, M., Vaissière, B. E., (2024) *Supplementing honey bee (Hymenoptera: Apidae) colonies with pollen increases their pollinating activity on nectariferous crops with anthers isolated from stigmas* Journal of Economic Entomology, Volume 117, Issue 1, Pages 43–57, <https://doi.org/10.1093/jee/toad222>

- [Champetier et al. 2015] Champetier, A., Sumner, D. A, Wilen, J. E. (2015) *The bioeconomics of honey bees and pollination*. Environmental and Resource Economics, 60, 143-164.
- [Chu 1955] Chu, J. T. (1955). *On bounds for the normal integral*. Biometrika, 42(1/2), 263-265.
- [Clement and Le Conte et al. 2018] Clement, H. (directeur d'ouvrage), Le Conte, Y. (chapitre 2) et al. (2018). *Le traité rustica de l'apiculture, chapitre 2 : la vie sociale de la colonie*. ISBN 978-2-8153-1267-7
- [Colin et al. 2022] Colin, Théotime, Warren, Ryan J., Quarrell, Stephen R., Allen, Geoff R., and Barron, Andrew B. (2022). *Evaluating the Foraging Performance of Individual Honey Bees in Different Environments with Automated Field RFID Systems*. Ecosphere, 13(5): e4088. <https://doi.org/10.1002/ecs2.4088>
- [Cook et al. 2021] Cook, D., Blackler, A., McGree, J., Hauxwell, C. (2021). *Thermal impacts of apicultural practice and products on the honey bee colony*. Journal of Economic Entomology, 114(2), 538-546.
- [Desfonds and Garcia De Cortazar Atauri 2020] Desfonds, V. and Garcia De Cortazar Atauri, I. (2020) *Phenology Data - UMR EMMAH - INRAE - BDD PHETEC V3* Recherche Data Gouv <https://doi.org/10.15454/CLYPS4>
- [Di Pasquale et al. 2013] Di Pasquale G, Salignon M, Le Conte Y, Belzunces LP, Decourtye A, Kretzschmar A, et al. (2013). *Influence of Pollen Nutrition on Honey Bee Health: Do Pollen Quality and Diversity Matter?* PLoS ONE, <https://doi.org/10.1371/journal.pone.0072016>
- [Döcke et al. 2019] Döke, M. A., McGrady, C. M., Otieno, M., Grozinger, C. M., Frazier, M. (2019). Colony size, rather than geographic origin of stocks, predicts overwintering success in honey bees (Hymenoptera: Apidae) in the Northeastern United States. Journal of Economic Entomology, 112(2), 525-533. <https://doi.org/10.1093/jee/toy377>
- [ECJRC 2022] European Commission, Joint Research Centre (JRC) (2022) *EU-CROPMap 2022*. European Commission, Joint Research Centre [Dataset] PID: <http://data.europa.eu/89h/555e5d1d-1aae-4320-a716-2e6d18aa1e7c>
- [Fewell et al. 1991] Fewell, J. H., Ydenberg, R. C., Winston, M. L. (1991). *Individual foraging effort as a function of colony population in the honey bee, Apis mellifera L.* Animal behaviour, 42(1), 153-155. [https://doi.org/10.1016/S0003-3472\(05\)80618-9](https://doi.org/10.1016/S0003-3472(05)80618-9)
- [Free and Racey 1968] Free, J. B., Racey, P. A. (1968). *The effect of the size of honeybee colonies on food consumption, brood rearing and the longevity of the bees during winter*. Entomologia Experimentalis et Applicata, 11(2), 241-249.
- [Greenleaf et al. 2007] Greenleaf, S.S., Williams, N.M., Winfree, R. et al. (2007). *Bee foraging ranges and their relationship to body size*. Oecologia, 589-596 <https://doi.org/10.1007/s00442-007-0752-9>
- [INRIA 2018] INRA (2018). *Base de Données Géographique des Sols de France à 1/1 000 000 version 3.2.8.0, 10/09/1998* <https://doi.org/10.15454/BPN57S>,
- [Kohli and Anstett] Kohli, M., Anstett, M.C. *A mathematical modelization of the energy content of an Apis mellifera beehive*. Manuscript to be submitted.
- [Kohli 2025] Kohli, M. (2025). *ApiThriveModel*. Zenodo. <https://doi.org/10.5281/zenodo.16105253>
- [Kovac et al. 2007] Kovac, H., Stabentheiner, A., Hetz, S. K., Petz, M., Crailsheim, K. (2007). *Respiration of resting honeybees*. Journal of insect physiology 53(12), 1250-1261. <https://doi.org/10.1016/j.jinsphys.2007.06.019>
- [Mitchell 2019] Mitchell, D. (2019). *Thermal efficiency extends distance and variety for honeybee foragers: analysis of the energetics of nectar collection and desiccation by Apis mellifera*. Journal of the Royal Society Interface, 16(150), 20180879 <https://doi.org/10.1098/rsif.2018.0879>
- [Myerscough 1993] Myerscough, M. R. (1993). *A simple model for temperature regulation in honeybee swarms*. Journal of Theoretical Biology, 162(3), 381-393. <https://doi.org/10.1006/jtbi.1993.1094>
- [Nachtigall et al. 1995] Nachtigall, W., Hanauer-Thieser, U., Mörz, M. (1995). *Flight*

*of the honey bee VII: metabolic power versus flight speed relation.* Journal of Comparative Physiology B, 165, 484-489. <https://doi.org/10.1007/BF00261303>

[Ocko and Mahadevan 2014] Ocko, S. A., Mahadevan, L. (2014). *Collective thermoregulation in bee clusters.* Journal of The Royal Society Interface, 11(91), 20131033 <https://doi.org/10.1098/rsif.2013.1033>

[Omholt and Lonvik 1986] Omholt, S. W., Lønvik, K. (1986). *Heat production in the winter cluster of the honeybee, Apis mellifera. A theoretical study.* Journal of theoretical biology, 120(4), 447-456. [https://doi.org/10.1016/S0022-5193\(86\)80038-8](https://doi.org/10.1016/S0022-5193(86)80038-8)

[Polya 1949] Pólya, G. (1949). *Remarks on computing the probability integral in one and two dimensions.* Proceedings of the Berkeley Symposium on Mathematical Statistics and Probability (No. 1, p. 63). Berkeley: University of California Press.

[Ratnieks and Shackleton 2015] Ratnieks Francis L. W., Shackleton Kyle (2015) *Does the waggle dance help honey bees to forage at greater distances than expected for their body size?* Frontiers in Ecology and Evolution. <https://doi.org/10.3389/fevo.2015.00031>

[Rodney and Purdy 2020] Rodney, S., and Purdy, J. (2020) *Dietary requirements of individual nectar foragers, and colony-level pollen and nectar consumption: a review to support pesticide exposure assessment for honey bees.* Apidologie 51(2), 163-179. <https://doi.org/10.1007/s13592-019-00694-9>

[Stabentheiner 2021] Stabentheiner, A., Kovac, H., Mandl, M., Käfer, H. (2021). *Coping with the cold and fighting the heat: thermal homeostasis of a superorganism, the honeybee colony.* Journal of Comparative Physiology A 207(3), 337-351. <https://doi.org/10.1007/s00359-021-01464-8>