

Forum Paper

Author-formatted document posted on 05/04/2024

Published in a RIO article collection by decision of the collection editors.

DOI: <https://doi.org/10.3897/arphapreprints.e124639>

Prototype Biodiversity Digital Twin: Honey Bees in Agricultural Landscapes

Jürgen Groeneveld,  Tomáš Martinovič,  Tuomas Rossi,  Ondrej Salamon, Kata Sara-aho, 
Volker Grimm

1 Prototype Biodiversity Digital Twin: Honey Bees in Agricultural 2 Landscapes

3

4 Jürgen Groeneveld¹⁾, Tomas Martinovic²⁾, Tuomas Rossi³⁾, Ondrej Salamon²⁾, Kata Sara-aho³⁾,
5 Volker Grimm^{1,4,5)}

6

7 ¹⁾Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling, Permoserstr. 15,
8 04318 Leipzig, Germany; <https://orcid.org/0000-0003-2338-4636>

9 ²⁾IT4Innovations, VSB – Technical University of Ostrava, 17. listopadu 2172/15, 708 00 Ostrava-Poruba, Czech
10 Republic

11 ³⁾CSC – IT Center for Science Ltd., P.O. Box 405, 02101 Espoo, Finland

12 ⁴⁾University of Potsdam, Plant Ecology and Nature Conservation, Zeppelinstraße 48 A, 14471 Potsdam, Germany;
13 ORCID: 0000-0002-3221-9512

14 ⁵⁾German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig,
15 Germany

16 Abstract

17 Honey bees are vital to human well-being and are under multiple stresses. We need to be able to
18 assess the viability and productivity of honey bee colonies in different landscapes and under
19 different management and climate change scenarios. We have developed a prototype digital
20 twin, HONEYBEE-pDT, based on the BEEHAVE model, which simulates foraging, population
21 dynamics and *Varroa* mite infestation of a single honey bee colony. The main input data are land
22 cover maps and daily weather data. Users can run the pDT for a specific site or for larger areas,
23 up to the whole of Germany. Hive weight data from hundreds of hives will be used for calibration
24 and validation.

25 Keywords

26 Pollination, biodiversity, honey bees, multiple stressors, agricultural landscapes, resilience

27 Introduction

28 Pollinators are ubiquitous in ecosystems and play a critical role in our food supply, although the
29 risks of their decline, including to biodiversity, are not fully understood. Of particular importance
30 for crop pollination (Garibaldi et al. 2013) and wild plant biodiversity are honey bees (*Apis*
31 *mellifera*; Potts et al. 2016). Despite being a managed species, they are severely affected by
32 climate change, emerging parasites and diseases, modern agricultural land use and possibly
33 inappropriate beekeeping practices. In Europe, winter colony losses have increased to nearly 20%
34 in recent decades (Gray et al. 2022), and in the USA, annual losses can reach 50% (Steinhauer et
35 al. 2021).

36 While single stressors, such as modern pesticides, may play an important role, the current general
37 consensus is that the combination of multiple stressors impairs the resilience of honey bee

38 colonies. Even if each stressor has no detectable effect at the colony level, their combination can
39 lead to colony mortality (Henry et al. 2017). However, empirically quantifying the effects of
40 stressors and their combination on honey bees is challenging. Bee colonies, even from the same
41 apiary, show large variation in behaviour, which would require a large number of replications. In
42 addition, most stressors, such as extreme weather, gaps in forage availability or parasites and
43 pathogens, are virtually impossible to control.

44 Numerous simulation models have therefore been developed to support and extrapolate
45 empirical research (Becher et al. 2013, Chen et al. 2021, EFSA et al. 2021), but so far only one of
46 these, BEEHAVE (Becher et al. 2014), appears to be both available and able to link within-hive
47 dynamics with foraging in a dynamic agricultural landscape (EFSA et al. 2021).

48 BEEHAVE is a typical high-resolution ecological model: it has a relatively small spatial extent. It
49 represents only the landscape around a single hive, i.e. 5 x 5 km². As such, it cannot be used to
50 assess the status of honey bees and their habitat across regions, countries or beyond. Existing
51 workflows for BEEHAVE rely on maps of fields and crops in the surrounding landscape, which are
52 rarely available, as are data to test model predictions of colony performance. BEEHAVE has been
53 used in more than 25 studies (Appendix I), but its use to support policy development at national
54 or European level has been limited. Such policies include important aspects of the Common
55 Agricultural Policy (CAP) of the European Communities. To support the development of such
56 policies, but also to assist farmers and beekeepers and their associations in developing
57 sustainable and biodiversity-friendly practices, it would be necessary to extend the scope and
58 predictive power of BEEHAVE towards a Digital Twin (DT), taking into account the specific
59 challenges of developing a DT for biodiversity conservation (Koning et al. 2023).

60 Objectives

61 As a first step, a prototype DT, HONEYBEE-pDT, will be developed to enable the automated
62 application of the BEEHAVE model for the whole of Germany. This includes two types of
63 applications. First, to produce maps of Germany that visualise, for example, the number of adult
64 bees before winter or the amount of honey that has been produced during a year. Therefore,
65 BEEHAVE is run on a raster with a resolution of 5 km. Second, to run BEEHAVE for specific hive
66 locations, users only need to specify the coordinates of the hive. The users can also modify the
67 model parameters and the parameters of the floral resources. HONEYBEE-pDT can be run via a
68 web interface on supercomputers such as LUMI hosted by CSC - IT Centre for Science in Finland
69 or on cloud environments. The pDT can also be used for education and training in sustainable
70 practices.

71 Workflow

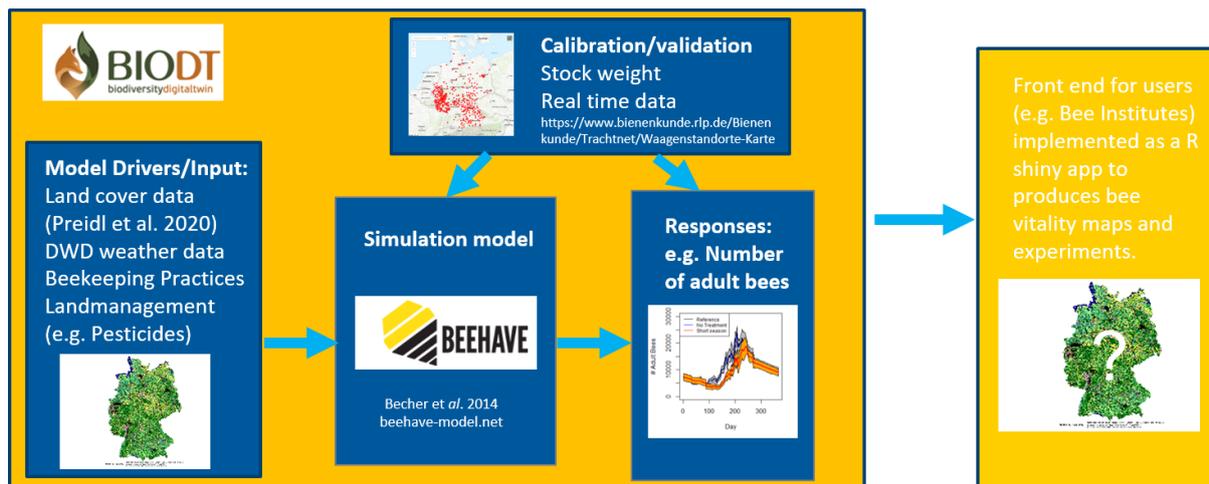


Fig. 1. Overview of the prototype HONEYBEE-pDT (see text for details).

72
73

74

75 Figure 1 provides an overview of the HONEYBEE-pDT. The user GUI is implemented as an R Shiny
76 application and the workflow is executed using LEXIS (Golasowski et al. 2022). Scripts have been
77 developed to specify the input data (drivers: land cover data and weather data) and to transform
78 the input data into input files that can be read into the BEEHAVE simulation model. The input of
79 weather data is done using the R package *rdwd*. The simulation experiments are also specified
80 and executed by an R script using the *nrx* package (Salecker et al. 2019). The execution of the
81 HONEYBEE-pDT has been parallelized to take advantage of high performance computing
82 capabilities as described in the Performance section. The HONEYBEE-pDT can be applied to other
83 countries where data on land cover, conversion of land use type to nectar and pollen resources,
84 and weather data are available.

85

86 Data

87 The pDT requires land cover data, weather data and the specification of model parameters and
88 flower resource parameters. In the pDT, the land cover data is based on a map by Preidl and
89 colleagues (2020), which provides information on 19 different land use types, e.g. crops such as
90 oilseed rape or grassland. The data are freely available on the Pangea server
91 (<https://doi.org/10.1594/PANGAEA.910837>). The data comes as raster data and needs to be
92 converted into polygons for our application. We use the R package *terra* to manipulate the land
93 use data (<https://cran.r-project.org/web/packages/terra/index.html>. As requested on 21
94 December 2022). The conversion of land cover types into floral resources is done by a lookup
95 table that can be specified by the user; default values will be provided based on previous
96 BEEHAVE applications. We request weather data using an API provided by the R package *rdwd*
97 (<https://cran.r-project.org/web/packages/rdwd/index.html>. As requested on 21 December 2022).
98 Daily sunshine hours and daily maximum temperatures from the nearest DWD weather station
99 are requested and converted into daily foraging hours. The weather data are freely available.
100 There are data gaps in the DWD data, so we plan to replace the DWD data input with another
101 product using the building block to download data from the Copernicus platform
102 (<https://cds.climate.copernicus.eu/>). Other input options, such as beekeeping practices, can be

103 customised by the user. In addition to the input data, it is planned to use monitoring data from
104 the TrachNet project (Otten and Berg 2018, Johannesen et al. 2022), where weight changes of
105 more than 500 hives in Germany are recorded. These data will be used for calibration and
106 validation. Currently, the data can be accessed by anyone via a web interface. Access through this
107 web interface is not feasible within this project, as it would require a manual download. The host
108 of the data has provided us with the full data set. We plan to develop a workflow to request
109 subsets of this data. The automatic download procedure will be used internally in the beginning,
110 but it is intended to make the data and data requests available to everyone.

111 So far, HONEYBEE-pDT is limited to Germany, but the workflows can be applied to other
112 countries if the relevant data, such as land cover maps, are available.

113 Model

114 BEEHAVE (Becher et al. 2014) is a simulation model implemented in NetLogo (Wilensky 1999) and
115 is freely available (<https://beehave-model.net>). BEEHAVE consists of three modules: colony,
116 foraging and mite module. The colony module runs with daily time steps. It describes age cohorts
117 of larvae, worker bees and drones. These dynamics are driven by the daily egg laying rate of the
118 queen, which is imposed by a hump-shaped distribution with a maximum in early summer.

119 The foraging module is agent-based, with one agent representing 100 bees. It simulates the
120 foraging behaviour of bees, including scouting for new rewarding floral resources in the
121 landscape and recruiting foragers via a waggle dance that communicates the foraging efficiency
122 of particular flower fields. Foragers collect nectar and pollen in the given landscape, but only
123 when the weather permits. The temporal resolution of the foraging module is implicit and takes
124 into account flight and handling time in seconds.

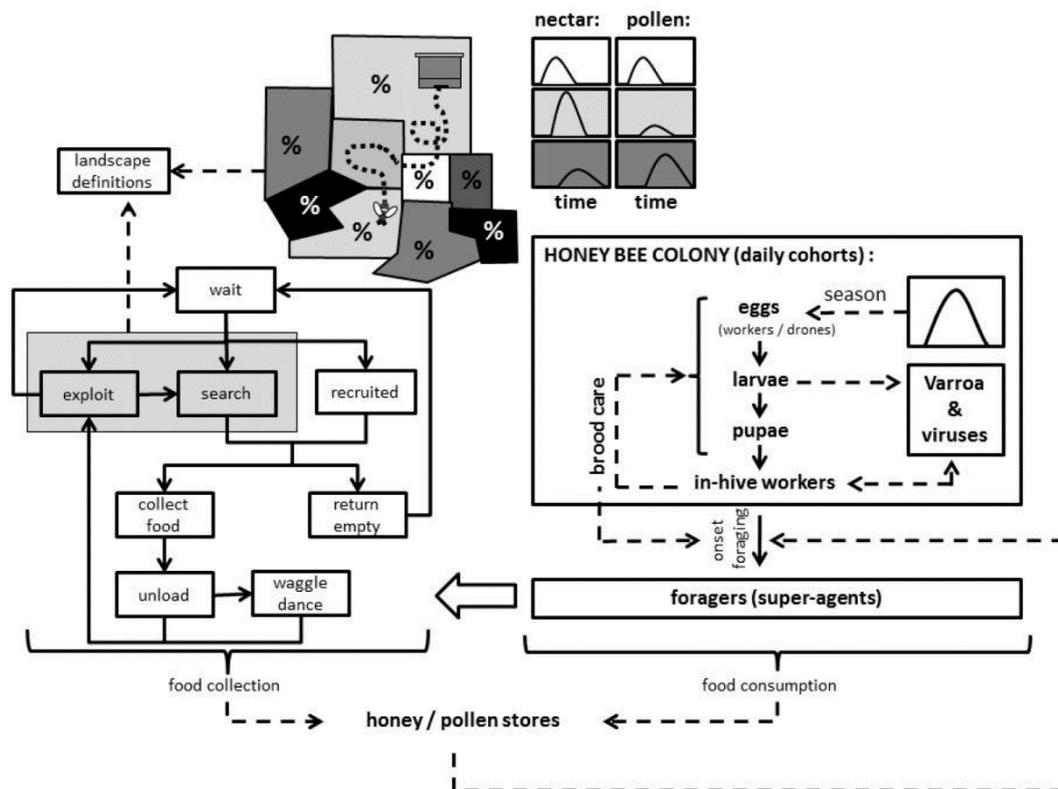
125 The mite model represents the dynamics of the Varroa mite population in the hive. Mites can be
126 either inside the brood cells or phoretic, i.e. attached to an adult bee. Mites transmit viruses that
127 increase the mortality of infected larvae or adult bees. The mite module includes optional control
128 measures, such as treatment with acaricides. Other optional beekeeping practices include honey
129 harvesting and swarm control.

130 BEEHAVE can be run with stylized settings for theoretical studies, i.e. all floral resources in the
131 landscape are represented by two resource patches not representing a real landscape. However,
132 it is also possible to import landcover and weather data for specific locations and years. The
133 landscape is represented as a list of fields, or patches, that provide nectar and/or pollen sooner
134 or later in the year. Each patch is characterized by its distance from the hive, the likelihood of
135 detection by foragers, the flowering period, the nectar and pollen supply and the handling time
136 for the bees. The latter increases with increasing use of the patch, i.e. the foraging efficiency, for
137 example, the resources of a patch can change over the course of a day. Weather data on
138 temperature and rainfall are converted into the number of foraging hours per day, as bees do not
139 forage in rain and low temperatures. BEEHAVE comes with example data sets for a landscape in
140 England. The input file for BEEHAVE is a text file that can be compiled manually or using the
141 software tool BEESCOUT (Becher et al. 2016). The BEEHAVE implementation
142 `Beehave_BeeMapp2015` (<https://beehave-model.net>), includes additional features for setting up
143 the model; this is the version used for the digital twin prototype presented here.

144 BEEHAVE was implemented in NetLogo (Wilensky 1999), a software platform and programming
145 language based on Java and Scala. NetLogo is specifically designed for implementing agent-

146 based models and provides tools for assembling a graphical user interface (GUI). Both BEEHAVE
 147 and NetLogo are freely available on the Internet and run on all major operating systems.
 148 BEEHAVE comes with detailed documentation of the model in ODD format (Grimm et al. 2020)
 149 and its code, as well as a tutorial and user manual. It has been used in more than 20 studies
 150 (Appendix 1).

151 Figure 2 provides an overview of the main model components of BEEHAVE: foraging,
 152 demographics of honey bees and Varroa mites. Please note that the user of the pDT will not
 153 interact with BEEHAVE directly, but through the BioDT GUI.



154
 155
 156 Fig. 2: Overview of the BEEHAVE model from the model description (ODD protocol).

157 FAIRness

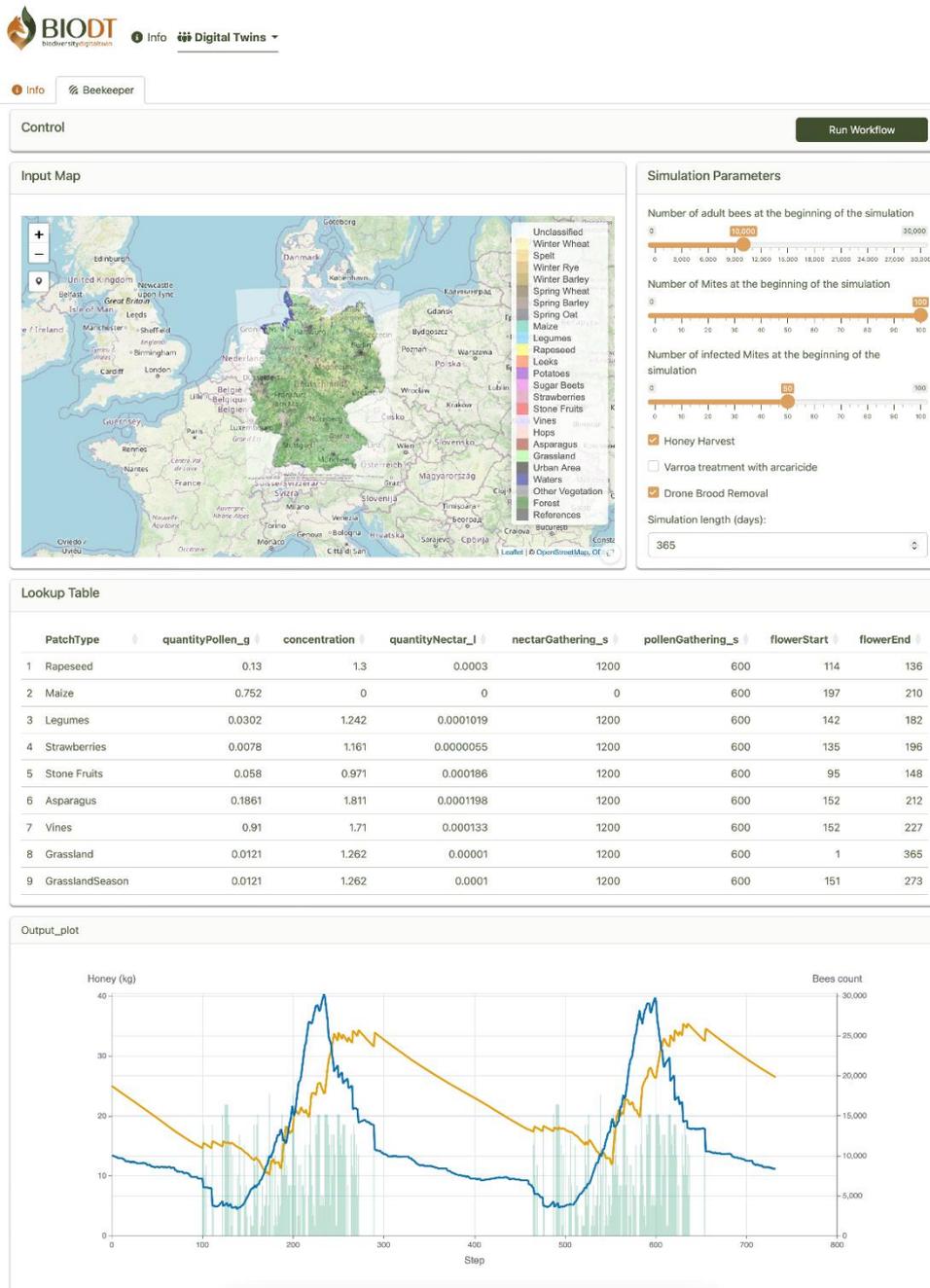
158 The BEEHAVE model is well documented and freely accessible. The BEEHAVE version used and all
 159 developed scripts are published as open source on the BioDT GitHub repository
 160 (<https://github.com/BioDT>). All input data is freely available (see DATA for details). Currently
 161 model outcomes of the HONEYBEE-pDT will not be stored and its up to the user how to manage
 162 the data.

163 Performance

164 The simulation experiments are specified and executed by R scripts using the *nlr*x package
165 (Salecker et al. 2019). The software required for executing the model (NetLogo, Java, R with *nlr*x
166 and other packages) have been bundled in a Docker container image that can be pulled and
167 executed on the CPU partition of the LUMI supercomputer through Apptainer / Singularity and
168 on a cloud through Docker. The execution of the containerized BEEHAVE model has been
169 parallelized on LUMI over individual inputs by using HyperQueue task scheduler. As an
170 exploratory study, we used the pDT to predict the number of surviving bees and honey storage
171 using a regular grid spanning around 3500 locations in Germany, based on the surrounding land
172 cover types and weather data. By utilizing the developed parallelization scheme, this calculation
173 took about an hour on eight LUMI-C nodes. As a rough estimate, the same calculation would
174 have taken more than a week on a regular laptop. While the run configuration on LUMI requires
175 still optimization for maximum efficiency, it is clear that the capability to execute the pDT in
176 parallel over hundreds or thousands of cores and to leverage the large computing capacity of
177 LUMI-C is highly advantageous. The containerized solution here provides also cleanly deployable
178 environment for the pDT and directly enables also execution on cloud environment for the
179 workloads that do not need extensive computing resources.

180 Interface and outputs

181 The communication between the user and the pDT is done by a R shiny application. The user can
182 vary parameters of the model and the floral resources. In addition, a location within Germany can
183 be chosen. As outputs the number of adult bees, honey production and flight time are visualized.
184 A screenshot of the GUI for the site specific application is shown in Figure 3.



185

186 Figure 3: Screenshot of GUI of the HONEYBEE-pDT

187

188 **Integration and sustainability**

189 During the duration of the project we already have run the pDT on different HPCs (LUMI and
 190 Karolina). Thus, in principle the pDT can easily move places. One option after the end of the
 191 project is to host the HONEYBEE-pDT using resources from the Helmholtz Association to which
 192 the first and the senior authors of this paper are belonging to.

193 The HONEYBEE-pDT would benefit from links with other DT initiatives such as DestineE and EOSC,
194 as information on extreme events, droughts and other environmental information is crucial for
195 reliable prediction of honey bee flight and foraging behaviour. It would also be beneficial to
196 attempt to link the HONEYBEEpDT with DTs of vegetation DTs such as the GRASSMIND DT.

197 Application and impact

198 The prototype presented here, HONEYBEE-pDT, demonstrates the concept of a digital twin for
199 supporting two important aspects of biodiversity conservation, pollination and agricultural land
200 use. DTs are intended to support decisions in a more robust and relevant way than traditional
201 models. The two defining characteristics of DTs are that (1) their inputs are regularly updated and
202 their outputs are regularly compared to new monitoring data for calibration and validation, and
203 (2) they cover spatial scales that are relevant to stakeholders, including farmers and policy
204 makers.

205 Turning a simulation model such as BEEHAVE into a DT requires infrastructure and expertise far
206 beyond that typically available for modellers. Expertise was required to create data structures and
207 workflows for key relevant input data, to create workflows for running BEEHAVE in parallel on a
208 supercomputer, to containerise these workflows and the many complex software tools required,
209 and to create a professional GUI. The infrastructure required to run BEEHAVE at all relevant spatial
210 scales was a supercomputer such as LUMI. While the modellers involved would not have had the
211 time and expertise to create HONEYBEE-pDT on their own, the data and computer scientists
212 involved would not have been able to take a model like BEEHAVE off the shelf and plug it into
213 their workflows and infrastructure, as this would have required expertise in modelling and honey
214 bee ecology.

215 Certainly, frequent meetings and updates were needed to develop a mutual understanding of all
216 the elements of the pDT, but the effort was well worth it, as the results and the prospect of the
217 final, fully implemented DT far exceeded our expectations. Biodiversity modellers have always
218 struggled with the choice between large-scale models that are too unrealistic at the local scale,
219 and small-scale models that are realistic but too small in scale to be useful for supporting
220 management and policy development. HONEYBEE-pDT was an important milestone in the
221 adoption of the concept of DTs for biodiversity research, management and conservation (De
222 Koning et al. 2023). This will enable a wide range of applications with highly relevant impacts.

223 HONEYBEE-pDT is aimed at different end-users. Firstly, we want beekeepers to simulate a virtual
224 honey bee colony at a location of interest to them and compare the simulation results with their
225 own experience and give us feedback. As it is difficult for us in the academic world to reach the
226 practitioners, we work closely with the German bee institutes and present at their annual
227 meetings. We have also organised workshops and training on the BEEHAVE model to disseminate
228 our tools. As a second target group we have identified other researchers. At our user workshop in
229 Leipzig in November we realised that we need to allow them to upload customised versions of
230 the BEEHAVE simulation model so that they can use the pDT for their work. The same goes for
231 the third target group, industry. Companies such as Bayer also use BEEHAVE and may be
232 interested in using a service such as the HONEYBEE-pDT, but they would want to use their own
233 version of BEEHAVE, which includes a pesticide exposure and effects module (Preuss et al. 2022).
234 In theory, -pDT can also be used by national and European policy makers to optimise CAP

235 greening scenarios, by farmers and their associations to develop biodiversity-friendly cropping
236 systems and pesticide use, and by beekeepers and their associations to optimise beekeeping
237 practices, in particular *Varroa* mite control.

238 Acknowledgements

239 This study has received funding from the European Union's Horizon Europe research and
240 innovation programme under grant agreement No 101057437 (BioDT project,
241 <https://doi.org/10.3030/101057437>). Views and opinions expressed are those of the author(s)
242 only and do not necessarily reflect those of the European Union or the European Commission.
243 Neither the European Union nor the European Commission can be held responsible for them. We
244 acknowledge the EuroHPC Joint Undertaking for awarding this project access to the EuroHPC
245 supercomputer LUMI, hosted by CSC (Finland) and the LUMI consortium through a EuroHPC
246 Development Access call (<https://www.lumi-supercomputer.eu/acknowledgement>). This work was
247 supported by the Ministry of Education, Youth and Sports of the Czech Republic through the e-
248 INFRA CZ (ID:90254). We also acknowledge CSC – IT Center for Science, Finland, for
249 computational resources. We acknowledge IT4Innovations National Supercomputing Center and
250 the use of Karolina (<https://www.it4i.cz/pro-uzivatele/povinnosti-uzivatele>).

251 Reference

252

253 Becher, M. A., Osborne, J. L., Thorbek, P., Kennedy, P. J., & Grimm, V. (2013). Towards a systems
254 approach for understanding honeybee decline: a stocktaking and synthesis of existing models.
255 *Journal of Applied Ecology*, 50(4), 868-880.

256 Becher, M. A., et al. (2014). BEEHAVE: a systems model of honeybee colony dynamics and
257 foraging to explore multifactorial causes of colony failure. *Journal of Applied Ecology* 51(2): 470-
258 482.

259 Becher, M. A., Grimm, V., Knapp, J., Horn, J., Twiston-Davies, G., & Osborne, J. L. (2016).
260 BEESCOUT: A model of bee scouting behaviour and a software tool for characterizing
261 nectar/pollen landscapes for BEEHAVE. *Ecological modelling*, 340, 126-133.

262 Chen, J., DeGrandi-Hoffman, G., Ratti, V., & Kang, Y. (2021). Review on mathematical modeling of
263 honeybee population dynamics. *Mathematical Biosciences and Engineering*, 18(6).

264 EFSA (European Food Safety Authority), Ippolito A, Focks A, Rundlöf M, Arce A, Marchesi M, Neri
265 FM, Szentes Cs, Rortais A and Auteri D, 2021. Analysis of background variability of honey bee
266 colony size. EFSA supporting publication 2021:EN-6518. 79 pp. doi:10.2903/sp.efsa.2021.EN-6518

267 Garibaldi, L. A., et al. (2013). "Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee
268 Abundance." *Science* 339(6127): 1608.

269 Golasowski, Martin, et al. (2022). The LEXIS platform for distributed workflow execution and data
270 management. *HPC, Big Data, and AI Convergence Towards Exascale*. Taylor & Francis, 2022.

271 Gray, A., et al. (2022). Honey bee colony loss rates in 37 countries using the COLOSS survey for winter
272 2019-2020: the combined effects of operation size, migration and queen replacement. *Journal of*
273 *Apicultural Research*.

274 Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., DeAngelis, D. L., ... & Ayllón, D.
275 (2020). The ODD protocol for describing agent-based and other simulation models: A second

- 276 update to improve clarity, replication, and structural realism. *Journal of Artificial Societies and*
277 *Social Simulation*, 23(2).
- 278 Henry, M., Becher, M. A., Osborne, J. L., Kennedy, P. J., Aupinel, P., Bretagnolle, V., ... & Requier, F.
279 (2017). Predictive systems models can help elucidate bee declines driven by multiple combined
280 stressors. *Apidologie*, 48(3), 328-339.
- 281 Johannesen, J., Wöhl, S., Berg, S., & Otten, C. (2022). Annual fluctuations in winter colony losses of
282 *Apis mellifera* L. are predicted by honey flow dynamics of the preceding year. *Insects*, 13(9), 829.
- 283 de Koning, K., Broekhuijsen, J., Kühn, I., Ovaskainen, O., Taubert, F., Endresen, D., ... & Grimm, V.
284 (2023). Digital twins: dynamic model-data fusion for ecology. *Trends in Ecology & Evolution*.
- 285 Otten, C.; Berg, S. TrachtNet 5.0—Die Bundesweite elektronische Trachtbeobachtung ist für jeden
286 nutzbar (2018) *Bienen Nat.* 18–19.
- 287 Potts, S. G., et al. (2016). "Safeguarding pollinators and their values to human well-being." *Nature*
288 540(7632): 220-229.
- 289 Preidl, S., Lange, M., & Doktor, D. (2020). Introducing APiC for regionalised land cover mapping
290 on the national scale using Sentinel-2A imagery. *Remote Sensing of Environment*, 240, 111673.
- 291 Preuss, T. G., Agatz, A., Goussen, B., Roeben, V., Rumkee, J., Zakharova, L., & Thorbek, P. (2022).
292 The BEEHAVEecotox Model—Integrating a Mechanistic Effect Module into the Honeybee Colony
293 Model. *Environmental Toxicology and Chemistry*, 41(11), 2870-2882.
- 294 Salecker, J., Sciaini, M., Meyer, K. M., & Wiegand, K. (2019). The nlr r package: A next-generation
295 framework for reproducible NetLogo model analyses. *Methods in Ecology and Evolution*, 10(11),
296 1854-1863.
- 297 Steinhauer, N., et al. (2021). Prioritizing changes in management practices associated with
298 reduced winter honey bee colony losses for US beekeepers. *Science of the Total Environment* 753.
- 299 Wilensky, U. (1999). NetLogo. Center for Connected Learning and Computer-based Modeling,
300 Northwestern University. Evanston, IL.
- 301
- 302

303

304 Appendix Table S1: List of all BEEHAVE applications.

305

306

-
- 307 1. Becher, M.A., Grimm, V., Thorbek, P., Horn, J., Kennedy, P.J., Osborne, J.L., 2014. **BEEHAVE: a**
 308 **systems model of honeybee colony dynamics and foraging to explore multifactorial causes of**
 309 **colony failure**. *Journal of Applied Ecology* 51(2) 470-482.
- 310 2. Rumke, J.C., Becher, M.A., Thorbek, P., Kennedy, P.J., Osborne, J.L., 2015. **Predicting honeybee**
 311 **colony failure: Using the BEEHAVE model to simulate colony responses to pesticides**.
 312 *Environmental Science & Technology* 49(21) 12879-12887.
- 313 3. Horn, J., Becher, M.A., Kennedy, P.J., Osborne, J.L., Grimm, V., 2016. **Multiple stressors: using**
 314 **the honeybee model BEEHAVE to explore how spatial and temporal forage stress affects**
 315 **colony resilience**. *Oikos* 125(7) 1001-1016.
- 316 4. McMahon, D.P., Natsopoulou, M.E., Doublet, V., Fürst, M., Waging, S., Brown, M.J., Gogol-
 317 Döring, A., Paxton, R.J., 2016. **Elevated virulence of an emerging viral genotype as a driver of**
 318 **honeybee loss**. *Proceedings of the Royal Society B: Biological Sciences* 283(1833) 20160811.
- 319 5. Henry, M., Becher, M.A., Osborne, J.L., Kennedy, P.J., Aupinel, P., Bretagnolle, V., Brun, F.,
 320 Grimm, V., Horn, J., Requier, F., 2017. **Predictive systems models can help elucidate bee**
 321 **declines driven by multiple combined stressors**. *Apidologie* 48(3) 328–339.
- 322 6. Thorbek, P., Campbell, P.J., Sweeney, P.J., Thompson, H.M., 2017a. **Using BEEHAVE to explore**
 323 **pesticide protection goals for European honeybee (*Apis mellifera* L.) worker losses at different**
 324 **forage qualities**. *Environmental Toxicology and Chemistry* 36(1) 254-264.
- 325 7. Thorbek, P., Campbell, P.J., Thompson, H.M., 2017b. **Colony impact of pesticide-induced**
 326 **sublethal effects on honeybee workers: A simulation study using BEEHAVE**. *Environmental*
 327 *Toxicology and Chemistry* 36(3) 831-840.
- 328 8. Agatz, A., Kuhl, R., Miles, M., Schad, T., Preuss, T.G., 2019. **An evaluation of the BEEHAVE model**
 329 **using honey bee field study data: Insights and recommendations**. *Environmental Toxicology*
 330 *and Chemistry* 38(11) 2535-2545.
- 331 9. Prado, A., Pioz, M., Vidau, C., Requier, F., Jury, M., Crauser, D., Brunet, J.-L., Le Conte, Y., Alaux,
 332 C., 2019. **Exposure to pollen-bound pesticide mixtures induces longer-lived but less efficient**
 333 **honey bees**. *Science of the Total Environment* 650 1250-1260.
- 334 10. Requier, F., Rome, Q., Chiron, G., Decante, D., Marion, S., Menard, M., Muller, F., Villemant, C.,
 335 Henry, M., 2019. **Predation of the invasive Asian hornet affects foraging activity and survival**
 336 **probability of honey bees in Western Europe**. *Journal of Pest Science* 92 567-578.
- 337 11. Schmolke, A., Abi-Akar, F., Hinarejos, S., 2019. **Honey bee colony-level exposure and effects in**
 338 **realistic landscapes: An application of BEEHAVE simulating clothianidin residues in corn pollen**.
 339 *Environmental Toxicology and Chemistry* 38(2) 423-435.
- 340 12. Schmolke, A., Abi-Akar, F., Roy, C., Galic, N., & Hinarejos, S. 2020. **Simulating honey bee large-**
 341 **scale colony feeding studies using the BEEHAVE model—Part I: Model validation**.
 342 *Environmental Toxicology and Chemistry*, 39(11), 2269-228
- 343 13. Abi-Akar, F., Schmolke, A., Roy, C., Galic, N., Hinarejos, S., 2020. **Simulating honey bee large-**
 344 **scale colony feeding studies using the BEEHAVE model—Part II: Analysis of overwintering**
 345 **outcomes**. *Environmental Toxicology and Chemistry* 39(11) 2286-2297.

- 346 14. Carter, L.J., Agatz, A., Kumar, A., Williams, M., 2020. **Translocation of pharmaceuticals from**
347 **wastewater into beehives**. *Environment International* 134 105248.
- 348 15. Requier, F., Rome, Q., Villemant, C., & Henry, M. 2020. **A biodiversity-friendly method to**
349 **mitigate the invasive Asian hornet's impact on European honey bees**. *Journal of Pest Science*,
350 93(1), 1-9.
- 351 16. Bulson, L., Becher, M.A., McKinley, T.J., Wilfert, L., 2021. **Long-term effects of antibiotic**
352 **treatments on honeybee colony fitness: A modelling approach**. *Journal of Applied Ecology* 58(1)
353 70-79.
- 354 17. European Food Safety Authority (EFSA), Ippolito, A., Focks, A., Rundlöf, M., Arce, A., Marchesi,
355 M., Neri, F.M., Rortais, A., Szentes, C., Auteri, D., 2021. **Analysis of background variability of**
356 **honey bee colony size**. EFSA supporting publication 2021:EN-6518. 79pp.
357 doi:10.2903/sp.efsa.2021.EN-6518.
- 358 18. Grindrod, I., Martin, S.J., 2021. **Parallel evolution of Varroa resistance in honey bees: a common**
359 **mechanism across continents?** *Proceedings of the Royal Society B* 288(1956) 20211375.
- 360 19. Horn, J., Becher, M. A., Johst, K., Kennedy, P. J., Osborne, J. L., Radchuk, V., & Grimm, V. 2021.
361 **Honey bee colony performance affected by crop diversity and farmland structure: a modeling**
362 **framework**. *Ecological Applications*, 31(1), e02216.
- 363 20. Schott, M., Sandmann, M., Cresswell, J.E., Becher, M.A., Eichner, G., Brandt, D.T., Halitschke, R.,
364 Krueger, S., Morlock, G., Düring, R.-A., 2021. **Honeybee colonies compensate for pesticide-**
365 **induced effects on royal jelly composition and brood survival with increased brood**
366 **production**. *Scientific Reports* 11(1) 62.
- 367 21. Baden-Böhm, F., Thiele, J., Dauber, J., 2022. **Response of honeybee colony size to flower strips**
368 **in agricultural landscapes depends on areal proportion, spatial distribution and plant**
369 **composition**. *Basic and Applied Ecology* 60 123-138.
- 370 22. Nearman, A., VanEngelsdorp, D., 2022. **Water provisioning increases caged worker bee lifespan**
371 **and caged worker bees are living half as long as observed 50 years ago**. *Scientific Reports* 12(1)
372 18660.
- 373 23. Preuss, T.G., Agatz, A., Goussen, B., Roeben, V., Rumkee, J., Zakharova, L., Thorbek, P., 2022. **The**
374 **BEEHAVEecotox model—integrating a mechanistic effect module into the honeybee colony**
375 **model**. *Environmental Toxicology and Chemistry* 41(11) 2870-2882.
- 376 24. Reiner, D., Spangenberg, M.C., Grimm, V., Groeneveld, J., Wiegand, K., 2022. **Chronic and acute**
377 **effects of imidacloprid on a simulated BEEHAVE honeybee colony**. *Environmental Toxicology*
378 *and Chemistry* 41(9) 2318-2327.
- 379 25. Schödl, I., Odemer, R., Becher, M.A., Berg, S., Otten, C., Grimm, V., Groeneveld, J., 2022.
380 **Simulation of Varroa mite control in honey bee colonies without synthetic acaricides:**
381 **Demonstration of Good Beekeeping Practice for Germany in the BEEHAVE model**. *Ecology and*
382 *Evolution* 12(11) e9456.
- 383 26. Agatz, A., Miles, M., Roeben, V., Schad, T., van der Stouwe, F., Zakharova, L., Preuss, T.G., 2023.
384 **Evaluating and explaining the variability of honey bee field studies across Europe using**
385 **BEEHAVE**. *Environmental Toxicology and Chemistry* 42(8) 1839-1850.
- 386 27. Requier, F., Fournier, A., Pointeau, S., Rome, Q., Courchamp, F. 2023. **Economic costs of the**
387 **invasive Yellow-legged hornet on honey bees**. *Science of the Total Environment*, 898, 165576.
- 388 28. Singer, A., Lückmann, J., Becher, M., Jakoby, O., Metz, M., 2023. **Effects of brood termination**
389 **rate on colony viability—A BEEHAVE modelling study how timing, magnitude and duration of**
390 **effects determine colony strength**. *Julius-Kühn-Archiv*(474).

391

392

393