

SyrFitSources: An agent-based model to investigate the effects of land use on the population dynamics of aphidophagous hoverflies

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ABSTRACT

Aphidophagous hoverflies are affected by insect decline, which is partly caused by habitat loss due to intensified agriculture. We present SyrFitSources, an agent-based model (ABM) for investigating the effect of land use on the population dynamics of the aphidophagous hoverfly *Episyrphus balteatus* on landscape scale in Central Europe. SyrFitSources considers 1) the life cycle of *E. balteatus*, 2) the resources of the larvae, i.e., aphids, 3) the resources of the imagines, i.e., pollen and nectar, and 4) the effect of insecticides on aphids and on syrphid larvae. For model testing, analysis, calibration, and evaluation, we used pattern-oriented modeling to compare the ABM results with observed numbers of active *E. balteatus* in 13 landscapes in Southern Germany in 2011. SyrFitSources reproduced these activity patterns. In 14 sensitivity experiments, we investigated the effects of stage-dependent mortality, migration, feeding, and reproduction on imaginal density. The effects were generally small, where variation of migration-related parameters had the largest effect on imaginal density. An additional resource-reduction scenario of aphids and floral resources suggests that the reduction of aphids has a stronger effect on the density of *E. balteatus* than that of floral resources. Two scenarios on the effect of insecticides on hoverfly larvae indicate that hoverfly populations are more strongly influenced by the insecticide-related reduction of aphid populations than by the direct effect of insecticides on hoverfly larvae. We conclude that SyrFitSources is a valuable tool for applied sciences, e.g., to assess ecological effectiveness of biodiversity measures in agricultural landscapes.

1. Introduction

During the last years, the declining insect diversity has gained increasing attention, especially since the “Krefeld study” (Hallmann et al., 2017), where severe losses in the biomass of flying insects were reported in Germany over 27 years. Declining abundances and species richness of insects were observed in different parts of the world (Biesmeijer et al., 2006; Potts et al., 2010; Wagner, 2020). Some of the drivers causing the decrease of arthropod diversity and abundance are agricultural intensification, land use change, the use of pesticides, and climate change (Goulson, 2019; Potts et al., 2010; Wagner, 2020). The diversity and abundance of hoverflies (Diptera: Syrphidae), also known

as syrphids, declined in several Western and Central European countries (Barendregt et al., 2022; Biesmeijer et al., 2006; Hallmann et al., 2021; Powney et al., 2019). Some syrphid species partially migrate from Central Europe to the Mediterranean and South Europe in autumn and return again from the south in spring, while some individuals of those species remain in Central Europe (Gatter and Schmid, 1990; Wotton et al., 2019). Especially the number of aphidophagous species migrating to the south declined by 97 % in Southern Germany from the 1970s to the 2010s (Gatter et al., 2020). A similar decrease in abundance of aphidophagous hoverflies was found in a Dutch forest between 1982 and 2021 by Barendregt et al. (2022).

Like butterflies and bees, syrphid imagines feed on pollen and nectar.

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However, depending on the species, their larvae feed on decaying matter (saprophagous) or plants (herbivorous), prey on aphids (aphidophagous), or parasitize the nests of ants and bumblebees, feeding on the larvae of the hosts (Rotheray and Gilbert, 2011). Unlike bees, syrphids do not exercise brood care beyond finding places with resources for their larvae where they lay eggs. Because of their different diets as larvae and imagines, aphidophagous syrphids fulfill a dual ecosystem function of pollination and pest control of aphids (Dunn et al., 2020).

Both resources of aphidophagous hoverflies, aphids and floral resources, generally decreased in the last decades (Baude et al., 2016; Bell et al., 2020; Crossley et al., 2021; Ewald et al., 2015). Land use change has caused reduction of floral resources, which is associated with the decrease of several flower visiting insect species, as it was shown for Great Britain (Baude et al., 2016). For syrphids in particular, the abundance and richness of floral resources has a positive effect on their abundance and species richness in different land-cover types (Cole et al., 2017). To the best of our knowledge, it is not known how the abundance of aphids affects the abundance of aphidophagous hoverflies. However, aphid densities declined significantly or at least showed trends of decrease in different regions of the temperate climate zone across the Northern Hemisphere (Bell et al., 2020; Crossley et al., 2021; Ewald et al., 2015). Further, the increase of pesticide usage correlated significantly with insect abundance in the last decades (Ewald et al., 2015) and is also assumed to be an important driver of syrphid decrease (Barendregt et al., 2022).

Taking together different studies on syrphid ecology and behavior can help to understand how food limitation influences the population dynamics of hoverflies. Formalizing the existing knowledge in an agent-based model (ABM) can be a powerful tool in this context. Recent studies introduced ABMs taking into account the interactions of species and resources within a landscape for solitary bees (Everaars and Dormann, 2014; Schmolke et al., 2023), honey bees (Becher et al., 2014), and bumblebees (Becher et al., 2018; Twiston-Davies et al., 2021). As far as we know, the only published spatiotemporally explicit ABM for syrphids is *Hover-Winter* (Arrignon et al., 2007), which explores how the landscape influences the hibernation pattern of *Episyrphus balteatus* in Southern France. Because of its focus, *Hover-Winter* uses a simple module for nectar resources and does not model the life cycle of syrphids.

As the decline of syrphids is attributed to many factors, we investigate the relationships between syrphids and their food sources over their whole life cycle in spatially explicit landscapes. For this purpose, we have developed SyrFitSources (Syrphid's Fitness dependent on Resources), a spatiotemporally explicit ABM for syrphids, applicable to landscapes in Central Europe. The model investigates the impact of land use on the population dynamics of aphidophagous syrphids at landscape scale, taking resource availability and resource interaction of larval and imaginal *E. balteatus* into account. We chose the aphidophagous and migratory species *E. balteatus* as a model organism as it is very common in Europe and numerous studies on its behavior could be used for the parameterization of SyrFitSources. When building the model, we implemented:

1. the life cycle of *E. balteatus*,
2. resources of the larvae, namely aphids, and their phenology
3. resources of the imagines, namely pollen and nectar, and their phenology
4. the effect of insecticides on aphids and on syrphid larvae

We used pattern-oriented modeling (POM; Gallagher et al., 2021; Grimm et al., 2005) for model development with patterns observed in Southern Germany. To understand better the effects of uncertain or central parameters on the model outcomes, we examined 14 model parameters, which were selected depending on their uncertainty or their association with central processes of syrphid population dynamics in sensitivity experiments. To improve our understanding of the interplay of underlying mechanisms in SyrFitSources, we ran three scenarios.

First, we investigated the effects of resource reduction by decreasing the aphid carrying capacity of host plants and the quantity of nectar and pollen. Second, we investigated the effect of aphid reduction through insecticide applied above different thresholds of aphid densities on the population sizes of *E. balteatus*. And third, we investigated the effects of insecticide toxicity on the aphid-feeding larvae of *E. balteatus*.

SyrFitSources was designed to be used for quantifying the effect of different landscapes on syrphids. That also includes the possibility to test effects of agri-environment measures on syrphid populations. Our model could also be extended to support pesticide risk assessment similar to SolBeePop for solitary bees (Schmolke et al., 2023) or land management like BEE-STEWARD for bumblebees (Twiston-Davies et al., 2021). The code of SyrFitSources, example inputs and a full model description are publicly available (App et al., 2025), to encourage other scientists to use or adapt it for their own research.

2. Methods

The processes implemented in SyrFitSources are based on studies from 38 articles, article supplements, books and unpublished sources (Appendix A), including studies on behavior and physiology of different syrphid and other insect species. The code of SyrFitSources was implemented in NetLogo 6.2.2 (Wilensky, 1999), a programming language specifically designed for ABMs with an integrated user interface. The following section is a short outline of model components and structure. A full model description following the Overview, Design Concepts and Details (ODD) protocol (according to Grimm et al., 2006, 2020) can be found in App et al. (2025).

2.1. Summary ODD and model structure

Here, we give a brief description of SyrFitSources following the "Summary ODD" (according to Supplement 2 in Grimm et al., 2020): The overall purpose of our model is to model population dynamics of *E. balteatus* dependent on land use on landscape scale (Fig. 1). Specifically, we address the following question: How do land use affects the population dynamics of aphidophagous syrphids at landscape scale? To consider our model realistic enough for its purpose, we used the following patterns: 1. time of maximum number of active syrphid in a landscape, 2. The number of active syrphids in flowering fields is significantly higher than in maize fields, while neighboring maize fields have higher numbers of active syrphids than more distant fields, 3. higher syrphid abundances in Lower Bavarian landscapes compared to Lower Franconian landscapes (see Section 2.3). The model includes the following entities: The landscape is represented by a habitat network (Fig. 2), made of habitat agents and connections. Each habitat agent comprises plants and juvenile syrphids (juveniles), which are implemented as entities. Also, the imaginal syrphids (imagines) are implemented as individual entities. Because of the large number of state variables we only list the most important state variables characterizing these entities: The global environment is characterized by daily mean temperature and latitude, which affects the length of each day. Habitat agents are characterized by their area and a land cover type. The land cover type determines if the habitat agent is suitable for syrphids to overwinter or hibernate and if they are exposed to insecticides. Movement of imagines between habitat agents depends on the length and direction of reachable habitat agents and on the size of the neighboring habitat agent. The plants of a habitat agent are characterized by their species-specific phenology of pollen and nectar. Also, plants have a species-specific aphid carrying capacity and time of infestation. The juvenile syrphid agents correspond to one or more individuals at one of the consecutive stages: egg, first, second, and third larval instar, and pupa. Imagines differ in their sex, their current energy and time level, their location, number of eggs they carry, and the days they have spent active. The spatial extent ranges between one and a few square kilometers. The temporal resolution is one day and the temporal extent can be

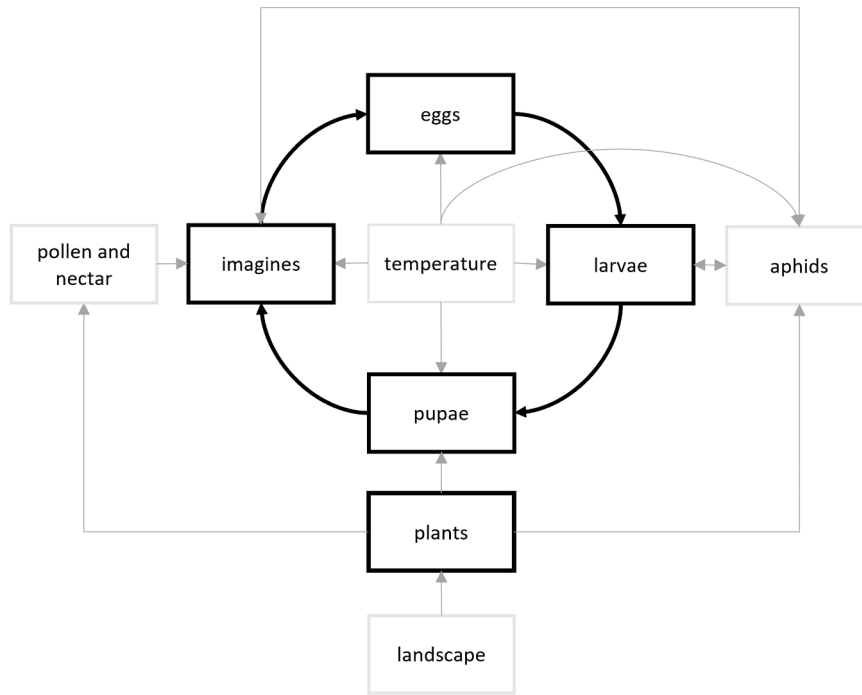


Fig. 1. Model structure of SyrFitSources. The modeled life cycle of *Episyrphus balteatus* is affected by resources provided by the landscape. Agents are marked by boxes with a black border. Grey boxes are the landscape, the mean daily temperature or the properties of plant agents. Syrphid imagines feed on pollen and nectar and the female syrphids lay their eggs into aphid colonies. The larval instars forage on aphids associated with the plants. Further, the mortality of pupae is connected with the plant species. The temperature affects the activity of imagines, stage duration of eggs, larval instars and pupae as well as the growth rate of the aphid colonies.

varied between one year and several years. The most important *processes* of the model, which are repeated every *time step*, are the update of nectar and pollen quantities of plants and the aphid densities of plants, the temperature dependent development of larvae, and their feeding on aphids. Further, the model includes the search of imagines for nectar and pollen on different habitat agents, their feeding on nectar and pollen, and the females' search for aphids to lay their eggs. The most important *design concept* of the model is the implementation of the basic principles that describe stage-dependent population dynamics of syrphids which were coupled to plant phenology and aphid availability in landscapes.

2.1.1. Representation of landscapes, plants, and aphids

To reduce the computational effort, each delimitable land use unit of the landscape, such as a field, was represented as a single or multiple immobile agents comprising multiple contiguous raster cells of the land cover type. These are further referred to as habitat agents. This

corresponds to the concept of BEEHAVE and BumbleBEEHAVE (Becher et al., 2014, 2018). For aggregation of raster cells into a habitat agent we extended an algorithm from BEESCOUT (Becher et al., 2016, 2018), which is used to create the landscape input for BEEHAVE and BumbleBEEHAVE. This algorithm allows to separate a large field into several habitat agents instead of one (Becher et al., 2016; Fig. 2). The landscape was then only represented by those habitat agents. Their locations were defined by the mean x and y coordinates of the aggregated raster cells and the habitat agent's area was the sum of the area of the raster cells it contains. Our extension enabled us to include more than four or nine landcover types in the model area. We implemented movement of hoverflies among habitat agents based on a habitat network (Fig. 2). Each land-cover type was characterized by a specific plant community and its corresponding plant coverage. The plant-specific quantities of pollen and nectar were scaled to the plant coverage, which allowed us to calculate the floral resources for habitat agents in a similar approach as

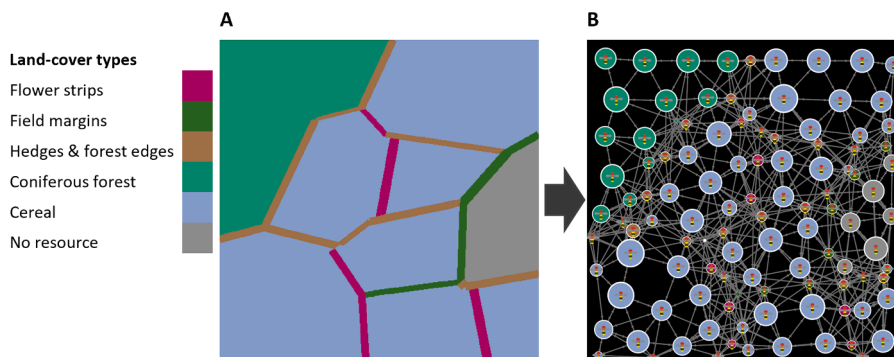


Fig. 2. For SyrFitSources, A) the spatial raster data is transformed to a B) discrete habitat agent network. The grey lines depict the connections between the habitat agents (circles). Large fields are shown as big circles, small linear structures like hedges or flower strips as small circles. The transformation of raster data into a habitat agent network can be achieved by an internal process of SyrFitSources. Alternatively, an already compiled habitat agent network can be inserted directly from a text file.

in BEEHAVE and BumbleBEEHAVE (Becher et al., 2014, 2018).

Similar as the quantity of nectar and pollen, the carrying capacity of a plant was scaled by the plant coverage. The aphid population dynamics were implemented with a logistic growth equation. We used a temperature dependent growth rate provided by Wu et al. (2014) and reduced it to 75 % due to model calibration. For the aphid population decline, we used equations of Bianchi et al. (2007) and modified them for SyrFitSources. A decline term was subtracted from the temperature dependent growth rate after the aphid population has exceeded its time dependent climax. We assumed that the degradation of the growth rate begins at 40 % of the time span between start and end of infestation.

2.1.2. Insecticides

Aphids are controlled with insecticides which can have strong lethal effects on syrphid larvae, and also sublethal effects, which still affect the imagines after insecticide exposure as larvae (Moens et al., 2011). According to the findings of Tenhumberg (1993), we assumed that the populations of aphids do not break down completely after insecticide application, but have a reduced growth rate. So, we implemented insecticide mortality of aphids as reduced population growth rate for 30 days as found after the application of a LC₃₀ concentration of a thiacloprid/deltamethrin mixture in a laboratory experiment (Majidpour et al., 2020). Lethal effects of insecticides on syrphid larvae were integrated into the model, but in our standard model version the effect is neglected, as we do not know which insecticides were used in our model regions and SyrFitSources results were reasonable without insecticide mortality.

2.1.3. Representation of imagines and scheduling of their daily tasks

Imagines have a daily amount of time [s], which they invest into processes similarly as bees and bumblebees in BEEHAVE and BumbleBEEHAVE (Becher et al., 2014, 2018). This daily amount of time depends on sunrise and sunset, calculated dependent on latitude and day of the year. Further, imagines maintain an amount of energy [J] through nectar and/or pollen feeding, which also is invested in daily processes. Both sexes of *E. balteatus* need nectar, pollen, and honeydew (sugar-rich excretion of aphids) for increased longevity (van Rijn et al., 2013), but we do not know the exact proportions of eaten nectar to pollen. Therefore, we simplified the diet to only nectar for vital processes of both sexes. Though, in the model structure, we implemented the possibility for the imagines to feed partly or completely on pollen for vital processes. In this case, the parameter *feeding_pollen_nectar_ratio* can be changed from zero (no pollen) to a value up to maximal one (only pollen) to set the proportion of pollen compensating the energy deficit. Female imagines additionally feed on pollen when producing eggs, similarly as it was observed for the syrphid *Rhingia campestris* (Haslett, 1989). For simplicity's sake we did not consider the honey dew production of aphids. When day length falls below the threshold of 11.65 h, females stop producing eggs and gain fat for overwintering (Hondelmann and Poehling, 2007). Searching for food is repeated until all imagines have fed or until their time or energy resources are depleted. In the next sub-step, the males return to woody structures, where they hover to mate with unfertilized females. This was based on the observation that males often hover near tree groups and forest clearings (Schneider, 1948). After the males have arrived at the woody structures or have depleted their time and energy resources, gravid females search for aphids on their current habitat agent in order to lay eggs there. If they do not find any aphids, they leave the habitat agent to search for aphids on a neighboring habitat agent. This is repeated until they have laid all eggs or their time or energy resources are depleted. If thereafter females still have energy and time left, it is assumed that they search for forest edges as place to stay overnight or to hibernate (Arrignon et al., 2007). As hedges can be viewed as forest edges without forest (Ellenberg and Leuschner, 2010) we included hedges as overnight and hibernation habitats. When a female is not fertilized, it directly searches for woody structures. After all individuals have performed their

daily tasks or used up their daily time, they remain inactive. When they run out of energy, they die. Individuals of both sexes of syrphids emigrate in summer and autumn (Hlaváček et al., 2022).

2.1.4. Activity, mortality, and metabolism of imagines

The probability that an imago is active increases with temperature (Arrignon et al., 2007; Gilbert, 1985). Actively performed processes comprise feeding, search for aphids, hovering, and search for a habitat agent to overnight or hibernate. The number of active imagines per day on a habitat agent is the number of imagines that have entered this habitat agent on a day. Also, the switches of actively performed processes of an imago are counted and added to the number of active imagines on the habitat agent.

The mortality from freezing increases with decreasing temperature, which is calculated with a logistic equation from Arrignon et al. (2007) based on the observations of Hart and Bale (1997). Age mortality increases with increasing duration of active days after hatching from the pupa. This mortality rate was adapted to the Gompertz-Makeham equation (Kirkwood, 2015) based on mortality rates from a greenhouse experiment (Geusen-Pfister, 1987). We applied a time-dependent power function for the mortality rate of active imagines from Appendix S1 of Becher et al. (2014), based on a probably predation-related mortality rate of foraging bees, which was observed in the field (Visscher and Dukas, 1997).

We derived the energy consumption of active and inactive behavior of *E. balteatus* from the measured energy consumption of the syrphid *Eristalis tenax*, using equations to scale the energy consumption of insects with different size but same linear proportion (Sotavalta and Laulajainen, 1961). Regarding energy storage, the imagines in the model have fat depots of 5 % body weight (Hondelmann and Poehling, 2007) in addition to the energy stored in the cardiovascular system, which is based on the maximum flight time. Females can overwinter in Central Europe (Hondelmann and Poehling, 2007) and they gain up to 11 % body weight of fat, while this was not observed for males (Hondelmann and Poehling, 2007). Hence, we implemented the extra fat for hibernation to increase the female energy storage. As the likelihood of *E. balteatus* to reduce its ovaries and to enter diapause increases sharply below 11.65 h day length (Hondelmann and Poehling, 2007), the model induces winter metabolism on a daily base when the daylight drops below this threshold and an imago was inactive that day. As insects are exotherms, we set the rate of winter metabolism much lower than during inactivity at other times of the year. If daily temperature exceeds 0 °C, imagines can become active again.

2.1.5. Movement and migration

Connections between habitats were set to a maximum length of 200 m, which is the maximum distance of *E. balteatus*' perception (Arrignon et al., 2007). To reduce computational costs, we did not implement the perception of floral resources in the model, because this only led to a slight underestimation of the detection rates of floral resources in bees (S 2 of Becher et al., 2016), and we assumed that perception in syrphids is more or less similar to bees. Hoverflies, however, can detect vertical landmarks (Collett and Land, 1975) and, thus, we assumed that they can sense forest and other shrubby land-cover types inside their perception range and fly there directly.

The movement probability of an imago is dependent on the distance and area size of neighboring habitat agents. The closer and the larger the other habitat agent, the higher the probability to move there. This is based on results from a study on *E. balteatus* and *Eupeodes corollae*, where both species were caught in pan traps in different distances from a phacelia strip (Wratten et al., 2003). Bees and bumblebees move through the landscape at 2.96 and 3.22 m s⁻¹, respectively, while searching for floral resources (derived from Osborne et al., 2013 and Wright, 2013 in Becher et al., 2016). The syrphids *Eristalis* spp. and *Volucella pellucens* were assumed to fly 8 m s⁻¹ in direct flight (Collett and Land, 1978). However, we assumed that *E. balteatus* moves slowly

with 1 m s^{-1} , as it is lighter than the aforementioned syrphid and bee species. We also assumed that insects do not take the direct path while they move in the landscape, which results in lower velocity.

As syrphid immigration has been observed in spring (Fisler and Maracchi, 2023; Wotton et al., 2019), *E. balteatus* imagines migrate into the landscape in SyrFitSources between 1st May and 31st June. In spring, a total of 4700 syrphids km^{-2} migrate into the landscape, according to observations from South Britain (Wotton et al., 2019). Many individuals of *E. balteatus* emigrate between beginning or mid of July and mid or end of September (Gatter and Schmid, 1990; Wotton et al., 2019). Therefore, the imagines in the model can leave the landscape between 1st July and 14th September. Emigration was implemented as a triangular function that calculates the probability of an imago leaving between the beginning and end of emigration, with the highest probability of emigration around 7th and 8th August. We chose 0.05 as the maximum probability of emigration, a proportion that prevents population collapse in SyrFitSources. The simulated median number of emigrating *E. balteatus* is about 30,000 individuals km^{-2} , which is higher than the observed maximum of about 22,000 km^{-2} *E. balteatus* km^{-2} emigrating out of South Britain (Wotton et al., 2019), but still in the same order of magnitude.

2.1.6. Reproduction and oviposition

In the laboratory, females become fertile after 8 to 12 days at 23 °C. For a fecund female, the number of potentially laid eggs per day increases over nine days from initially around 60 up to 150 and then decreases again (Branquart and Hemptinne, 2000). We fitted this pattern observed in the laboratory with a third order polynomial regression (R Core Team, 2022) for the first 30 days of fecundity. When a female is fecund for >30 days, the number of potentially laid eggs in the model remains constant after the 30th day as females can still lay eggs up to 100 days after hatching from the egg (Geusen-Pfister, 1987).

The pollen which females have fed for egg production is transferred one-to-one to egg mass in SyrFitSources. Female syrphids seem to avoid to lay their eggs into aphid colonies if conspecific eggs or larvae are present (Almohamad et al., 2009). Based on Figures 10, 13, 17, and 18 from Tenhumberg (1993), we assumed that the eggs and larvae of syrphids in established colonies never exceed a ratio of two to 100 aphids. Accordingly, female hoverflies in SyrFitSources only lay eggs on a plant until this ratio is reached. Because the ratio of eggs and larvae to aphids can be much higher in young aphid colonies (Kan, 1988), we implemented a function which raises the potential ratio of eggs and larvae to aphids at the beginning of the aphid infestation of a plant.

2.1.7. Representation of juveniles

One juvenile agent comprises all individuals which were laid as egg on the same day on the same plant of a habitat agent. The development time of the juvenile stages only depends on temperature. According to laboratory experiments, it takes around 60 days to complete the juvenile stages at 7.5 °C, but it takes only around 21 days at 20 °C (Ankersmit et al., 1986). For each day, the day of transition to the next stage or hatching is calculated based on the mean temperature of all days a juvenile was exposed to.

A part of the eggs and pupae dies during the transition to the next stage. For eggs we used the high laboratory mortality of a greenhouse experiment (Geusen-Pfister, 1987) and mortality rates of pupae were based on parasitization rates found in an Italian field study (Sommaggio et al., 2014). The mortality of the larvae is dependent on the number of aphids eaten (Putra and Yasuda, 2006). Therefore, we fitted a logistic equation on the proportion of surviving larvae as a function of the number of aphids eaten from the figures of Putra and Yasuda (2006) with nls (R Core Team, 2023).

Further, the voracity of larvae depends on aphid density and describes the daily uptake of aphids. Because the larval voracity of the first instar is much lower than that of the second and third (Putra and Yasuda, 2006), we fitted an equation on voracity data from Putra and Yasuda

(2006) via nls (R Core Team, 2023) resembling a Holling's type II functional response (Holling, 1959). The number of eaten aphids per day and larvae (second and third instar) per stem follows an equation in Tenhumberg (1995) resembling Holling's type III functional response (Holling, 1959). Both equations describe an approximate saturation at a given density of prey. Because aphids are clumped at lower densities (Ohnesorge and Viereck, 1983), we used Tenhumberg's parameterization for larval voracity per stem on a square meter.

2.2. Code testing

To ensure that SyrFitSources' code works correctly, we made use of NetLogo's internal control tools, e.g. plots, monitors and print statements, as suggested Railsback and Grimm (2019). With those control tools we examined the dynamics of several state variables, the model schedule and whether the processes were implemented correctly. Additionally, we visualized model outputs to evaluate if processes are ecologically plausible and correspond to field observations. Many of the equations in SyrFitSources were individually implemented in advance in R (R Core Team, 2022, 2023), checked for the ecological plausibility of their outcomes, and adjusted if necessary. Resulting response plots can be found in the ODD protocol.

2.3. Pattern-oriented modeling

In the following chapter, we present a field study as basis for applying a POM approach to execute the modelling cycle (Gallagher et al., 2021; Grimm and Railsback, 2005). This includes (i) assembling hypotheses for essential processes and structures and (ii) model testing e.g., calibration (adjusting parameter values) of uncertain parameters (e.g., aphid growth rate, aphid phenology of the most abundant crops and forest trees as well as imaginal flight velocity and maximum probability of emigration to reproduce the patterns).

2.3.1. Model areas

We used POM for reproducing the number of active syrphids based on observations of *E. balteatus* from a field study of the Bavarian State Institute for Agriculture (Bayerische Landesanstalt für Landwirtschaft, LfL). The field study included 13 landscapes in Bavaria, Germany (seven in Lower Franconia and six in Lower Bavaria) and aimed at detecting effects of flower areas on the species richness and abundance of arthropods and arachnids (Wagner et al., 2014). For the experimental design, three Malaise traps were set up in each landscape: one in a flower area, another one in a neighboring maize field, and the third in a maize field around 500 m remote from the other traps. The traps were placed in June (seven days from 13.06. to 20.06.2011 and seven days from 20.06. to 27.06.2011), July (seven days from 07.07. to 14.07.2011 and seven days from 14.07. to 21.07.2011), and August (seven days from 15.08. to 22.08.2011 and eight days from 22.08. to 30.08.2011).

The syrphids *E. balteatus* and *Eu. corollae* can travel at least 200 m from a phacelia strip into the surrounding landscape (Wratten et al., 2003). Due to the mobile lifestyle of *E. balteatus*, which moves between flower resources, egg-laying sites, and shrubs during the same day, the moving distance could even be >200 m. The model area was defined by bounding boxes with a minimum distance of 1000 m from the malaise traps, to avoid edge effects. The model areas of the 13 landscapes varied from about 6 to 10 km^2 .

In order to create land-cover layers of the model areas, crop and land-cover information from administrative data of the LfL was aggregated to similar crops or land-cover types to simplify the input. For forests, we used the 'Dominant Tree Species Map' for Germany (DTSG, Blickensdörfer et al., 2024). Again, we aggregated similar tree species. For small woody structures, e.g., hedges, we used the 'Small Woody Features' of 2015 (SWF, Copernicus programme, 2019). We combined the various geospatial data to create a comprehensive land-cover raster with 2 m resolution. For details on the aggregation of land-cover types and

the landscape analysis, see Appendix B.

Each land-cover type has its specific plant community with different coverage of the plant species. For most arable land-cover types, we simply assumed 100 % cover of the defining crop. For other land-cover types like hedges, flower areas, and field paths we assigned a specific plant coverage based on species lists or vegetation relevés. For the precise coverage of plants in all land-cover types, see Appendix C. We calculated mean daily temperature for each landscape from hourly data of the nearest weather station of the German Weather Service (*Deutscher Wetterdienst*, DWD) for the year 2011. For both regions the mean annual temperature is very similar (Lower Bavaria: 9.26 ± 7.62 °C, Lower Franconia: 9.90 ± 7.12 °C). For more detailed information on the daily temperatures, see Appendix D.

2.3.2. Floral resources and aphids

To parameterize the land-cover types of the model areas with plants, we used floral traits (phenology, pollen quantity, nectar quantity, density of floral units) of 72 plant species and genera from the FloRes Database (*Baden-Böhm et al., 2022b*), which is a compilation from different sources. We added further 11 plants, like crops or conifers, which were partially present in FloRes or not at all, mostly as aphid resource. For further information and the precise parameterization of floral resources per plant, see Appendix E.

The maximum carrying capacity for the aphid populations on plant species was estimated from different sources. We used the carrying capacities of 1250 aphids per m² on field margins given in *Bianchi et al. (2007)* on most herbaceous plants at 100 % coverage. For oak and shrubs, we used the carrying capacity of 200 aphids per m² of forests given in *Bianchi et al. (2007)*. Since very few syrphid species, but not

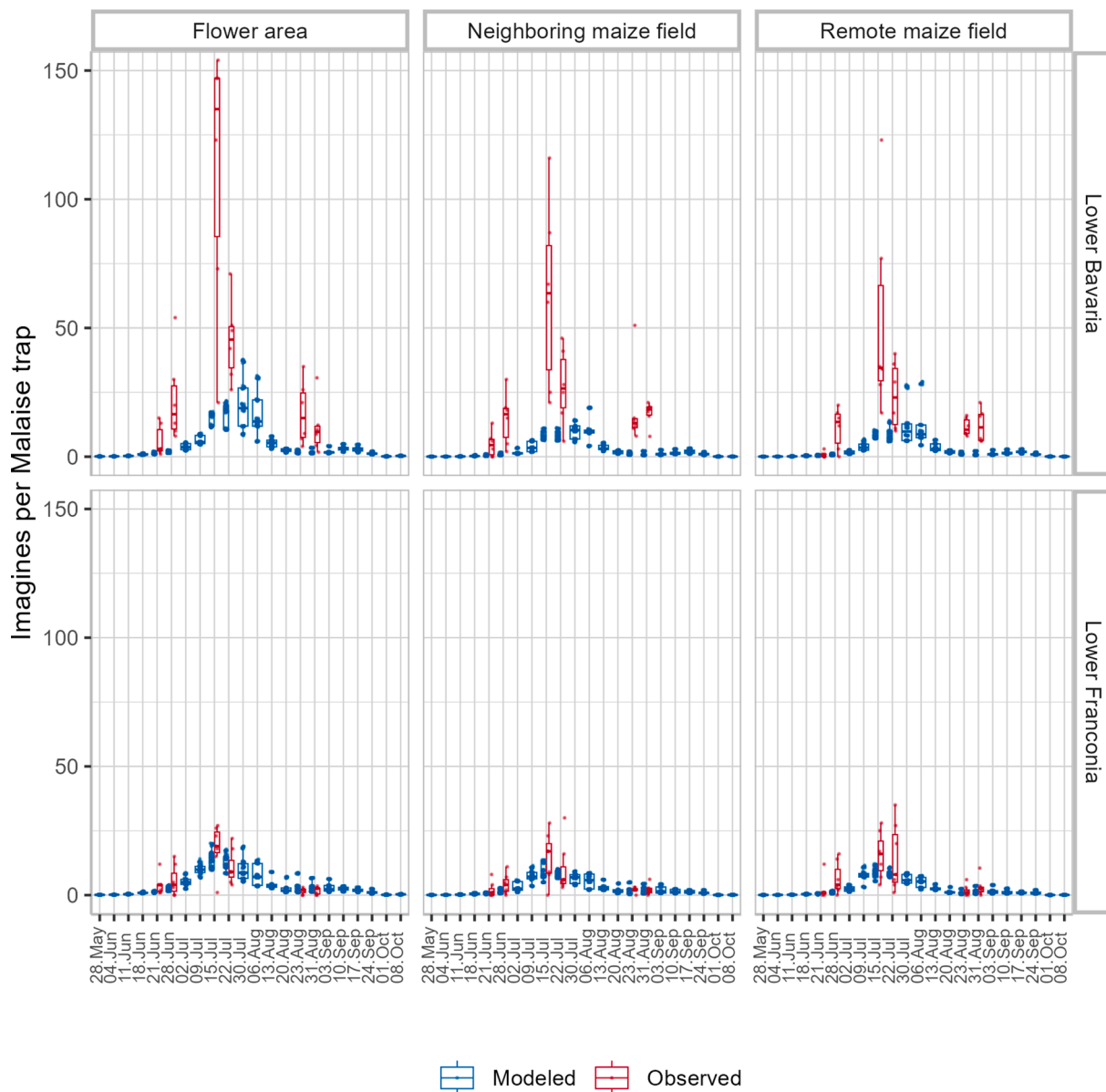


Fig. 3. Comparison of simulated numbers and field-observed numbers of active imaginal *Episyrrhus balteatus* in two Bavarian regions, comprising six landscapes in Lower Bavaria and seven landscapes in Lower Franconia (based on field observations from 2011). In each landscape three Malaise traps were set up: one in a flower area, one in a neighboring maize field, and one in a maize field remote from the flower area. The simulated numbers of active imagines were summed up for seven days to recreate the sampling design with Malaise traps from the field. For the period when no traps were set in the landscapes, the cumulated number of active imagines is shown here for every seventh day. The first and third quartiles delimit boxes of active imagines across all landscapes, the middle line marks the median and the boxes' whiskers have 1.5th length of the boxes.

E. balteatus, feed on beech aphids (Sadeghi et al., 2014), beech forests do not host aphids in SyrFitSources. Seed treatment with insecticide was common at the beginning of the 2010s and reduces the capacity of aphids to around a half or even lower on wheat (Abd-Ella, 2016). So, we halved the capacity in cereal given by Bianchi et al. (2007) to 5000 aphids per m². We also used the halved capacity for maize, soy, potato, and sugar beet. The capacity of spruce with 70,000 aphids per m² was assessed through the leaf area index of spruce (Schleppi et al., 1999), the area of spruce needles (Krause et al., 2012), and the density of aphids per needle on spruce (Straw et al., 2011). The recommended tree density per ha is lower for pine than for spruce of similar height (Schober, 1995). Therefore, we scaled the aphid capacity for pine down to 26,697 aphids per m² based on the ratio of pines to spruces per ha. For detailed calculations and the parameterization of aphid infestation on plants, see Appendix F.

For oak, spruce, and pine as well as spring cereal, winter cereal, potato, and sugar beet we did not have sufficient information on the floral traits. However, as they provide aphids, we added them as aphid resources; however, we did not consider them as pollen and nectar resources, because we had no information about their pollen and nectar quantity. For further information and the precise parameterization of aphids per plant, see Appendix G.

2.3.3. Patterns for pattern-oriented modeling

We interpreted the numbers of individuals caught by the malaise traps as active imagines because they only can catch flying syrphids. From the field observations in Bavaria, we derived three patterns for POM (Fig. 3):

Table 1

Parameters that were varied in the sensitivity experiments.

Process	Parameter name	Description	Unit
Feeding	<i>feeding_pollen_nectarratio</i>	Proportion of pollen in diet for vital processes	[-]
Emigration	<i>emigrate_start_d</i>	Begin of emigration	[d]
	<i>emigrate_end_d</i>	End of migration	[d]
	<i>emigration_proportion</i>	Proportion of emigrating flies at climax of emigration	[-]
Immigration	<i>immigrate_start_d</i>	Begin of migration	[d]
	<i>immigrate_end_d</i>	End of migration	[d]
	<i>immigrating_flies</i>	Numbers of flies migrating into the landscape	[individuals km ⁻²]
Movement	<i>Fligh_velocity</i>	Flight velocity between habitat agents	[m s ⁻¹]
Mortality	<i>mortality_eggs</i>	Egg mortality	[-]
	<i>MortalityForaging_per_s</i> (scaled by <i>mortality_factor_imago</i>)	Mortality of active imagines	[s ⁻¹]
Reproduction and oviposition	<i>egg_larvae_aphid_ratio</i>	Maximum ratio of syrphid eggs and larvae to aphids	[-]
	<i>enhance_oviposition_ratio</i>	Factor of enhancement of <i>egg_larvae_aphid_ratio</i> in young aphid colonies	[-]
	<i>fertilization_m2_factor</i>	Area where fertilization occurs at 100% with one male present	[m ²]
Start population	<i>startpopulation</i>	initial population of syrphids after model initialization	[m ²]

1. The temporal pattern of active *E. balteatus* throughout the year. In both regions numbers of active imagines increased in June, peaked in July, and decreased in August to similar numbers as in June. We assumed that the timing of active imagines peak is most important and allowed a deviation of one week in the model results. As the maximum of active imagines lasted mostly around one week in the field, the decrease of imaginal activity in the model should occur at the latest one week after the decline in the field. In late summer, the number of simulated active imagines should have declined to the same level as in spring.
2. As a spatial pattern we used the differences in numbers of active syrphids in flower areas compared to maize fields. In Bavaria the active imagines peak in July are distinctly higher in the flower fields than in the maize fields while the number of active imagines in neighboring maize fields are slightly higher than in the remote ones. The model results should show the same ranking.
3. As pattern that indicates SyrFitSources ability to reproduce regional differences in syrphid dynamics, we used the difference in maximum of active syrphid between Lower Bavaria and Lower Franconia. At median, it is about five times higher in Lower Bavarian flower fields than in Lower Franconian ones.

In the model, each Malaise trap was represented by the nearest habitat agent with an area greater than 2000 m² of the same land-cover type as where the trap was set up. To compare the observed and simulated number of active imagines, we summed up the model results of total numbers of active imagines on the habitat agent seven days before the Malaise traps were emptied and scaled them to 2.3 m², as this was the area a trap covered. In the period when no traps were set in the landscapes, the total number of simulated active imagines (feeding, oviposition, and search for woody structures) was calculated for every seventh day of the year, except for the days before and after the traps were set. We did not include hovering males into simulated numbers of active imagines on the habitat agent because we assumed that they are unlikely to be captured by a Malaise trap due to the stationarity of hovering. For each landscape, we conducted ten model runs.

2.4. Sensitivity experiments

We conducted sensitivity experiments with SyrFitSources for all 13 Bavarian landscapes, investigating the effect of varying single parameters on the daily density of imagines during summer (01.06.2011 to 31.08.2011). Because densities are very low during spring, autumn, and winter and the peak density occurs in summer, the strongest effects of the variation of parameter values should be visible in the summer. We focused on the 14 most important or uncertain parameters related to feeding, migration, stage dependent mortality, reproduction, and oviposition (Table 1). Parameters were mostly varied in an observed range referred through literature. In other cases, when a parameter could only be roughly estimated, we varied mostly in descending and ascending powers or doubled and halved the parameter. We ran 10 simulations for each parameter variation over one year. See Appendix H for the standard values of 14 parameters and their variation for the sensitivity experiments.

2.5. Reducing resources and experiments for assessing the effect of insecticides

Because both floral resources and aphids declined in the last decades, we conducted an experiment on resource reduction to explore which resource has a stronger limiting effect in the 13 Bavarian landscapes. Here, we reduced each of the available floral resources and the carrying capacity of the aphids to 10, 1, 0.1, 0.01, 0.001, and 0.0001 % of their standard parameter values. These standard values were the floral resources and the carrying capacity for aphids as implemented for model evaluation (see Section 2.3.2).

One of the drivers of insect decline is assumedly the effect of pesticides (Wagner, 2020), so we varied the threshold of applying insecticides (*threshold_apply_insecticide*) against aphids. All other parameter values were kept unchanged. We used a low threshold for application (1000 aphids m^{-2}), an intermediate one (2000 aphids m^{-2}), and none at all (5000 aphids m^{-2} , i.e., the capacity of aphids on most crops because SyrFitSources needs a threshold for crops). However, the seeds of crops were always treated with insecticide, even in the scenario without insecticides, limiting the capacity of aphids (Abd-Ella, 2016).

As the mortality of syrphid larvae differs among the type of insecticides, we varied the mortality (*mortality_sprayed*) based on observed values according to Moens et al. (2011), keeping the standard values of the other parameters unchanged. For further details on how the different insecticide mortality rates of syrphid larvae were parameterized, see Appendix H. Similar to the sensitivity experiment we ran 10 simulations for each variation of thresholds of insecticide application and larval insecticide mortality of syrphids for one year using the same spatial input and weather data as for the sensitivity experiment.

3. Results

3.1. Results of pattern-oriented modeling

SyrFitSources was able to reproduce the three observed patterns from Lower Bavaria and Lower Franconia (Fig. 3): First, SyrFitSources reproduced the temporal pattern of active *E. balteatus* throughout the year. The following model simulations correspond to the field observations: (i) the imaginal densities increased from mid to late June, (ii) the maximum of active imagines was reached in mid-July, as in the field study in Lower Franconia, and (iii) the simulated active imagines declined towards the end of August. Only the simulated peak of active imagines in Lower Bavaria between the end of July and the beginning of August was delayed by two weeks compared to the peak observed in the field. Second, as in the field study, the simulated peak of active imagines on the flower areas were higher than those on the maize fields in Lower Bavaria. In contrast to the field observations, however, the simulated numbers of active imagines in the neighboring and distant maize fields in Lower Bavaria did not differ. Similar patterns were reproduced for

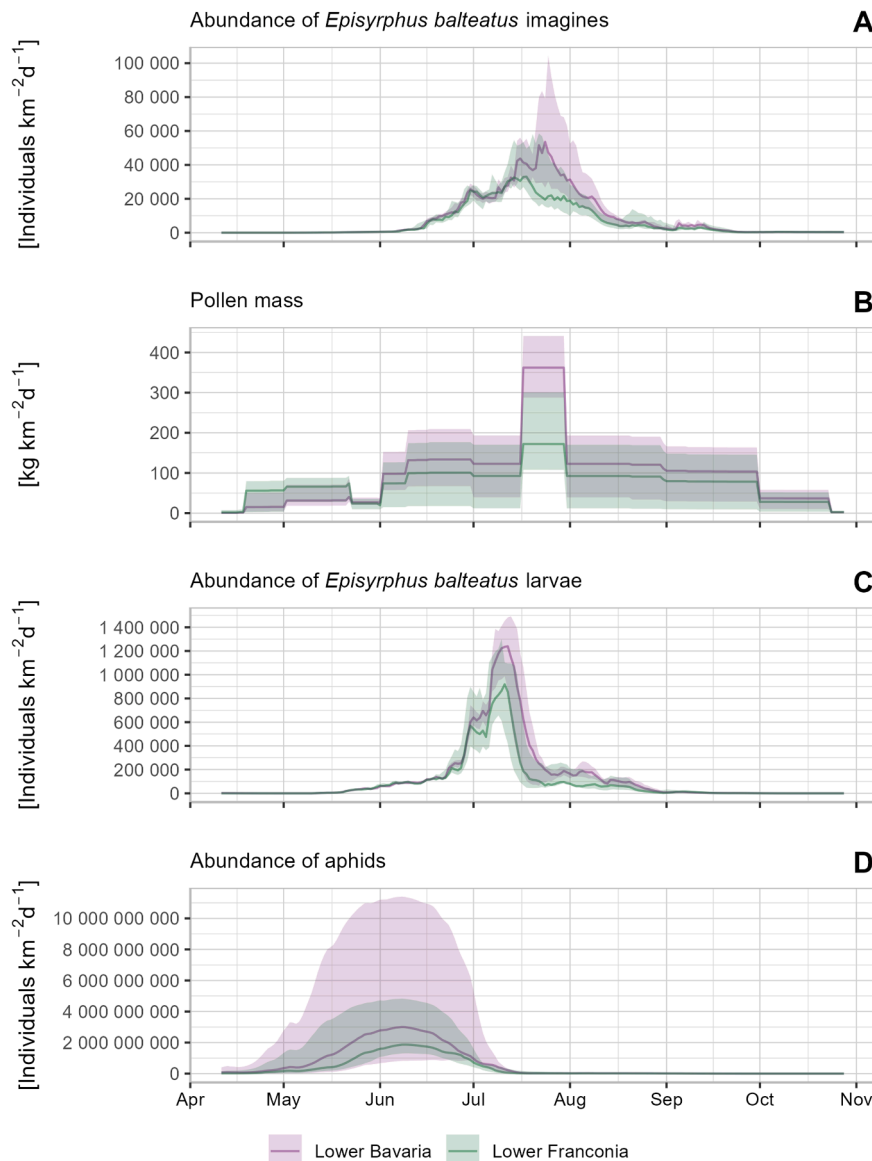


Fig. 4. Results from SyrFitSources. Simulated median with 5 and 95 % quantile of **A** density of *Episyrphus balteatus*, **B** quantity of pollen, **C** density of syrphid larvae, and **D** density of aphids on landscape scale for six landscapes in Lower Bavaria and seven landscapes in Lower Franconia. Solid lines are the median values for each region.

Lower Franconia, although the differences between the number of active imaginal syrphid in flower areas and maize fields were not observed in the field study for Lower Franconia. Third, in line with the results of the field study, the simulated peaks for active imagines were up to two times higher in Lower Bavarian flowering areas than in Lower Franconia, although the differences were less pronounced than in the field study (up to eight times higher numbers of active imagines in Lower Bavaria, see Fig. 3). In contrast to what was observed in the field, the simulated number of active imagines in the Lower Bavarian maize fields did not exceed the simulated numbers in the Lower Franconian maize fields as clearly.

To better understand the interplay between the temporal dynamics of active syrphids and their resources, we show these dynamics in distinct graphs in Fig. 4. The pattern of imaginal density differed strongly from the pattern of pollen quantity on landscape scale (Fig. 4A & B). The overall imago densities between Lower Bavaria and Lower Franconia showed similar temporal patterns, but differed in numbers. In Lower Franconia the peak was around 30,000 imagines km⁻² in mid-July and in Lower Bavaria it was around 50,000 imagines km⁻² around a week later. In both landscapes the density of imagines dropped remarkably to around 5000 imagines km⁻² in mid-August and was stable at a low level until mid-September. In late September, the density

dropped to around 350 imagines km⁻² in Lower Bavaria and 162 imagines km⁻² in Lower Franconia. The pollen quantity showed different "plateaus" according to the flowering time of the main crops (maximum at 360 kg km⁻² in Lower Bavaria and 170 kg km⁻² in Lower Franconia during the flowering time of maize in July).

The temporal patterns of larvae and aphid density are similar at different quantities (Fig. 4C & D). In Lower Bavaria, the larval density increased more strongly than in Lower Franconia (12×10^5 and 9×10^5 larvae km⁻²). The aphid density peaked a month earlier (3×10^9 aphids km⁻² in Lower Bavaria; 2×10^9 aphids km⁻² in Lower Franconia) than the larval density and the aphid density declined to low numbers (27×10^6 aphids km⁻² in Lower Bavaria and 14×10^6 aphids km⁻² in Lower Franconia) at the end of July. The density of syrphid larvae exhibits a time lag of two to four weeks as compared to aphid density.

To better understand the habitat use of syrphids that emerges from SyrFitSources, we show imago densities during their active time period in different habitats in Fig. 5. The simulated patterns of active imagines were similar in the different land-cover types, but numbers differ dependent on availability of nectar (Fig. 5A & B). In all land-cover types, the number of active imagines peaked in July. The highest number of active imagines was simulated in hedges (median: 4.95 imagines m⁻² at 19th July) because the imagines use hedges for staying overnight and for

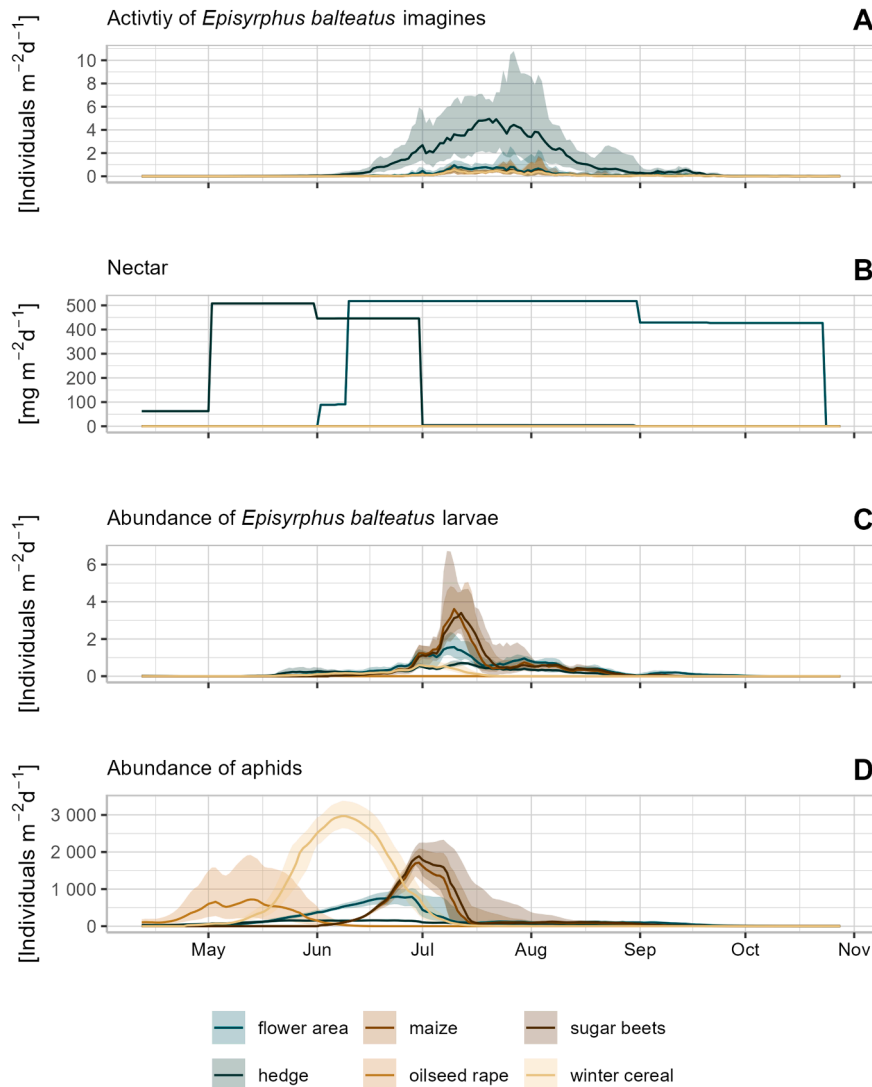


Fig. 5. Results from SyrFitSources. Simulated median with 5 and 95 % quantile of A active imagines of *Episyrphus balteatus*, B quantity of reachable nectar, C the density of larvae of *E. balteatus*, and D density of aphids in selected land-cover types in six landscapes in Lower Bavaria and seven landscapes in Lower Franconia with each 10 replications. The solid lines are the median values for each land-cover type.

hibernation independent of quantities of nectar, which are depleted after June. The number of active imagines in the flower areas were lower than in the hedges (0.96 m^{-2} at 9th July), but still higher than in the crops ($0.55\text{--}0.59 \text{ m}^{-2}$ between 10th July to 26th July).

The simulated density of larvae in six selected land-cover types is

strongly dependent on the overall density of aphids in the landscape (Fig. 5C & D). In comparison to the numbers of active imagines (Fig. 5A), the highest density of larval hoverflies occurred in maize (median: $3.61 \text{ larvae m}^{-2}$ on 9th July) and sugar-beet fields ($3.4 \text{ larvae m}^{-2}$ on 11th July) as both crops showed high aphid densities in July, when aphid

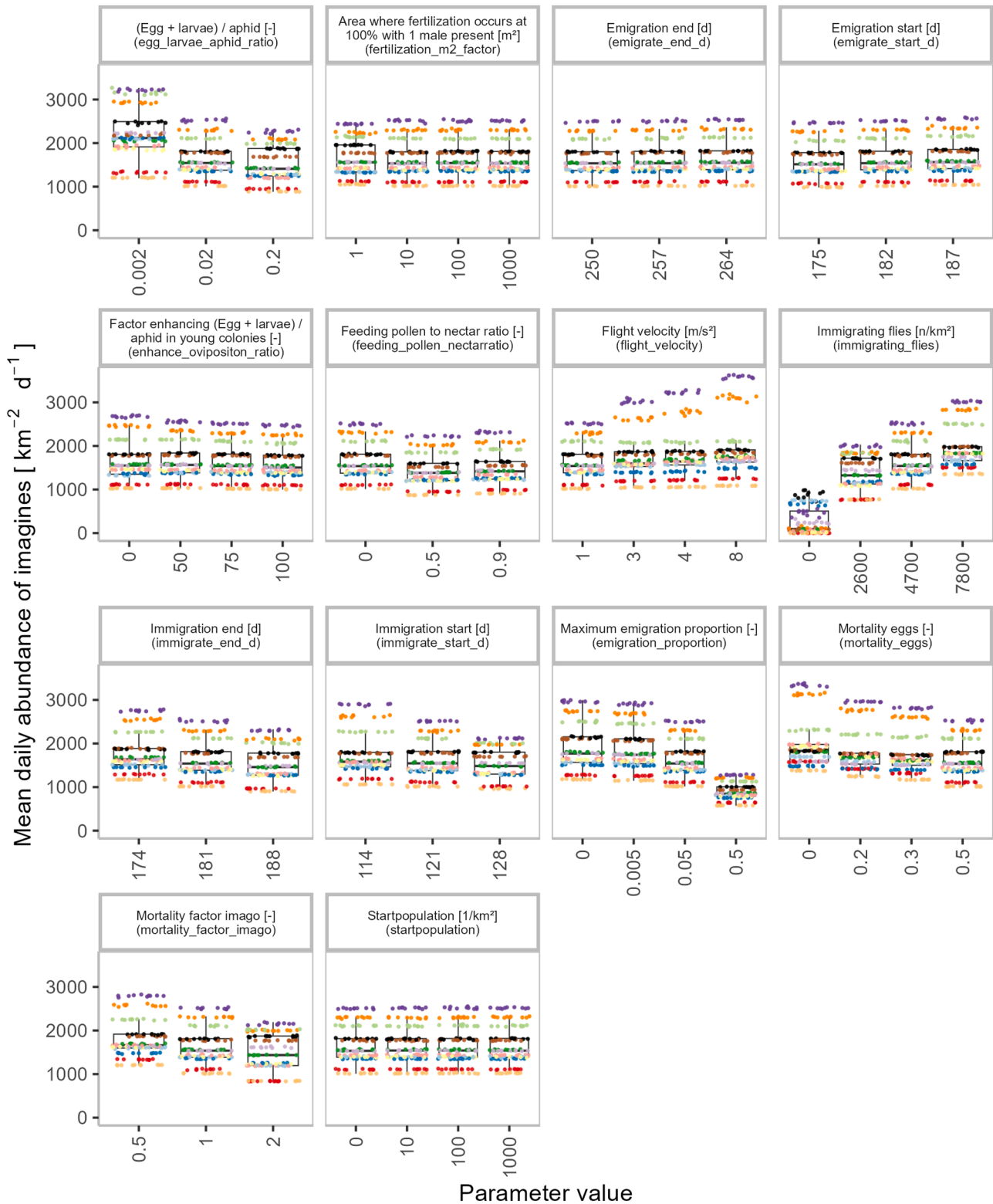


Fig. 6. Sensitivity experiments with SyrFitSources for the daily density of syrphid imagines during summer (01.06.2011 to 31.08.2011). The values of 14 parameters were varied for 13 landscapes in South Germany with 10 replications each. Different colors indicate results from different landscapes. The first and third quartiles delimit boxes of the mean daily density in all landscapes, with the median indicated as vertical line and the whiskers having 1.5th length of the boxes.

densities were already low on other land-cover types. In maize and sugar beets, the maximum capacity for aphids ($5000 \text{ aphids m}^{-2}$) and the threshold for applying insecticide ($2000 \text{ aphids m}^{-2}$) were mostly not reached (medians: $1713 \text{ aphids m}^{-2}$ in maize and $1887 \text{ aphids m}^{-2}$ in sugar beets on 29th June). The maximum densities of syrphid larvae occurred in winter cereals ($0.60 \text{ larvae m}^{-2}$ on 29th June) around two weeks earlier than in flower areas ($1.56 \text{ larvae m}^{-2}$ on 9th July) and hedges ($0.7 \text{ larvae m}^{-2}$ on 11th July). For aphids, the lowest peak resulted in oilseed rape (median: $721 \text{ aphids m}^{-2}$ on 12th May) and the highest densities were provided in winter cereals (median: $2971 \text{ aphids m}^{-2}$ on 8th June). Hence, aphid densities were much higher in crops than in flower areas ($794 \text{ aphids m}^{-2}$ on 23th June).

3.2. Sensitivity experiments

Altogether, variation of values for most parameters only had a small effect on the mean density of imaginal syrphids during summer (Fig. 6). Variation of parameter values affecting migration or the numbers of eaten aphids showed a clear impact on the mean summer density. At low egg-and-larvae-to-aphid ratio, the predation pressure on aphids was low, leading to higher aphid densities and, consequently, to high densities of imaginal syrphids in summer. Moreover, variation of migrating hoverflies led to an increase or decrease of imaginal density, respectively. When no imagines migrated into the study areas the populations went extinct in most landscapes. When the end of immigration happened later, the mean summer densities decreased slightly. Increasing the maximum proportion of emigrating imagines resulted in decreasing lower mean abundance of imaginal syrphids in summer. Higher flight velocity of the imagines also increased the densities of imagines in some landscapes. Increased mortality of eggs and imagines resulted in a moderate decrease of mean density in summer.

3.3. Effects of reducing resources and of insecticides

The reduction of aphids had a stronger effect on the mean daily density of *E. balteatus* imagines in summer than the reduction of floral resources in SyrFitSources (Fig. 7). Reducing the capacity for aphids to

one tenth led to a decline in mean densities of *E. balteatus* by around a half. A similar decline of imagines occurred when the floral resources were reduced to one thousandth.

Insecticides affected the mean summer density of imaginal syrphids more indirectly through their impacts on decreasing aphids and less through their toxicity on syrphid larvae (Fig. 8). An increase of the threshold of aphid densities for insecticide application increased the mean density of imagines in summer strongly because this resulted in higher densities of aphids, which the syrphid larvae could eat. Increasing the toxicity of insecticides on larvae decreased the mean summer density of imagines moderately.

4. Discussion

4.1. Pattern-oriented modeling

With SyrFitSources, we developed, as far as we know, the first spatiotemporally explicit ABM that comprehensively models the entire life cycle and the resources and habitats of all stages of syrphids. SyrFitSources is a complex model, integrating important processes of the ecology and life cycle of aphidophagous syrphids. The representation of processes in the model was based on a comprehensive body of literature, which comprised studies of different syrphid and insect species, their behavior and their physiology (Appendix A). Despite uncertainties related to those many sources which we used to parameterize and test SyrFitSources, we were able to reproduce general patterns of active *E. balteatus* as observed in field. The strong increase of active *E. balteatus* in spring and the decline in late summer simulated in SyrFitSources correspond to field studies from Central Europe, which were performed in different regions (Grosser and Klapperstück, 1977; Ssymank, 2001; Stollár, 1968). Thus, SyrFitSources well reproduced general patterns of active *E. balteatus*. However, the model underestimated the number of active syrphids compared to field observations in Lower Bavaria and also the difference between Lower Bavaria and Lower Franconia. The reason may be that both regions did mostly not differ substantially in median coverage of land-cover types per landscape with exception of maize, rape, deciduous and coniferous woods (Fig. 1 in Appendix B).

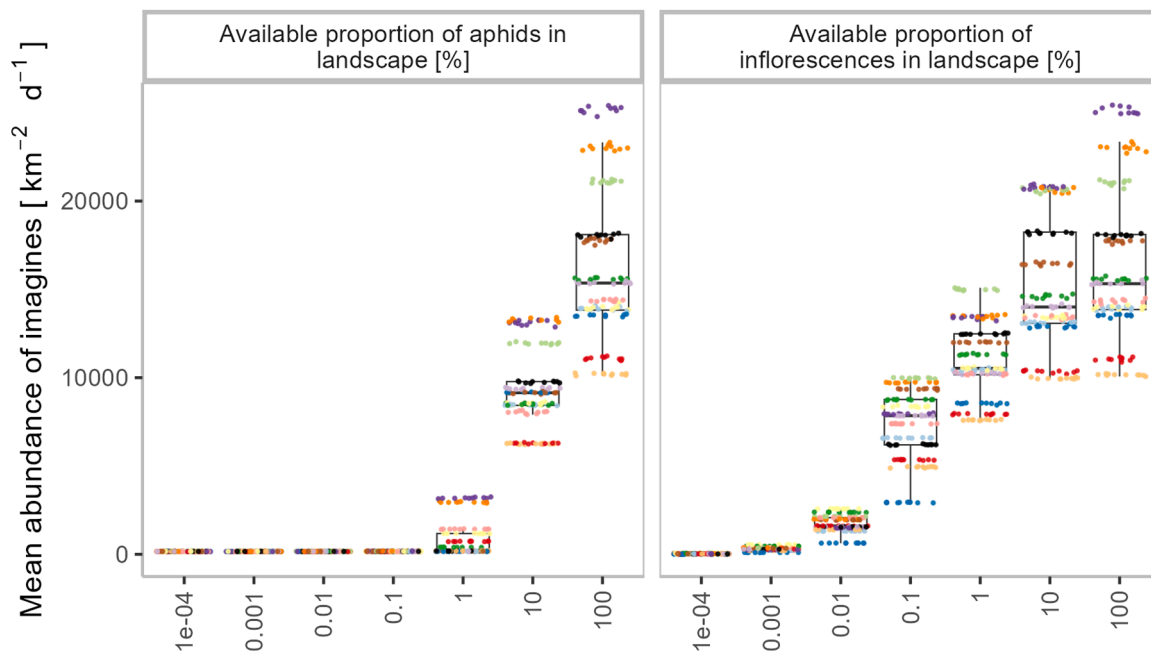


Fig. 7. Effect on the mean imaginal syrphid density in summer (01.06.2011 to 31.08.2011) after proportionally reducing the carrying capacity for aphids on plants and the proportion of floral resources in SyrFitSources for 13 landscapes in South Germany with ten replications of each landscape. Different colors depict results for different landscapes. The first and third quartiles delimit boxes of the mean daily density in all landscapes, with the median indicated as vertical line and the whiskers having 1.5th length of the boxes.

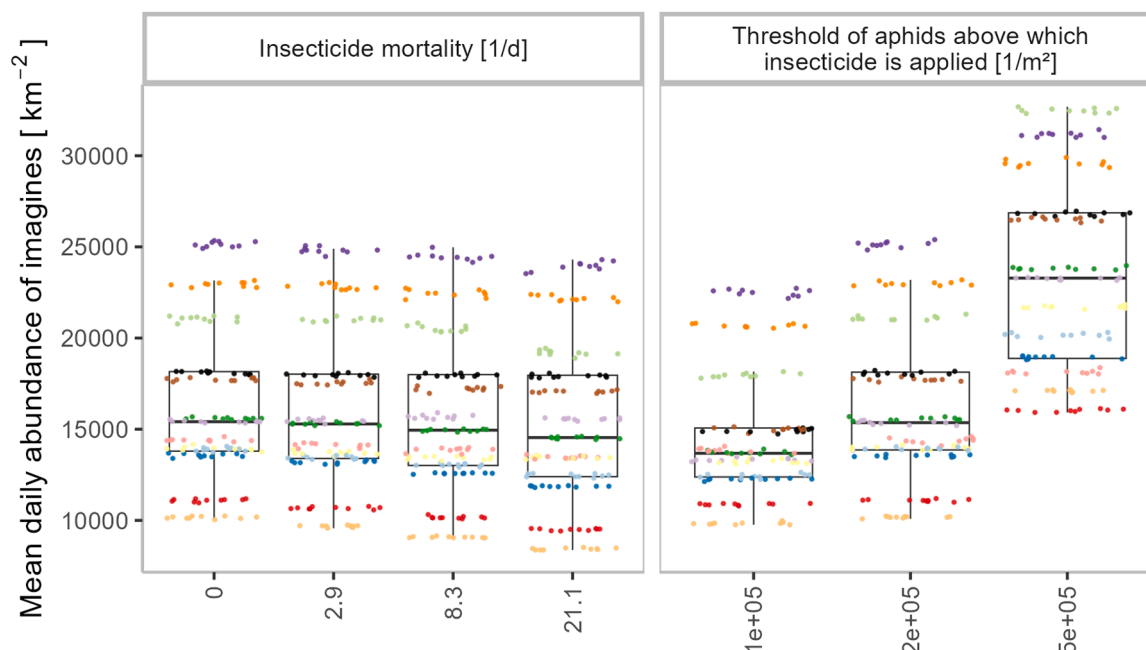


Fig. 8. Effect of insecticides mortality of syrphid larvae and threshold of aphids when insecticide is applied on the density of syrphid imagines in summer (01.06.2011 to 31.08.2011) in SyrFitSources for 13 landscapes in South Germany for ten replications of each landscape. Different colors depict results for different landscapes. The boxes delimit first and third quartiles of the mean daily density across all landscapes, the middle line sings the median and the boxes' whiskers have 1.5th length of the boxes.

Further, we implemented land-cover types in both regions with the same plant communities (Appendix C).

On transect walks in Scotland, syrphids were observed more frequently in habitats with high coverage of flowers than in habitats with low coverage of flowers and they were more active in hedges than in intensively managed wheat or barley (Cole et al., 2017). SyrFitSources reproduced these patterns of habitat-specific active imagines in hedges and in flower areas compared to winter cereals. These findings do not imply that flower-rich habitats per se increase the density of aphidophagous syrphids, because the resource-reduction scenarios suggest that the overall density of *E. balteatus* is much stronger affected by the density of aphids than by the density of flowers (quantity of pollen and nectar) at landscape scale. So, it is likely that flower-rich habitats attract *E. balteatus* from the surrounding landscape and cause accumulation of flies comparable to the concentration effect of pan traps in surroundings with low resources (Westerberg et al., 2021). Likewise, higher numbers of active imagines in flower areas resulted from SyrFitSources for Lower Bavaria, where more landscapes had high proportions of coniferous forests, than Lower Franconia (Fig. 1 in Appendix B), which resulted probably from the high capacity of conifers for aphids in SyrFitSources.

While SyrFitSources simulated realistic numbers of active *E. balteatus* imagines, it underestimated the density of *E. balteatus* larvae in cereals about one order of magnitude compared to the observations by Chambers and Adams (1986). When scaling up Tenhumberg's (1993) and Salveter's (1998) observations of larval density per stem in wheat, with assumed 500 stems m⁻², their observations were in the same magnitude as in Chambers and Adams (1986). However, the timing of the larval peak density in cereals from SyrFitSources is comparable to field observations (Chambers and Adams, 1986; Tenhumberg, 1993). Regarding habitat types, syrphid larvae showed lower densities in sown herb strips compared to wheat in May, June, and July in the field (Salveter, 1998). With SyrFitSources, we could not reproduce this difference in density for flower areas compared to winter cereals, but larval densities were quite equally distributed over most land-cover types with aphid-infested plants, except for maize and sugar beets in June and July. One explanation for this mismatch is that female *E. balteatus* in SyrFitSources are

not selective on aphid species as it was observed in the field (Gilbert, 2005). Hence, they spread their eggs more evenly in SyrFitSources over the habitats than it might be in reality. Salveter (1998) as well stated that eggs and larvae were mostly found on some spontaneously growing weeds, such as *Cirsium spec.*, while other strongly infested plants were without eggs and larvae inside the herb strip. Thus, the absolute numbers of simulated larvae density should be treated carefully unless imagines in SyrFitSources do not select aphid colonies for larvae according to specific preferences (Gilbert, 2005).

During the preparation for SyrFitSources' publication, Mansier and van Rijn (2024) published a spatial implicit but temporal explicit differential equation model for aphidophagous syrphids. This models' purpose was to investigate land use-related predator-prey dynamics of syrphids and aphids in order to improve biological pest control. This differential equation model gave partly similar results like SyrFitSources. For most of the habitats the densities of larvae were similar at peak and occurred around the same time. Though larval density in early crops with flower margins in the differential equation were around a magnitude larger than SyrFitSources results for winter cereals and peaked around a month later. A similar pattern was observed in late crops with flower margins. The maximum densities of the imagines from the differential equation model were similar to the number of active imagines at peak resulted from SyrFitSources except for the hedges. There was a time shift of maximum densities of the differential equation model by one month comparing to SyrFitSources results. The simulated maximum in SyrFitSources was around the beginning of July while the maximum density of imagines simulated by the differential equation model was only reached one month later. Though the timing of the peak occurs in all examined habitats in SyrFitSources around early July, whereas it occurred in all three habitats of the differential equation model around early August. That difference may be caused by gradual satiation of imagines dependent of floral density in the differential equation model (Appendix of Mansier and van Rijn, 2024) whereas satiation is binarily achieved by exceeding a certain threshold of energy in SyrFitSources. Likewise, reproduction was implemented as saturation curve dependent on aphid density in the differential equation model (Appendix of Mansier and van Rijn, 2024), whereas female imagines lay at constant

rate eggs until a certain ratio of eggs and larvae to aphids is exceeded in SyrFitSources.

4.2. Effects of resource reduction on *Episyrphus balteatus* population dynamics

The density of aphids had a strong effect on the density of *E. balteatus*, while the decrease of floral resources had a weaker effect. In the large body of literature, the significant effects of syrphid larvae on aphids were discussed (Almohamad et al., 2009; Dunn et al., 2020; Omkar and Mishra, 2016; Tenhumberg and Poehling, 1995), but to the best of our knowledge, only few studies like the one by Mansier and van Rijn (2024) discussed the effect of aphid density on syrphid density. Also, it was assumed that high aphid abundance in a previous year increased the abundance of aphidophagous *Eu. corollae* in Sweden leading to high numbers of emigrating imagines in 1981 (Svenson and Janzon, 1984). This suggests a strong effect of aphid abundance on aphidophagous syrphids, similar as it was simulated with SyrFitSources. Nevertheless, floral abundance and richness are an important aspect of syrphid ecology, which is positively associated with activity and densities on patch scale (Alison et al., 2022; Cole et al., 2017). Similar to our findings, a saturation effect of floral cover density was found for predatory syrphids in Wales, underlining the importance of floral resources especially at low densities (Alison et al., 2022). This effect could explain, why in other studies covering syrphids no effect of the abundance of floral resources on syrphid abundance could be found (Ferrante et al., 2025; Power et al., 2016). For many plant species, information on floral resources, such as phenology, density of floral units, quantity of nectar and pollen is currently limited or scattered over multiple publications (Baden-Böhm et al., 2022b). Therefore, only a subset of the plants in the flower-strip seed mixture and in plant communities of some landscape elements like the field paths and hedges could be implemented in the model.

4.3. Effects of insecticides on *Episyrphus balteatus* population dynamics

Surprisingly, the direct larval insecticide mortality had a minor effect on the overall summer density of imaginal *E. balteatus* resulted from SyrFitSources, although increased pesticide usage is assumed to be an important driver of syrphid decrease (Barendregt et al., 2022). These results from SyrFitSources suggest that insecticide usage on its own has a small negative impact on syrphid abundance, but combined with other causes it leads to a strong decline (Wagner et al., 2021). However, a strong decline of simulated imaginal density induced by the decrease of aphids from insecticides was remarkable. This suggests that the reported strong decrease of aphidophagous syrphids (Barendregt et al., 2022; Gatter et al., 2020) is mostly caused by reduced aphids as observed in the field (Bell et al., 2020; Crossley et al., 2021; Ewald et al., 2015). Still, the total direct effect of pesticides on syrphid density might be stronger in reality because potential mortality of imagines due to insecticides is not taken into account in SyrFitSources. Also, sublethal effects on imaginal females, which came in contact with insecticides as larvae, like reduced fertility (Moens et al., 2011) should be added for a comprehensive assessment.

4.4. Limitations

The aphid module performed well in the first half of the year up to the typical midsummer crash of the aphid population (Karley et al., 2004). Nevertheless, the aphid module underestimated the aphid numbers in autumn, when a second aphid peak was often observed (Bombosch, 1964, 1965, 1966; Karley et al., 2004). Simulations for periods longer than one year must be run with caution due to the underestimation of aphids in autumn. This probably lowers the number of imagines that enter hibernation and underestimates the abundance in the next year. That could be an important factor regulating the syrphid

abundance in the following year, as a report from Sweden suggests (Svenson and Janzon, 1984).

As mentioned above, a comprehensive pesticide risk assessment would demand an adaptation of the current insecticide module. This also includes a revised parameterization according to a broader range of common pesticides. Some insecticides have no lethal effect at all and some are very poisonous for the larvae (Moens et al., 2011). Also, sublethal effects, like reduced fertility, on the imagines, which came in contact as larvae with insecticides, differ strongly among the used insecticides (Moens et al., 2011).

Surprisingly, SyrFitSources underestimated the number of active *E. balteatus* in Lower Bavaria. We would have expected higher numbers of active imagines there, as the proportion of coniferous forests in Lower Bavaria is often higher. Coniferous forests provide aphids as a food resource in spring and summer and shelter in fall and winter. We assume that the underestimation of active imagines due to the fact that SyrFitSources does not simulate the effect of temperature on the life span of the imagines. At good feeding condition the lifespan of the tropical/subtropical syrphid *Ischiodon scutellaris* is at 30 °C around half to two third lower than at 20 °C (Lal and Haque, 1955). Female *E. balteatus* of unknown age that were caught or reared in late summer could at least survive around 112 to 119 days at median during a warm winter in Northern Germany (Hondelmann and Poehling, 2007). Hence, in SyrFitSources the lifespan of hibernating imagines is probably underestimated as temperature dependence of aging is not considered. Instead, the average of lifespans observed in a greenhouse experiment with fluctuating temperature between 15 and 35 °C (Geusen-Pfister, 1987) was used in the model. This may lead to overestimated mortality and lower density of imagines in autumn, winter, and spring when the temperature is mostly cooler than 15 °C. We suppose that the underestimated lifespans in autumn and spring as well as lower densities of hibernating *E. balteatus* due to underestimated aphid densities in autumn might lead to lower densities in the next summer in SyrFitSources compared to observations from the field. The results of the sensitivity experiments indicate that without immigration the mean spring and summer densities are much lower than in the standard scenarios. This may imply that *E. balteatus* populations in Central Europe heavily depend on migration from the Mediterranean, though this conclusion should be treated with caution due to probably underestimated densities of hibernating flies in SyrFitSources.

4.5. Potential applications

SyrFitSources was developed for modeling land use scenarios on syrphids. More elaborated analyzes of resource composition and configuration, as done for spatial distribution of flower strips for honeybees (Baden-Böhm et al., 2022a) with BEEHAVE (Becher et al., 2014), are also possible with SyrFitSources. Further potential applications of SyrFitSources are case studies, e.g., on the effects of agri-environmental measures as done by Baden-Böhm et al. (2023) for the buff-tailed bumblebee (*Bombus terrestris*) with BumbleBEEHAVE (Becher et al., 2018). With this type of scenario building, SyrFitSources can contribute to a deeper understanding of the demands of syrphids at landscape scale, from which management options for their targeted promotion can be derived. Although a pesticide assessment is not recommended in the current state of SyrFitSources, it might be a promising tool to be further developed in the future.

5. Conclusions

SyrFitSources is to our knowledge the first spatiotemporally explicit agent-based model for aphidophagous syrphids, which includes the complete life cycle and also spatiotemporally explicit availability of resources for syrphid larvae and imagines. In our study, we showed that SyrFitSources was able to reproduce population dynamics from field observations. We recommend that SyrFitSources should be validated on

independent field observations, based on additional monitoring data on *E. balteatus*. This may improve the parameterization and prediction accuracy of the model and also facilitate the temporal and spatial upscaling of these field studies. SyrFitSources can be applied to landscape scenarios concerning the resources of imagines and larvae. Therefore, SyrFitSources should be tested on case studies of several real landscapes and also in scenarios with artificially generated landscapes where selected land-cover types and heterogeneity can be gradually varied. Moreover, SyrFitSources may be developed further to address more specific questions in agricultural management related to, e.g., pesticide risk assessment, effectivity of biodiversity measures, or supply of pollination and biological pest control services.

Data statement

SyrFitSources' code, a complete model description and example inputs are available at <https://doi.org/10.5281/zenodo.13956913> (App et al., 2025). The used parameterization of plants, aphids and the coverages of plants per land-cover type for testing, analyzing, calibration and evaluation of the model and for sensitivity experiment are available in the appendices. Due to data privacy, the used geodata, the exact locations and catches of the Malaise-traps cannot be made available.

CRediT authorship contribution statement

Mario App: Writing – original draft, Visualization, Software, Methodology, Conceptualization. **Niels Hellwig:** Writing – review & editing, Software. **Anne-Kathrin Schneider-Hohenbrink:** Writing – review & editing. **Johannes Burmeister:** Writing – review & editing. **Boris Schröder:** Writing – review & editing. **Jan Thiele:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2025.111098](https://doi.org/10.1016/j.ecolmodel.2025.111098).

Data availability

The model code is shared on the repository Zenodo. The data used for pattern-oriented modeling is not open due to data privacy.

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