Persefone.jl: Modelling Biodiversity in Dynamic Agricultural Landscapes

Daniel Vedder[1,2,3*], Marco C. Matthies[1,3], Gabriel Díaz Iturry[1,3,4], Guy Pe'er[1,3]

Agricultural landscapes are highly dynamic, constantly changing in space and time due to the effects of farm management and environmental factors. To forecast the effects of changes in agricultural systems on biodiversity, we need to understand these landscape dynamics and how they impact different species. Here, we present Persefone.jl, an open-source process-based model of agricultural landscapes and animal species. The model simulates farm management, crop growth, and wildlife animal species using daily time steps in multiple Central European farming regions. We describe the model's structure and carry out initial simulation experiments, showing that the it replicates multiple qualitative and quantitative empirical patterns. We then discuss the model's design principles and possible applications in basic and applied research, including as a tool for policy evaluations. Finally, we give an outlook on prospective further developments of the software.

Keywords: agricultural landscapes, farm management, biodiversity, policy, individual-based model

[1] Department of Biodiversity and People, Helmholtz Centre for Environmental Research - UFZ, Permoserstraße 15, 04318 Leipzig, Germany

[2] Institute of Biodiversity, Ecology and Evolution, Friedrich Schiller University Jena, Dornburger Straße 159, 07743 Jena, Germany

[3] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103 Leipzig, Germany

[4] Departamento de Física, Universidad Mayor de San Simón, C. Sucre Esq. Parque La Torre, Cochabamba, Bolivia

* corresponding author: daniel.vedder@idiv.de

1 Introduction

Farm management affects biodiversity in numerous ways. Some effects are direct, such as disturbances created by tillage, harvest, or pesticide application. Others are indirect, as agriculture shapes landscapes over space and time, both locally and regionally, for instance through the choice of crop rotation, the creation or removal of semi-natural habitat, or the flow of water and availability of nutrients. Together, these effects create spatiotemporal patterns of resource availability and disturbance that influence all non-domestic species living in agricultural landscapes (Vasseur et al., 2013). However, many of these impacts are hard to trace and understand, particularly as their effects are often context- and species-specific.

In Europe, widespread declines of farmland species have been documented for taxa such as birds and butterflies (e.g. Rigal et al., 2023; van Swaay et al., 2019). These have prompted numerous conservation efforts seeking to establish approaches such as wildlife-friendly farming and agroecology (Pywell et al., 2012; Runhaar, 2021). Many of these efforts are conducted at a policy level, using a combination of regulations and subsidies to enforce or encourage agroecological practices. Of particular importance, due to its scope and volume, is the EU's Common Agricultural Policy (CAP), although its practical benefits have been mixed (Pe'er et al., 2014; Pe'er et al., 2020).

From an ecological perspective, there are at least three challenges associated with the design of effective agri-environmental measures. First, the measures must fit in with all the other things farmers do: they must be practicable, and not countered by other management practices (Hölting et al., 2022). Second, they must take into account the varying ecological requirements and behavioural responses of different target species (Vickery et al., 2004). Third, they should be tailored to the bioclimatic and landscape contexts, as different contexts could enhance or reduce the effectiveness of any chosen measure (le Clech et al., 2024).

Simulation models can help assess the likely consequences of changes in agricultural practice, whether policy-induced or otherwise (Topping et al., 2019). While economic simulation models are already widely used for agricultural policy assessments, this is not yet the case for biodiversity models (Reidsma et al., 2018). In a recent review, we identified several reasons that contribute to this (Vedder et al., 2025): First, many current biodiversity models are very abstract, often simulating virtual species and landscapes rather than specific agroecosystems. Second, few biodiversity models simulate the impact of farm management and the spatio-temporal dynamics of landscapes. Third, few models combine ecological and economic perspectives, for example through jointly considering farmer decision-making, crop production, and biodiversity outcomes.

Here we present Persefone.jl, a model of animal populations in dynamic agricultural landscapes that is intended to address these issues. The model simulates management practices and crop growth on real landscapes, and combines this with a suite of individual-based models of wildlife animal species. This allows it to model the spatiotemporal population dynamics of its target species in response to environment and management. Its aim is to further ecological research into the interactions between agriculture and biodiversity, and to provide a platform for rapid policy assessment in the context of European agricultural landscapes.

2 Methods

2.1 Model structure

In the following, we describe the model structure of Persefone.jl using an abbreviated form of the ODD protocol (Grimm et al., 2006, 2010), following the guidance by Grimm et al. (2020) for large models. The full model documentation is available in the appendices and on the model website (https://persefone-model.eu), while a graphical summary of the model structure is provided in Fig. 1.

Persefone.jl is designed to fulfil two *purposes*:

1. To represent the spatiotemporal **landscape dynamics** created by arable farming in Europe, including crop rotations, plant growth, and yield formation.
2. To reproduce the **population dynamics** of a selection of wildlife animal species in response to environmental conditions and agricultural management, considering especially movement, reproduction, and mortality.

To this end, the model simulates three main *entities*, or agents: farmers, crop-growing fields, and wildlife animals. These are each represented by separate *submodels*, which are described in more detail in subsequent sections. All agents are located on and interact with the model landscape, which is created by reading in environmental *input data* for the simulated region. These include satellite-based land cover maps, field geometries, soil type maps, and daily weather data. All required input data are publicly available for Germany (Table 1), and the model website documents how to acquire and process them in order to set up a new study region.

In terms of *processes*, the farm submodel manages the fields in the landscape, choosing which crops to grow where and when to carry out management actions. The crop sub-

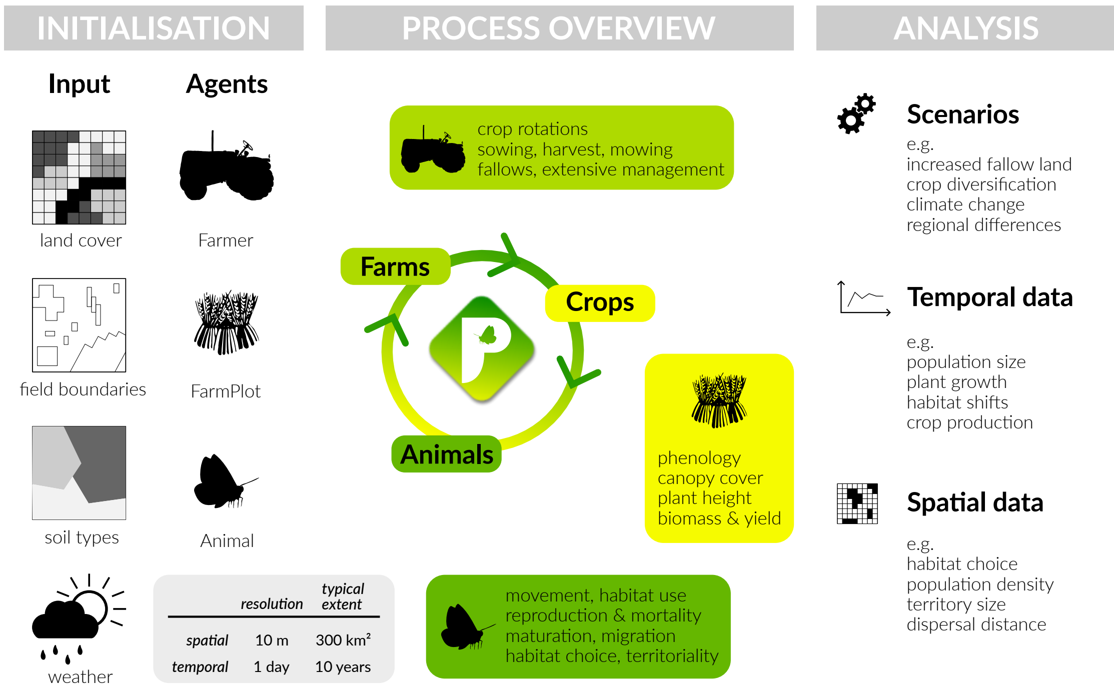

Figure 1: Graphical overview of Persefone.jl. The model contains three major submodels, simulating farm management, crop growth, and animal life cycles.

model simulates the growth of the crop plants on these fields over time, based on the environmental input and farm management. Finally, the animal submodel models the behaviour and life cycle of different indicator species, the individuals of which perceive and interact with the changing landscape created by the other submodels. The model runs at a landscape *scale*, with a spatial resolution of 10 m and daily updates, and a typical extent (depending on the configuration) of around 300 km^2 and 10 years.

The Persefone.jl software is open-source and can be downloaded via its website. It is implemented in Julia, a programming language designed for performant scientific computing (Bezanson et al., 2017). (The ".jl" suffix in the model name denotes that it is available as a Julia package.) Due to its significant computational demands, it is primarily intended to be run on a high-performance computing cluster (HPC). However, individual simulations can be run on a personal computer, and a simple graphical user interface is available for this purpose. For more details, see the user manual in Appendix A.

Table 1: Data sets used as input, for calibration, or for validation. All data are publicly available for our study regions. For links to the sources, see the user manual in Appendix A.

Data	Description	Purpose	Source
Land cover	Satellite-derived raster map of six different land cover classes (10 m resolution, year 2020).	input	mundialis GmbH & Co. KG
Field geometries	Shape files of all fields registered in the EU Land Parcel Information System (LPIS; in Germany: InVeKoS).	input	Thüringer Landesamt für Landwirtschaft und Ländlichen Raum
Soil types	Shape file map of soil types (i.e. different mixtures of clay, silt, and sand).	input	Bundesanstalt für Geowissenschaften und Rohstoffe
Weather	Daily observations of standard meteorological variables from the closest weather station.	input	Deutscher Wetterdienst
Crop phenology	Annual observations of the onset of growth stages (e.g. emergence, flowering, harvest) in different plant species.	calibration / validation	Deutscher Wetterdienst
Crop yield	Annual district-level average yields per hectare.	calibration / validation	Thüringer Landesamt für Statistik
Plant growth	Measurements of crop parameters (e.g. height, biomass) during the course of the growing season.	calibration	Reichenau et al. (2020)
Butterfly monitoring	Population trends of butterflies in Germany.	validation	Kühn et al. (2024)
Common bird monitoring	Population trends of common breeding birds in Germany.	validation	Busch et al. (2020)

2.1.1 Farm management

The farm submodel defines a FARMER agent who manages a collection of agricultural fields. In the current model version, a single agent is responsible for all fields in the region, and manages them using a set of configurable practices related to crop rotations, fallows, and grassland management (cf. Table 2).

Crop rotations are defined as a set of crops that are grown sequentially on a given field. Each crop is harvested when it is ripe (as determined by the crop submodel) and the next one sown according to its planting schedule (taken from the agronomic literature). Each year, a number of fields can be left fallow. Grassland is managed either intensively (with 4-5 cuts per year) or extensively (with 2 cuts per year). The proportion of meadows managed extensively is configurable, as is the proportion of arable land left fallow. Currently, management practices that are explicitly simulated are sowing, harvest, and mowing.

2.1.2 Crop growth

The purpose of the crop component is twofold: First, it simulates how agricultural landscapes change ecologically over the course of a year, as different stages of crop growth provide different degrees of habitat quality to wildlife species. Second, it estimates yields, enabling Persefone.jl to provide economically-relevant output alongside the ecological simulation results.

The crop submodel provides the FARMPLOT entity, which is initialised for every arable and grassland field in the simulated region. The farmer (see above) decides when the field is to be sown with a given crop, and when it is to be harvested or mown. Between sowing and harvest (and year-round for grassland) the crop component models how the plants on the field grow. Specifically, it simulates four main output variables: plant height, canopy cover, crop maturity, and yield. These values are available to both the farm and the animal components, and can be used for instance to decide when to harvest or to calculate habitat suitability.

To simulate these variables, Persefone.jl can use two different crop models. The primary crop model is AquaCrop, originally developed by the FAO and translated into Julia for use in Persefone.jl (Díaz Iturry et al., 2025). AquaCrop is an intermediate-complexity process-based crop model, which simulates plant growth and maturation based on water availability, meteorological parameters, and soil quality (Raes et al., 2009; Steduto et al., 2009). It has been used for numerous crops worldwide and is known to be quite reliable

Table 2: A selection of important model configuration parameters. The full list of parameters can be found in the user manual in Appendix A, species-specific parameters are given in Appendix C.

Parameter	**Default value**	**Description**
`seed`	2	The numeric value that is used to seed the random number generator. Simulation runs with identical configuration will have identical outcomes.
`startdate`	2011-01-01	Date on which to initialise the simulation.
`enddate`	2020-12-31	Date on which to terminate the simulation.
`region`	"jena"	Name of the region whose input files will be loaded to create the model landscape.
`farmmodel`	"BasicFarmer"	Which implementation of the farm submodel to use (currently, only one is available).
`croprotation`	["winter wheat", "winter rape", "maize", "winter barley"]	The name and order of crops to use as the crop rotation on arable fields.
`setaside`	0.04	Proportion of arable land set aside as annual fallow.
`extensivegrassland`	0.6	Proportion of grassland managed extensively.
`scenarios`	[ ]	Names of scenarios to apply. (Scenarios are functions that can change configuration settings during the course of a run, or otherwise modify the behaviour of the farm submodel.)
`fieldoutfreq`	"daily"	Frequency with which to output data related to field use and crop growth.
`cropmodel`	"almass,aquacrop"	Crop model(s) to use.
`targetspecies`	["MarbledWhite", "Skylark"]	List of animal species to simulate.
`popoutfreq`	"daily"	Frequency with which to output population-level data from the animal submodel.
`indoutfreq`	"monthly"	Frequency with which to output individual-level data from the animal submodel.

(Kostková et al., 2021; Mialyk et al., 2024). While there are default parameter values available for many crop types, to achieve maximum accuracy, the model needs to be calibrated with regionally-specific crop growth data. These can however be difficult to acquire.

Therefore, Persefone.jl complements AquaCrop with a second crop model, namely the vegetation component of the ALMaSS ecosystem model (Topping et al., 2003; Topping & Duan, 2024). This is a simple correlative model, predicting plant growth based on growing-degree days (i.e. temperature) and time of the year. While it is much less exact than AquaCrop (not least because it does not incorporate rainfall), it has parameters available for a wide range of crop types, and can also simulate grassland and some non-crop vegetation types. We therefore use it as a fallback for those crops and plants for which AquaCrop parameters are not available.

A fuller description of the two crop models, together with details about their calibration and validation, may be found in Appendix B.

2.1.3 Animal species

It is the animal submodel that produces the main ecological output of Persefone.jl, namely the abundance and distribution of the wildlife species over time and space. To do so, it models the behaviour, reproduction, and mortality of individual animals in the changing landscapes created by the other components.

Each target species is represented by a separate individual-based model, custom-coded with its own set of rules and parameters. Within each species model, the life cycle of the species is decomposed into a series of "life phases". These provide a conceptual framework to structure the differing behaviour and physiology of individuals across their lives, e.g. as a larva, on winter migration, or as a breeding adult (cf. Uchmański & Grimm, 1996). Practically, they are implemented as software functions that determine an individual's daily behaviour during each part of its life history, and decide when and under which conditions it switches to a different phase.

All species models can at any time access the full state of the simulation, such as the current weather, local land cover, or the state of crop plants in a given field. Individuals are notified of management actions affecting their current location, and can interact with other individuals, including those of different species. An integrated data logging system keeps track of a set of basic state variables, and can be extended by the species models to output more detailed information for model analysis.

2.2 Model setup

Following the above description of the fundamental model structure, we now describe how we set up Persefone.jl for our first study. The aim of this study was to demonstrate that the model is capable of reproducing spatiotemporal landscape dynamics as well as individual- and population-level patterns of ecologically very different animal species. For this, we simulated a bird and a butterfly species in three regions in Central Europe.

Persefone.jl was developed within the research project CAP4GI, which worked together with farmers in six regions in Germany to develop recommendations for novel agri-environment measures in the CAP (Velten et al., 2023). For the study we report here, the model has therefore been set up to simulate the three Thuringian regions in this project: Jena, Eichsfeld, and the Thuringian Basin. These range in size between 270 km^2 and 370 km^2 and form a gradient of increasing land use intensity (Fig. 2).

We used economic survey data from our study regions (G. Theilen, *pers. comm.*) to select a typical cropping sequence that is by default carried out on all arable fields in the model (with a randomised starting point): oilseed rape, winter wheat, silage maize, and winter barley. We calibrated AquaCrop for these four crops for each region, while using ALMaSS to model grass growth.

Next, we implemented and tested two animal species: the skylark *Alauda arvensis* and the marbled white *Melanargia galathea*. In both species, model design was kept deliberately simple, concentrating mainly on the environmental factors with the largest demographic impact, and the behavioural patterns directly affected by landscape and management. Other factors and behavioural patterns were ignored or strongly simplified, in order to keep the models to the minimum necessary complexity (Sun et al., 2016).

The skylark is a common and charismatic species of agricultural landscapes, which breeds on the ground in open areas. Though still common, it has lost over 50 % of its population in Germany over the past decades, due to various factors related to agricultural intensification (Busch et al., 2020). Of particular concern is the increased mortality due to a higher frequency of mowing in grassland, coupled with the increased proportion of less-favoured winter cereals, which pushes skylarks to breed preferentially in the (frequently mown) grassland. This ecological trap has been observed repeatedly and discussed extensively in the agroecological literature (e.g. Donald et al., 2002; Jenny, 1990; Poulsen et al., 1998).

The phase cycle of the skylark model (Fig. 3a) begins in spring, when the birds return from their winter migration. Males return first and begin to look for a territory of suitable size and location. Females return a little later and proceed to look for an unmated male

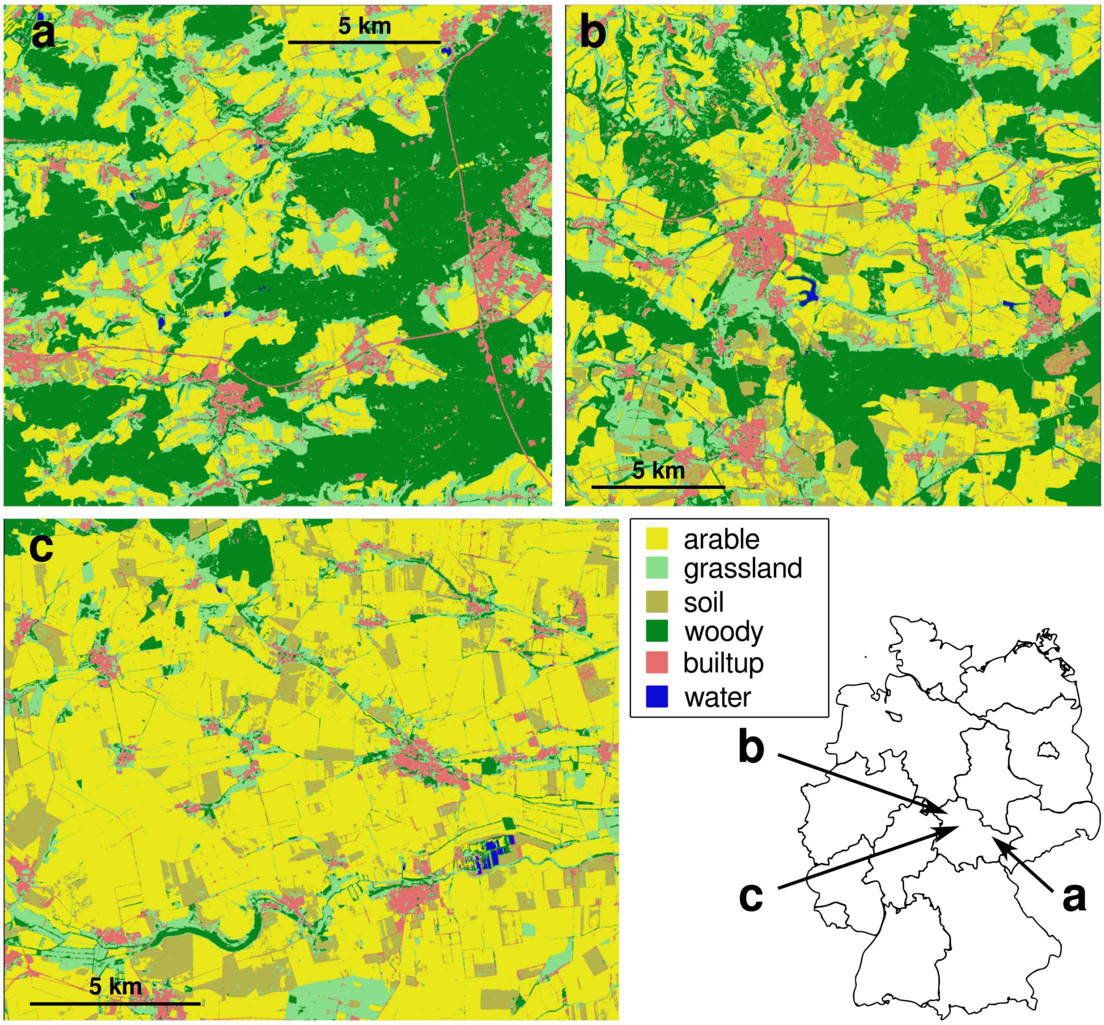

Figure 2: Regions simulated in this study: a) Jena, b) Eichsfeld, c) Thuringian Basin. Inset shows location of regions on a map of Germany. Landcover maps generated with data by mundialis GmbH & Co. KG (2021).

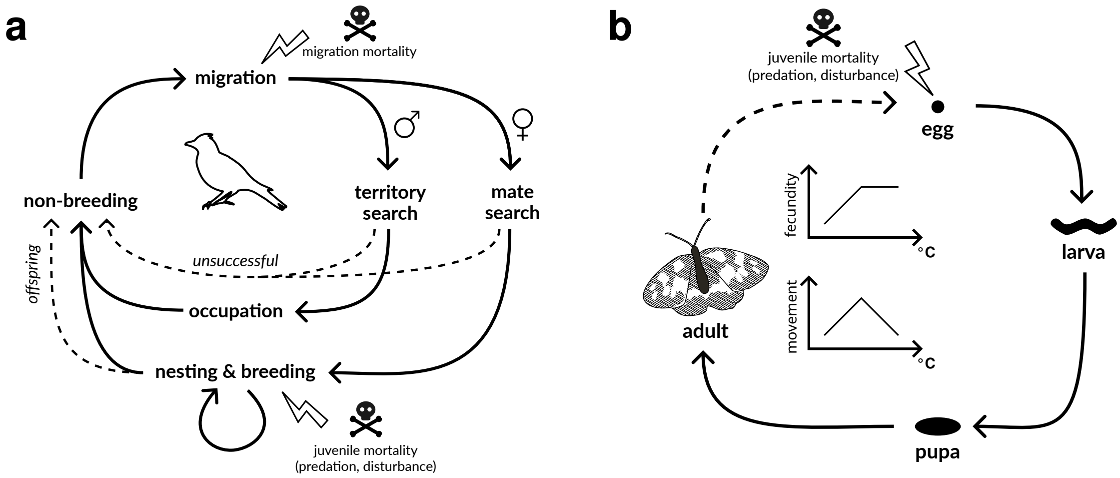

Figure 3: Animal model phase charts: a) Skylark *Alauda arvensis*, b) Marbled White *Melanargia galathea*.

with a territory with whom they can partner. After mating, a female will build a nest in the male's territory and raise a brood. If the brood has either fledged or is lost due to predation or harvest, she begins a new nest as long as the breeding season is not yet over. After the breeding season, skylarks forage non-territorially in small groups, before leaving for migration in autumn. Interaction with farm management thus revolves around breeding: crop growth affects territory and nesting site choice, and harvest/mowing is an important cause of mortality.

Marbled white butterflies are univoltine grassland specialists that fly in June–August. While highly abundant in some places, and showing a slight positive trend overall in Germany, they do not tolerate intensive grassland that is frequently mown (Reinhardt et al., 2021). They are also subject to strong population fluctuations caused by weather affecting their reproductive rate (Roy et al., 2001).

In the model (Fig. 3b), adult marbled whites are presumed to move randomly across suitable habitat, with a certain chance of crossing into unsuitable habitat. Only females are simulated, which lay a number of eggs each day as they fly. The distance moved and the number of eggs laid each day is temperature-dependent. As eggs and larvae develop on the ground, mortality from mowing is low; most is caused by predation (represented as a constant probability in the model). Thus, their main interaction with farm management is indirect, as they avoid grassland that has been fertilised or recently mown.

The full ODD documentation for both animal models is provided in Appendix C.

2.3 Model validation

Throughout the modelling process, we employed multiple techniques to ensure that the individual submodels and the complete model are adequate for their intended purpose (Troost et al., 2023). In this case, the first purpose defined above (landscape dynamics) is addressed by the farm and crop submodels; the second (population dynamics) by the animal component and its interactions with the rest of the model.

In addition to this scientific validation, we used software development best practices, including unit testing and code reviews, to verify the technical correctness of our software (Ropella et al., 2002; Vedder et al., 2021).

2.3.1 Landscape dynamics

The function of the farm submodel is to carry out the crop rotation and sow, harvest, and mow fields at the appropriate time. This was verified using visual inspection of field-level summary statistics, to track the sowing and harvest of the different crops over time.

The crop submodel is intended to produce reasonable estimates of crop growth and phenology under the given environmental conditions. We used publicly available data sets of district-level yield and phenology data from our study regions to calibrate the AquaCrop model, then used cross-validation to test the robustness of the calculated parameters. The ALMaSS crop model is currently only used to generate grass growth patterns, the sufficient correctness of which we confirmed visually. For more details on the calibration and validation of the crop component, see Appendix B.

2.3.2 Population dynamics

As is common in individual-based models, we were most concerned with the structural validation of our target species models, as our aim was to reproduce population dynamics from individual-level mechanisms (Troost et al., 2023). For this, we used pattern-oriented modelling (Gallagher et al., 2021; Grimm & Railsback, 2011), using the empirical literature to identify a set of ecological patterns at different spatial, temporal, and organisational scales for each species. We then tested whether these patterns emerge from the model output mechanistically, i.e. without having been explicitly programmed in.

For the skylarks, we looked at three different patterns. The first was the size of territories, which were generated procedurally in the model, and are known to vary depending on the landscape. The second was the choice of nesting habitat, which depends on the crops available and changes over the course of the breeding season. The third was the ecological trap described above, where the agricultural switch from spring to winter cereals pushes skylark nest-building onto frequently-mown grassland, resulting in population declines. To study these patterns, we set up a simulation experiment with four different scenarios, varying the grassland usage intensity (20 % or 80 % intensive grassland) and the use of winter-sown crops (spring wheat and spring barley or winter wheat and winter barley in the crop rotation). Each scenario was run for each region from 2011–2020.

For the marbled white, we considered multiple "simple" patterns: the number of eggs laid in a female's lifetime, the proportion of time spent moving through different habitats, the local population density, and the lifetime displacement distance. In addition, we selected a "complex" pattern, namely the population development as recorded by the German butterfly monitoring scheme (Kühn et al., 2024). This shows a strongly fluctuating, but overall decreasing trend from 2006 to 2015, followed by an increasing trend from 2016 to 2023. The fluctuations in the first period correlate with the previous year's mean summer temperature. These patterns we tested by running five replicate simulations in each region from 2006–2022.

Alongside this pattern-oriented modelling, we used exploratory simulations to test the response of the model to different parameter values and combinations, and to identify particularly sensitive parameters (see Appendix C for an overview of parameters and values tested).

3 Results

The model output shows how the modelled landscape changes over time due to farm management and crop growth. Fig. 4 shows this at a landscape perspective, tracking how the proportion of different crops changes over the course of several years, and how the average plant height of each crop changes over the growing seasons. Fig. 5 gives a field-level perspective, showing the development of the other four AquaCrop output variables (canopy cover, biomass, phenological stage, yield) from sowing to harvest. Fig. 6 shows validation of the AquaCrop model for silage maize, depicting goodness-of-fit of four output variables against empirical data from the three study regions. (For more details on the crop model validation, see Appendix B.)

The skylark model conforms well to the patterns against which we tested it. Territory sizes in the most intensive scenario ranged from 0.38–24.76 ha, with a median of 1.09 ha and an interquartile range of 0.81–1.56 ha. These values are coherent with the observations listed by Glutz von Blotzheim and Bauer (1985), which range between 0.17–46 ha,

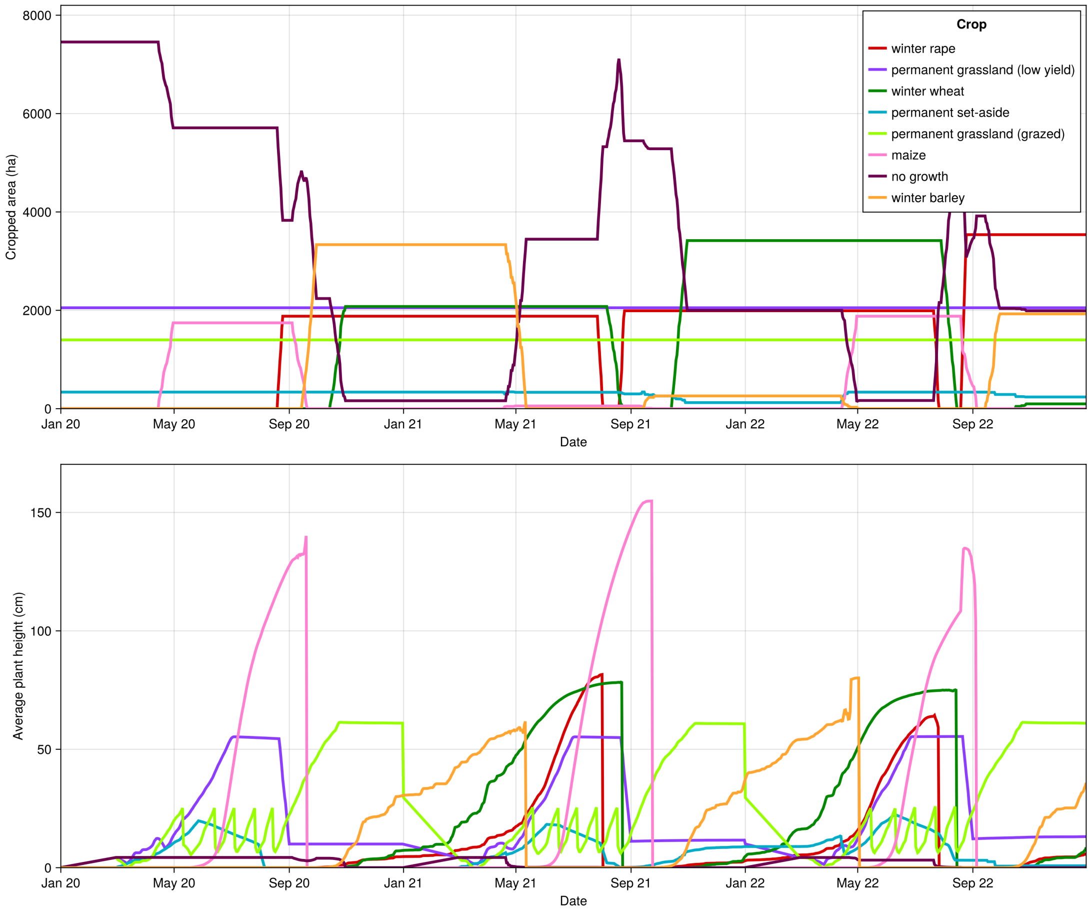

Figure 4: Field and crop dynamics generated by Persefone.jl, simulated in Jena from 2020–2022. Above: area of agricultural land sown with each crop type over time. Below: average plant height of crops over time. "No growth" refers to fields that are not currently sown with any crop (at the start of the simulation or between harvest and re-sowing).

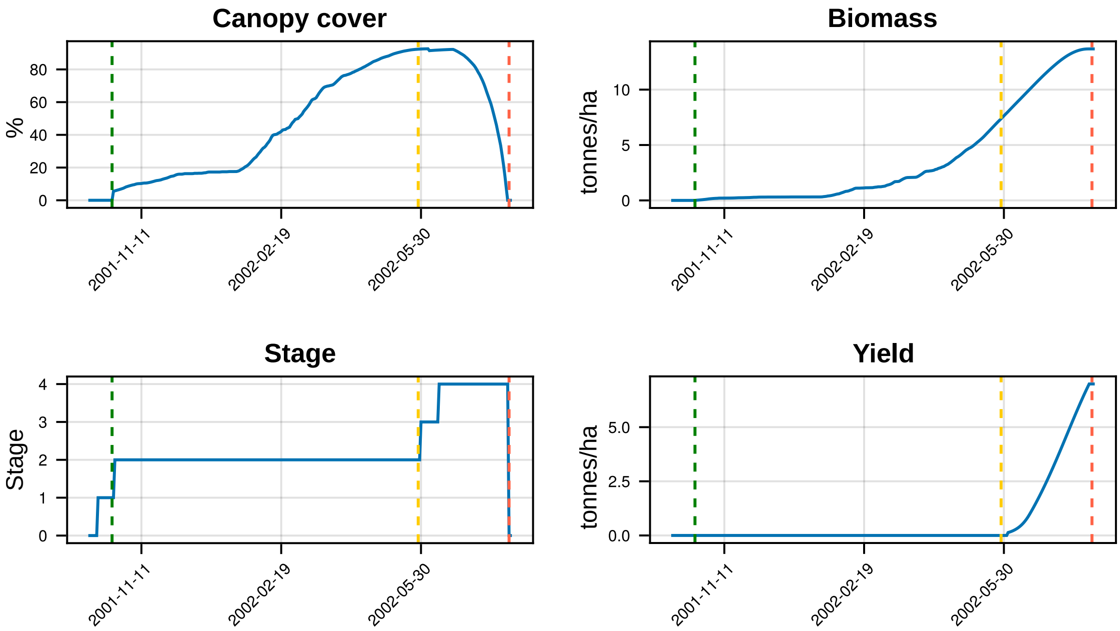

Figure 5: Output variables of the AquaCrop model, showing a simulation of winter wheat in the Jena region. Blue lines show model output over time. Dashed lines show empirically observed phenological dates from the region (green: emergence, yellow: flowering, red: harvest).

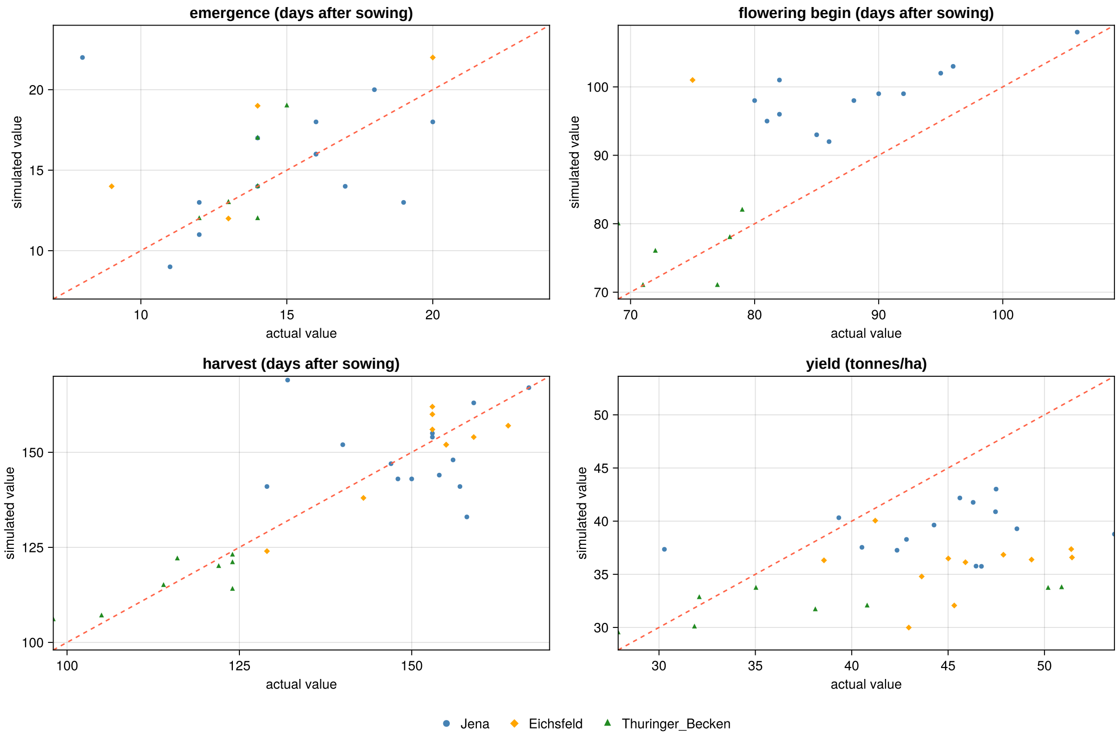

Figure 6: Output of the AquaCrop model compared to empirical data from the study regions, shown here for silage maize. The red line is the $x = y$ line, i.e. points above the line are overestimated, points below the line underestimated by the model.

and are most commonly around 0.5–1.5 ha. We also observe the effect that territory sizes in extensively used farmland are smaller—the scenario with the lowest land use intensity gave an interquartile range of 0.74–1.26 ha and a median of 0.96 ha. Thus, the species model successfully reproduces both the general size of territories as well as their landscape dependence.

Likewise, the choice of nesting habitat over the breeding season (Fig. 7) closely follows the description of Jenny (1990). In his observations, as in our model, grassland is always a favoured habitat; winter barley is almost never used, as it grows too quickly; winter wheat still occurs early in the breading season, but disappears later; while maize is more used in the later season. Overall, there is a decrease of nesting attempts towards the later breeding season, associated with a loss of suitable habitat. This shows that the species model's simple rules, in which nest site selection is primarily based on vegetation height, interacts with the crop submodel to recreate empirically observed patterns of nesting habitat.

The ecological trap of agricultural intensification is also very visible (Fig. 8). Across regions, skylark population grow in the scenario with mostly extensive grassland usage and spring-sown crops, while they decline in the scenario with intensive grassland usage and winter-sown crops. Scenarios with either intensive grassland usage or winter crops show intermediate but landscape-dependent trends: skylarks in the almost entirely arable Thuringian Basin respond very strongly to spring or winter crops, but little to grassland usage intensity, while the response is more mixed in the other regions.

For the marbled white, the collected lifetime variables also correspond well to known literature values (Fig. 9). Fecundity peaks at around 120 eggs/female, which is in the range given by Reinhardt et al. (2007). Lifetime displacement is usually below 1 km, but can reach up to 8 km, which agrees with the results of capture-mark-recapture studies (e.g. Vandewoestijne et al., 2004). In terms of movement, unmanaged and extensively managed grassland are the primary habitats used, although some dispersal movement through other habitat types also takes place (cf. Baguette et al., 2000; Lenda & Skórka, 2010).

In terms of the population development, the marbled white model replicates the Germany-wide trends to a certain extent (Fig. 10). As with the monitoring data, the model data too show an initial period of population decline, followed by stabilisation and (partly) increase. The effect of the weather can also be seen, with pronounced population peaks happening especially in 2007 and 2021, when a hot summer was followed by a cold one. However, the regionally-simulated populations do not follow the national monitoring data

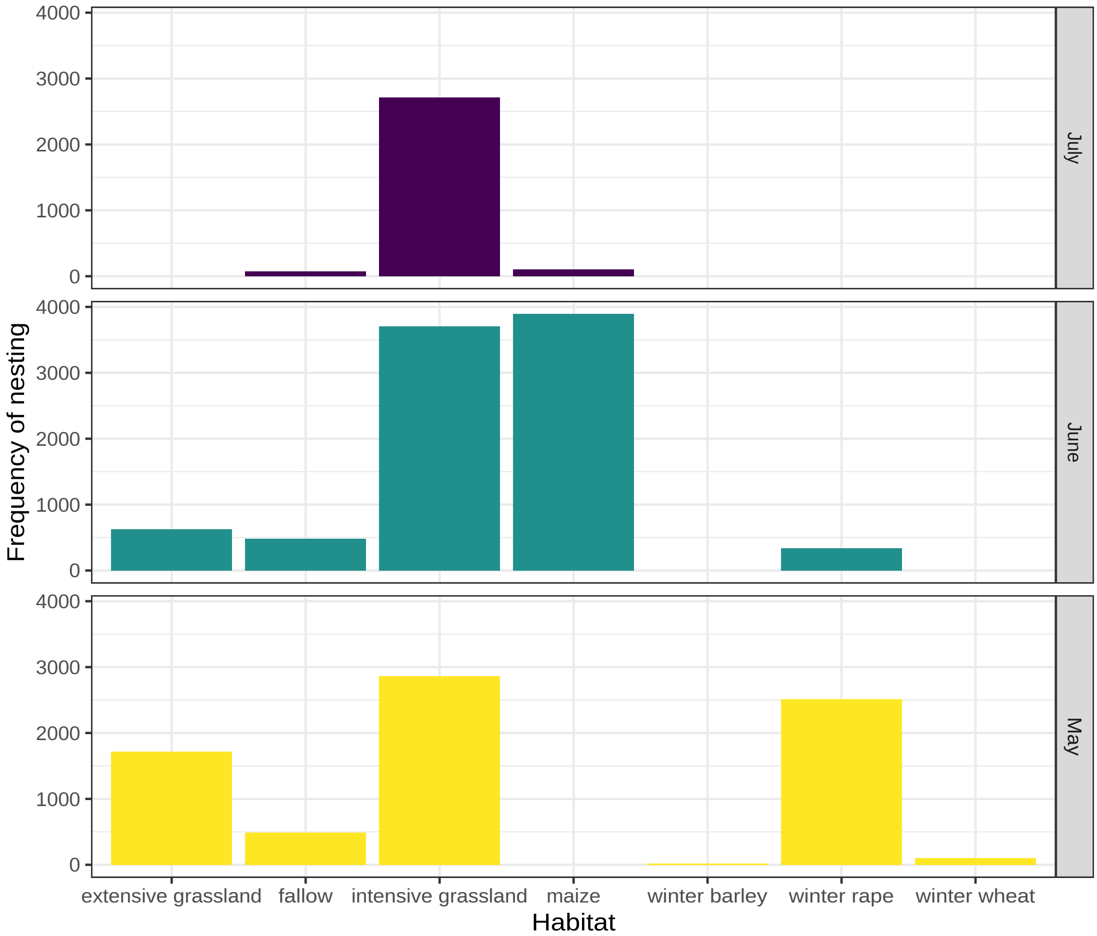

Figure 7: Habitat usage by nesting skylarks over the summer months. Data from a 10-year simulation run (2011-2020) in Jena under the intensive grassland / winter cereal scenario (cf. Fig. 8).

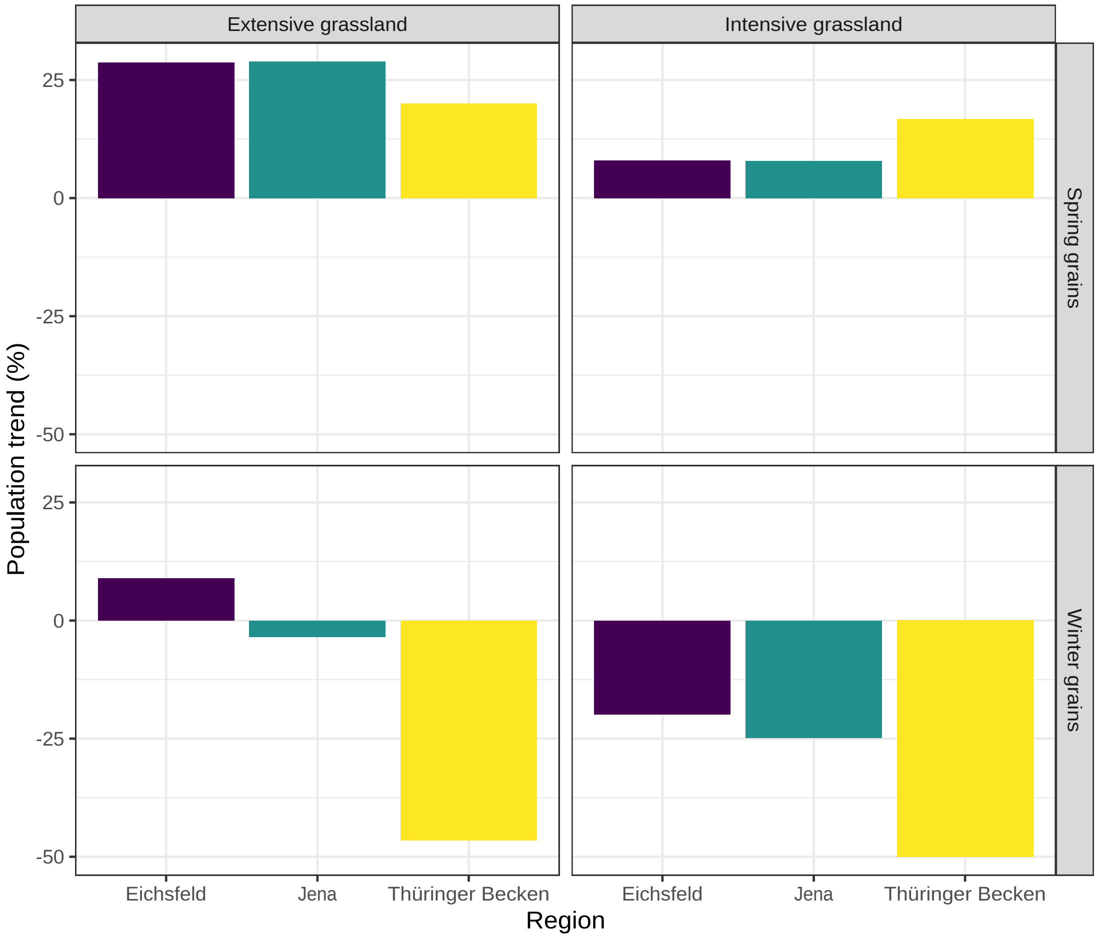

Figure 8: Skylark population trends in four different land-use scenarios in the three model regions. Trends are given as percentage increase/decrease after 10 simulated years (2011-2020).

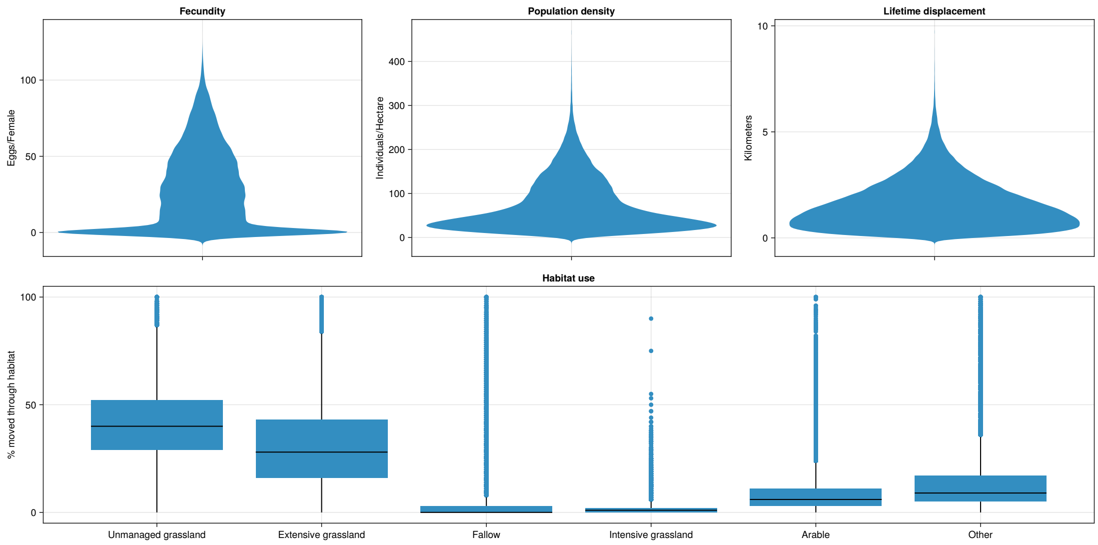

Figure 9: Pattern-testing for the marbled white model, showing several lifetime variables. Top left: Number of eggs laid by each female. Top center: Population density experienced by each individual (i.e. number of conspecifics in the surrounding hectare). Top right: Distance of the location at death from the location at birth for each individual. Bottom: Proportion of movement steps taken in different habitat types.

in detail: the year-to-year fluctuations are less pronounced in the model, and the degree of stabilisation or recovery after 2015 diverges quite widely. Indeed, differences in the weather in the three regions (Eichsfeld is coolest, Jena warmest) lead to quite different population trajectories. This suggests that the national trend hides significant regional variation, a hypothesis that could be tested with more detailed empirical data.

4 Discussion

4.1 Key features of Persefone.jl

Vedder et al. (2025) identified a need for new agroecological models that simulate real species and landscapes, explicitly represent farm management and landscape dynamics, and link ecological and economic perspectives. Persefone.jl is designed to fill this niche, in order to provide a model that can give insights into the interactions between agricultural management and wildlife species in European landscapes.

As the study results above show, Persefone.jl can successfully reproduce both landscape dynamics and population dynamics of real agroecosystems. One feature of the model

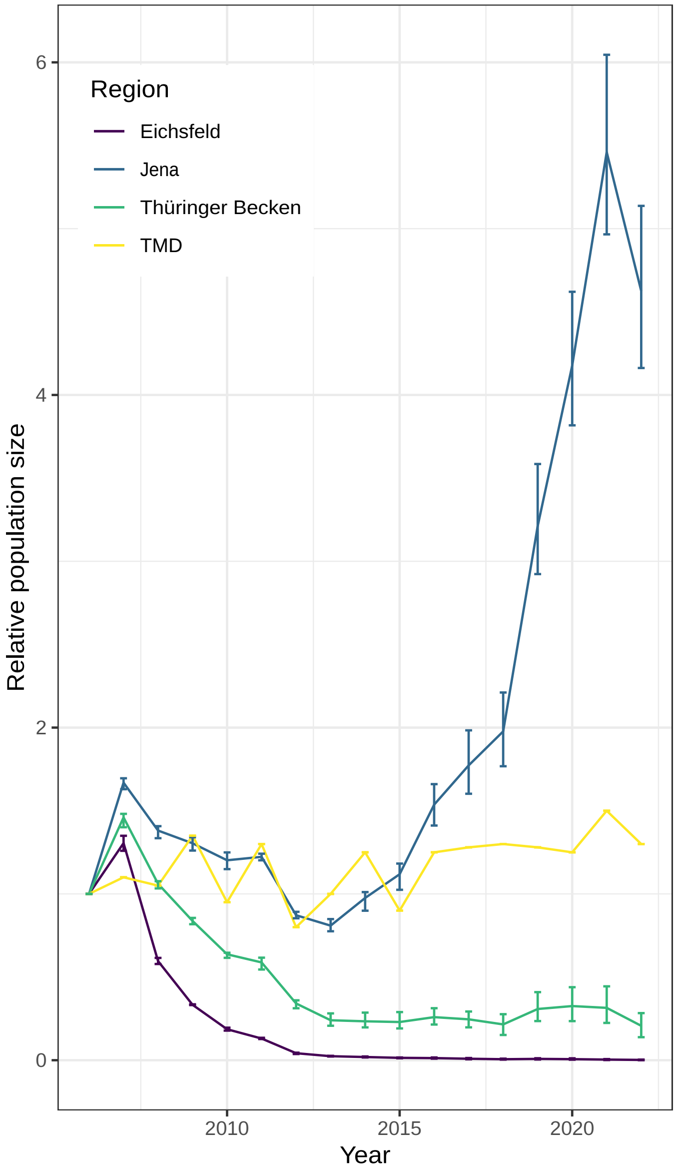

Figure 10: Marbled white population development in the three model regions from 2006 to 2022, compared with the national trend collected by the German butterfly monitoring scheme (TMD). Each line shows mean population size of five replicate simulation runs, relative to the population size in 2006; error bars show maximum/minimum values. TMD trends taken from Kühn et al. (2024).

that is particularly important to both of these aims is the inclusion of the crop growth submodel. As Vedder et al. (2025) argued, modelling crop growth is crucial for linking the human and natural domains of agriculture. One the one hand, explicitly modelling crops allows the model to track intra-annual changes to habitats and resources in the landscape, as well as disturbance events caused by farm management (Marrec et al., 2022; Vasseur et al., 2013). The importance of this for biodiversity is seen clearly in the example of the skylark model above. On the other hand, crop growth is the foundation of arable agriculture, and therefore key to including agronomic and economic perspectives. Modelling crops allows the farm submodel to take management decisions (e.g. date of harvest) dynamically, depending on annual conditions and not just a preset schedule. It also allows the model to collect data on yields, enabling an economic comparison of scenario outcomes as well as an ecological one. For these reasons, integrating crop growth in agroecological models is a major step towards a truly social-ecological modelling of agriculture.

Here, it should be noted that a comparable model to Persefone.jl is already available. This is ALMaSS, which has a long track record of use in agroecological research (e.g. Topping et al., 2003; Topping et al., 2019). While the aim and design of Persefone.jl and ALMaSS are quite similar (and we make use of their vegetation submodel), we understand our model to be a complement to ALMaSS in three ways. First, it is important for a research community to have multiple models studying the same question, as this leads to more robust understanding and predictions (Hooftman et al., 2022; Rosenzweig et al., 2013). Second, our modelling approaches differ: while ALMaSS embraces complexity and consistently chooses the highest-realism implementation option possible (cf. Topping et al., 2015), Persefone.jl pursues a policy of minimum-necessary complexity, leaving out any details that are not significantly important to the modelling purpose (Sun et al., 2016). And third, Persefone.jl gives a much greater priority to ease of use, transferability, and extensibility, with the intention that the software can be used by researchers independent of our own group.

This last point is important, as another feature of Persefone.jl is its strong focus on modularity and extensibility. The model is designed to be readily adaptable in three dimensions. First, configuring the model for a new study region can be done within a few hours, given the publicly available input data and the semi-automated import process (at least for regions within Germany). Second, implementing new animal species is doable in a matter of weeks. For this purpose, the animal submodel provides a domain-specific language (Holst & Belete, 2015) that has a succinct and readable syntax for defining new species, and also offers a set of inbuilt functions for common tasks. Third, the farm and crop submodels can be extended with new crop species and management scenarios, or even replaced with other equivalent submodels. The modular structure of the source code means that different implementations of these submodels can be slotted in, as long as they conform to a basic software interface (Vedder et al., 2024). This also opens up the possibility of coupling Persefone.jl to other agricultural or environmental models, such as models of farmer decision-making or soil processes. For all of these use cases, an emphasis on software quality and documentation is meant to ensure that the model can be successfully used by other researchers (McIntire et al., 2022; Vedder et al., 2021).

4.2 Potential for future research

With its integrated modelling of farm management, crop growth, and animal life cycles, Persefone.jl offers wide-ranging possibilities for agroecological research, spanning the continuum of basic to applied research.

In terms of basic research, Persefone.jl can provide a platform for modelling individual animal species in agricultural landscapes. For instance, the marbled white species model presented above could be used to further investigate the physiological mechanisms of temperature-dependence in butterfly population dynamics, ideally in a study that combines modelling with empirical work (as envisaged by Stillman et al., 2015). Other ecological modellers may also find the existing structure of Persefone.jl a useful basis to build their own species models on. Furthermore, the model's use of weather data means that questions related to climate change can be addressed by importing weather forecasts generated by climate models (Cabral et al., 2023), while the model's dynamic landscapes enable studies looking into the effects of intra-annual resource fluctuations and habitat changes (Katna et al., 2023; Schellhorn et al., 2015).

Beyond purely ecological research, Persefone.jl has the potential to become a tool for social-ecological research. Future expansions of the farm submodel (for example by coupling with existing agent-based models) can complement the model's biodiversity focus with a socio-economic perspective. This would allow pursuing new research questions, for instance tracing the impact of global market changes or behavioural factors on farmer decision-making and agroecosystems (cf. Drechsler, 2020). The simulation of crop growth in Persefone.jl also opens up the possibility of using it to study the feedback of biodiversity on food production through the action of ecosystem services, although this is currently still a major research challenge (Alexandridis et al., 2022; Seppelt et al., 2020).

Looking at more applied research questions, the ability to quickly set up new regions and management scenarios in Persefone.jl make it a promising instrument for policy advice. This, indeed, was one of our major reasons for creating the model, as currently there are few biodiversity models in active use in the EU policy arena (Candel, 2022; Reidsma et al., 2018). Here, the aim is to be able to provide rapid forecasts of the likely ecological effects of proposed policy changes (e.g. the recent derogation of the CAP's fallows regulation, or new agri-environment schemes), in order to support scientists and policy makers working on agricultural policy (cf. Pe'er et al., 2025; Will et al., 2021).

In outlook, our two highest priorities for the further development of Persefone.jl are the implementation of further animal species models and the integration of an economic farm submodel. Our aim is to build up a portfolio of indicator species models: wildlife species that cover a broad range of complementary niches, and can be considered representative of typical Central European agroecosystems. In addition, we will couple Persefone.jl to a socio-economic model of farmer decision-making, in order to explore some of the social-ecological and policy questions outlined above.

4.3 Conclusion

We present Persefone.jl, a process-based model of wildlife animal populations in dynamic agricultural landscapes. By simulating farm management, crop growth, and animal behaviour, we capture both direct and indirect effects of agriculture on species' demographics. Pattern-oriented modelling confirms that our mechanistic approach can reproduce empirically observed phenomena. We therefore make Persefone.jl available as a tool for agroecological research and policy evaluation.

Acknowledgements

The authors warmly thank the other members of the CAP4GI consortium for their excellent collaboration throughout the project, as well as our colleagues in the Department of Biodiversity and People for their support. DV, MCM, and GDI are funded through the project CAP4GI by the Federal Ministry of Education and Research (BMBF), within the framework of the Strategy, Research for Sustainability (FONA, www.fona.de/en) as part of its Social-Ecological Research funding priority, funding no. 01UT2102A. Responsibility for the content of this publication lies with the authors. DV, MCM, and GP gratefully acknowledge the support of iDiv, funded by the German Research Foundation (DFG–FZT 118, 202548816).

Data availability

The Persefone.jl source code and relevant input files are archived on Zenodo (https://doi.org/10.5281/zenodo.16993215). The development version is available at https://git.idiv.de/persefone/persefone-model.

Author contributions (CRediT)

DV: Conceptualization, Formal Analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing; MCM: Formal Analysis, Investigation, Software, Writing – review & editing; GDI: Formal Analysis, Investigation, Software, Writing – review & editing; GP: Conceptualization, Methodology, Funding acquisition, Supervision, Writing – review & editing

References

Alexandridis, N., Marion, G., Chaplin-Kramer, R., Dainese, M., Ekroos, J., Grab, H., Jonsson, M., Karp, D. S., Meyer, C., O'Rourke, M. E., Pontarp, M., Poveda, K., Seppelt, R., Smith, H. G., Walters, R. J., Clough, Y., & Martin, E. A. (2022). Archetype models upscale understanding of natural pest control response to land-use change. *Ecological Applications*, *32*(8), e2696. https://doi.org/10.1002/eap.2696

Baguette, M., Petit, S., & Quéva, F. (2000). Population spatial structure and migration of three butterfly species within the same habitat network: Consequences for conservation. *Journal of Applied Ecology*, *37*(1), 100–108. https://doi.org/10.1046/j.1365-2664.2000.00478.x

Bezanson, J., Edelman, A., Karpinski, S., & Shah, V. B. (2017). Julia: A Fresh Approach to Numerical Computing. *SIAM Review*, *59*(1), 65–98. https://doi.org/10.1137/141000671

Busch, M., Katzenberger, J., Trautmann, S., Gerlach, B., Dröschmeister, R., & Sudfeldt, C. (2020). Drivers of population change in common farmland birds in Germany. *Bird Conservation International*, *30*(3), 335–354. https://doi.org/10.1017/S0959270919000480

Cabral, J. S., Mendoza-Ponce, A., da Silva, A. P., Oberpriller, J., Mimet, A., Kieslinger, J., Berger, T., Blechschmidt, J., Brönner, M., Classen, A., Fallert, S., Hartig, F., Hof, C., Hoffmann, M., Knoke, T., Krause, A., Lewerentz, A., Pohle, P., Raeder, U., … Zurell, D. (2023). The road to integrate climate change projections with regional land-use–biodiversity models. *People and Nature*, *6*(5), 1716–1741. https://doi.org/10.1002/pan3.10472

Candel, J. (2022). EU food-system transition requires innovative policy analysis methods. *Nature Food*, *3*, 296–298.

Díaz Iturry, G., Matthies, M. C., Pe'er, G., & Vedder, D. (2025). AquaCrop.jl: A Process-Based Model of Crop Growth. *Journal of Open Source Software*, *10*(110), 7944. https://doi.org/10.21105/joss.07944

Donald, P. F., Evans, A. D., Muirhead, L. B., Buckingham, D. L., Kirby, W. B., & Schmitt, S. I. A. (2002). Survival rates, causes of failure and productivity of Skylark Alauda arvensis nests on lowland farmland. *Ibis*, *144*(4), 652–664. https://doi.org/10.1046/j.1474-919X.2002.00101.x

Drechsler, M. (2020). Model-based integration of ecology and socio-economics for the management of biodiversity and ecosystem services: State of the art, diversity and current trends. *Environmental Modelling & Software*, *134*, 104892. https://doi.org/10.1016/j.envsoft.2020.104892

Gallagher, C. A., Chudzinska, M., Larsen-Gray, A., Pollock, C. J., Sells, S. N., White, P. J. C., & Berger, U. (2021). From theory to practice in pattern-oriented modelling: Identifying and using empirical patterns in predictive models. *Biological Reviews*, 21. https://doi.org/10.1111/brv.12729

Glutz von Blotzheim, U. N., & Bauer, K. M. (Eds.). (1985). *Handbuch der Vögel Mitteleuropas (10,1 : Passeriformes ; T. 1); [Alaudidae - Hirundinidae]*. AULA-Verl.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jørgensen, C., Mooij, W. M., Müller, B., Pe'er, G., Piou, C., Railsback, S. F., Robbins, A. M., … DeAngelis, D. L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, *198*(1–2), 115–126. https://doi.org/10.1016/j.ecolmodel.2006.04.023

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol : A review and first update. *Ecological Modelling*, *221*, 2760–2768. https://doi.org/10.1016/j.ecolmodel.2010.08.019

Grimm, V., & Railsback, S. F. (2011). Pattern-oriented modelling: A 'multi-scope' for predictive systems ecology. *Philosophical Transactions of the Royal Society B*, *367*(1586), 298–310. https://doi.org/10.1098/rstb.2011.0180

Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., DeAngelis, D. L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A. S. A., Milles, A., Nabe-Nielsen, J., Polhill, J. G., Radchuk, V., Rohwäder, M.-S., Stillman, R. A., Thiele, J. C., & Ayllón, D. (2020). The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism. *Journal of Artificial Societies and Social Simulation*, *23*(2), 7. https://doi.org/10.18564/jasss.4259

Holst, N., & Belete, G. F. (2015). Domain-specific languages for ecological modelling. *Ecological Informatics*, *27*, 26–38. https://doi.org/10.1016/j.ecoinf.2015.02.005

Hölting, L., Busse, M., Bülow, S., Engler, J. O., Hagemann, N., Joormann, I., Kernecker, M. L., Larondelle, N., Sturm, A., Turkelboom, F., Wätzold, F., & Cord, A. F. (2022). Co-design: Working with farmers in Europe to halt the loss of biological diversity. *Ecological Solutions and Evidence*, *3*(3). https://doi.org/10.1002/2688-8319.12169

Hooftman, D. A., Bullock, J. M., Jones, L., Eigenbrod, F., Barredo, J. I., Forrest, M., Kindermann, G., Thomas, A., & Willcock, S. (2022). Reducing uncertainty in ecosystem service modelling through weighted ensembles. *Ecosystem Services*, *53*, 101398. https://doi.org/10.1016/j.ecoser.2021.101398

Jenny, M. (1990). Territorialität und Brutbiologie der FeldlercheAlauda arvensis in einer intensiv genutzten Agrarlandschaft. *Journal für Ornithologie*, *131*(3), 241–265. https://doi.org/10.1007/BF01640998

Katna, A., Thaker, M., & Vanak, A. T. (2023). How fast do landscapes change? A workflow to analyze temporal changes in human-dominated landscapes. *Landscape Ecology*, *38*(8), 2145–2155. https://doi.org/10.1007/s10980-023-01686-y

Kostková, M., Hlavinka, P., Pohanková, E., Kersebaum, K. C., Nendel, C., Gobin, A., Olesen, J. E., Ferrise, R., Dibari, C., Takáč, J., Topaj, A., Medvedev, S., Hoffmann, M. P., Stella, T., Balek, J., Ruiz-Ramos, M., Rodríguez, A., Hoogenboom, G., Shelia, V., … Trnka, M. (2021). Performance of 13 crop simulation models and their ensemble for simulating four field crops in Central Europe. *The Journal of Agricultural Science*, *159*(1–2), 69–89. https://doi.org/10.1017/S0021859621000216

Kühn, E., Musche, M., Harpke, A., Feldmann, R., & Settele, J. (2024). Tagfalter-Monitoring Deutschland: Auswertung 2005-2023. *Oedippus*, *42*, 12–45. https://www.ufz.de/export/data/6/298835_298188_Oedippus_42_klein.pdf

le Clech, S., van Bussel, L. G. J., Lof, M. E., de Knegt, B., Szentirmai, I., & Andersen, E. (2024). Effects of linear landscape elements on multiple ecosystem services in contrasting agricultural landscapes. *Ecosystem Services*, *67*, 101616. https://doi.org/10.1016/j.ecoser.2024.101616

Lenda, M., & Skórka, P. (2010). Patch occupancy, number of individuals and population density of the Marbled White in a changing agricultural landscape. *Acta Oecologica*, *36*(5), 497–506. https://doi.org/10.1016/j.actao.2010.07.002

Marrec, R., Brusse, T., & Caro, G. (2022). Biodiversity-friendly agricultural landscapes – integrating farming practices and spatiotemporal dynamics. *Trends in Ecology & Evolution*, *37*(9), 731–733. https://doi.org/10.1016/j.tree.2022.05.004

McIntire, E. J. B., Chubaty, A. M., Cumming, S. G., Andison, D., Barros, C., Boisvenue, C., Haché, S., Luo, Y., Micheletti, T., & Stewart, F. E. C. (2022). PERFICT: A Re-imagined foundation for predictive ecology. *Ecology Letters*, *25*(6), 1345–1351. https://doi.org/10.1111/ele.13994

Mialyk, O., Schyns, J. F., Booij, M. J., Su, H., Hogeboom, R. J., & Berger, M. (2024). Water footprints and crop water use of 175 individual crops for 1990–2019 simulated with a global crop model. *Scientific Data*, *11*(1), 206. https://doi.org/10.1038/s41597-024-03051-3

mundialis GmbH & Co. KG. (2021). *Landcover classification map of Germany 2020 based on Sentinel-2 data* (Geoscientific Information). Geoscientific Information. Retrieved August 5, 2025, from https://data.mundialis.de/geonetwork/srv/eng/catalog.search#/metadata/9246503f-6adf-460b-a31e-73a649182d07

Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., Collins, S., Dieterich, M., Gregory, R. D., Hartig, F., Henle, K., Hobson, P. R., Kleijn, D., Neumann, R. K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W. J., Turbé, A., … Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, *344*(6188), 1090–1092. https://doi.org/10.1126/science.1253425

Pe'er, G., Bonn, A., Bruelheide, H., Dieker, P., Eisenhauer, N., Feindt, P. H., Hagedorn, G., Hansjürgens, B., Herzon, I., Lomba, Â., Marquard, E., Moreira, F., Nitsch, H., Oppermann, R., Perino, A., Röder, N., Schleyer, C., Schindler, S., Wolf, C., … Lakner, S. (2020). Action needed for the EU Common Agricultural Policy to address sustainability challenges (K. Gaston, Ed.). *People and Nature*, *2*(2), 305–316. https://doi.org/10.1002/pan3.10080

Pe'er, G., Kachler, J., Herzon, I., Hering, D., Arponen, A., Bosco, L., Bruelheide, H., Finch, E. A., Friedrichs-Manthey, M., Hagedorn, G., Hansjürgens, B., Ladouceur, E., Lakner, S., Liquete, C., López-Hoffman, L., Pinto, I. S., Robuchon, M., Selva, N., Settele, J., … Bonn, A. (2025). Role of science and scientists in public environmental policy debates: The case of EU agrochemical and Nature Restoration Regulations. *People and Nature*, *n/a*(n/a). https://doi.org/10.1002/pan3.70064

Poulsen, J. G., Sotherton, N. W., & Aebischer, N. J. (1998). Comparative nesting and feeding ecology of skylarks Alauda arvensis on arable farmland in southern England with special reference to set-aside. *Journal of Applied Ecology*, *35*(1), 131–147. https://doi.org/10.1046/j.1365-2664.1998.00289.x

Pywell, R. F., Heard, M. S., Bradbury, R. B., Hinsley, S., Nowakowski, M., Walker, K. J., & Bullock, J. M. (2012). Wildlife-friendly farming benefits rare birds, bees and plants. *Biology Letters*, *8*(5), 772–775. https://doi.org/10.1098/rsbl.2012.0367

Raes, D., Steduto, P., Hsiao, T. C., & Fereres, E. (2009). AquaCrop—The FAO Crop Model to Simulate Yield Response to Water: II. Main Algorithms and Software Description. *Agronomy Journal*, *101*(3), 438–447. https://doi.org/10.2134/agronj2008.0140s

Reichenau, T. G., Korres, W., Schmidt, M., Graf, A., Welp, G., Meyer, N., Stadler, A., Brogi, C., & Schneider, K. (2020). A comprehensive dataset of vegetation states, fluxes of matter and energy, weather, agricultural management, and soil properties from intensively monitored crop sites in western Germany. *Earth System Science Data*, *12*(4), 2333–2364. https://doi.org/10.5194/essd-12-2333-2020

Reidsma, P., Janssen, S., Jansen, J., & van Ittersum, M. K. (2018). On the development and use of farm models for policy impact assessment in the European Union – A review. *Agricultural Systems*, *159*, 111–125. https://doi.org/10.1016/j.agsy.2017.10.012

Reinhardt, R., Sbieschne, H., Settele, J., Fischer, U., & Fiedler, G. (2007). *Tagfalter von Sachsen*. Entomofauna Saxonica.

Reinhardt, R., Harpke, A., Caspari, S., Dolek, M., Kühn, E., Musche, M., Trusch, R., Wiemers, M., & Settele, J. (2021). *Verbreitungsatlas der Tagfalter und Widderchen Deutschlands* (1., korrigierter Nachdruck). Eugen Ulmer KG.

Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., del Moral, J. C., Domşa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory, R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., . . . Devictor, V. (2023). Farmland practices are driving bird population decline across Europe. *Proceedings of the National Academy of Sciences*, *120*(21), e2216573120. https://doi.org/10.1073/pnas.2216573120

Ropella, G. E., Railsback, S. F., & Jackson, S. K. (2002). Software Engineering Considerations for Individual-Based Models. *Natural Resource Modeling*, *15*(1), 5–22. https://doi.org/10.1111/j.1939-7445.2002.tb00077.x

Rosenzweig, C., Jones, J. W., Hatfield, J. L., Ruane, A. C., Boote, K. J., Thorburn, P., Antle, J. M., Nelson, G. C., Porter, C., Janssen, S., Asseng, S., Basso, B., Ewert, F., Wallach, D., Baigorria, G., & Winter, J. M. (2013). The Agricultural Model Intercomparison and Improvement Project (AgMIP): Protocols and pilot studies. *Agricultural and Forest Meteorology*, *170*, 166–182. https://doi.org/10.1016/j.agrformet.2012.09.011

Roy, D. B., Rothery, P., Moss, D., Pollard, E., & Thomas, J. A. (2001). Butterfly numbers and weather: Predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, *70*(2), 201–217. https://doi.org/10.1111/j.1365-2656.2001.00480.x

Runhaar, H. (2021). Four critical conditions for agroecological transitions in Europe. *International Journal of Agricultural Sustainability*, *19*(3–4), 227–233. https://doi.org/10.1080/14735903.2021.1906055

Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, *30*(9), 524–530. https://doi.org/10.1016/j.tree.2015.06.007

Seppelt, R., Arndt, C., Beckmann, M., Martin, E. A., & Hertel, T. W. (2020). Deciphering the Biodiversity–Production Mutualism in the Global Food Security Debate. *Trends in Ecology & Evolution*, *35*(11), 1011–1020. https://doi.org/10.1016/j.tree.2020.06.012

Steduto, P., Hsiao, T. C., Raes, D., & Fereres, E. (2009). AquaCrop—The FAO Crop Model to Simulate Yield Response to Water: I. Concepts and Underlying Principles. *Agronomy Journal*, *101*(3), 426–437. https://doi.org/10.2134/agronj2008.0139s

Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., & Grimm, V. (2015). Making Predictions in a Changing World: The Benefits of Individual-Based Ecology. *BioScience*, *65*(2), 140–150. https://doi.org/10.1093/biosci/biu192

Sun, Z., Lorscheid, I., Millington, J. D., Lauf, S., Magliocca, N. R., Groeneveld, J., Balbi, S., Nolzen, H., Müller, B., Schulze, J., & Buchmann, C. M. (2016). Simple or complicated agent-based models? A complicated issue. *Environmental Modelling & Software*, *86*, 56–67. https://doi.org/10.1016/j.envsoft.2016.09.006

Topping, C. J., Hansen, T. S., Jensen, T. S., Jepsen, J. U., Nikolajsen, F., & Odderskær, P. (2003). ALMaSS, an agent-based model for animals in temperate European landscapes. *Ecological Modelling*, *167*(1), 65–82. https://doi.org/10.1016/S0304-3800(03)00173-X

Topping, C. J., Alrøe, H. F., Farrell, K. N., & Grimm, V. (2015). Per Aspera ad Astra: Through Complex Population Modeling to Predictive Theory. *The American Naturalist*, *186*(5), 669–674. https://doi.org/10.1086/683181

Topping, C. J., Dalby, L., & Valdez, J. W. (2019). Landscape-scale simulations as a tool in multi-criteria decision making to support agri-environment schemes. *Agricultural Systems*, *176*, 102671. https://doi.org/10.1016/j.agsy.2019.102671

Topping, C. J., & Duan, X. (2024). ALMaSS Landscape and Farming Simulation: Software classes and methods. *Food and Ecological Systems Modelling Journal*, *5*, e121215. https://doi.org/10.3897/fmj.5.121215

Troost, C., Huber, R., Bell, A. R., Van Delden, H., Filatova, T., Le, Q. B., Lippe, M., Niamir, L., Polhill, J. G., Sun, Z., & Berger, T. (2023). How to keep it adequate: A protocol for ensuring validity in agent-based simulation. *Environmental Modelling & Software*, *159*, 105559. https://doi.org/10.1016/j.envsoft.2022.105559

Uchmański, J., & Grimm, V. (1996). Individual-based modelling in ecology: What makes the difference? *Trends in Ecology & Evolution*, *11*(10), 437–441. https://doi.org/10.1016/0169-5347(96)20091-6

Vandewoestijne, S., Martin, T., Liégeois, S., & Baguette, M. (2004). Dispersal, landscape occupancy and population structure in the butterfly *Melanargia galathea*. *Basic and Applied Ecology*, *5*(6), 581–591. https://doi.org/10.1016/j.baae.2004.07.004

van Swaay, C. A. M., Dennis, E. B., Schmucki, R., Sevilleja, C., Balalaikins, M., Botham, M., Bourn, N., Brereton, T., Cancela, J., Carlisle, B., Chambers, P., Collins, S., Dopagne, C., Escobés, R., Feldmann, R., Fernández-García, J., Fontaine, B., Gracianteparaluceta, A., Harrower, C., … Roy, D. B. (2019). *The EU Butterfly Indicator for Grassland species: 1990-2017* (Technical Report). Butterfly Conservation Europe. www.butterfly-monitoring.net

Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.-M., & Baudry, J. (2013). The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agriculture, Ecosystems & Environment*, *166*, 3–14. https://doi.org/10.1016/j.agee.2012.08.013

Vedder, D., Ankenbrand, M., & Cabral, J. S. (2021). Dealing with software complexity in individual-based models. *Methods in Ecology and Evolution*, *12*(12), 2324–2333. https://doi.org/10.1111/2041-210X.13716

Vedder, D., Fischer, S. M., Wiegand, K., & Pe'er, G. (2024). Developing multidisciplinary mechanistic models: Challenges and approaches. *Socio-Environmental Systems Modelling*, *6*, 18701. https://doi.org/10.18174/sesmo.18701

Vedder, D., Rakowski, J., Kolb, L., Theilen-Loges, G., Lakner, S., & Pe'er, G. (2025). Building bridges between ecological and economic agent-based models of agriculture. https://doi.org/10.32942/X2GH1H

Velten, S., Kewes, C., Brudler, R., Marsden, K., & Theilen, G. (2023). Multi-level Exchange Platforms for Biodiversity Conservation in Agricultural Landscapes. *Social Innovations Journal*, *22*. Retrieved January 9, 2024, from https://socialinnovationsjournal.com/index.php/sij/article/view/6968

Vickery, J. A., Bradbury, R. B., Henderson, I. G., Eaton, M. A., & Grice, P. V. (2004). The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biological Conservation*, *119*(1), 19–39. https://doi.org/10.1016/j.biocon.2003.06.004

Will, M., Dressler, G., Kreuer, D., Thulke, H.-H., Grêt-Regamey, A., & Müller, B. (2021). How to make socio-environmental modelling more useful to support policy and management? *People and Nature*, *00*, 1–13. https://doi.org/10.1002/pan3.10207