



APPLE-POPDYN: an individual-based model linking apple-tree productivity and leaf miner infestation dynamics

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Abstract

The extent of crop damage caused by insect pests is economically significant and largely determined by the host selection behavior of individual pest species. According to the plant vigor hypothesis, herbivorous insects prefer vital over stressed plant parts. However, the feedbacks between insect behavior, plant performance, and insect population dynamics remain poorly understood. We developed the individual-based model APPLE-POPDYN to explore how different insect oviposition strategies affect apple tree productivity and insect phenology—feedbacks that are challenging to disentangle with experimental studies alone. The model is based on the interaction between the spotted tentiform leaf miner (*Phyllo-norycter blancardella*) and its host, the apple (*Malus domestica*). It allows for controlled modification of behavioral traits, thereby enabling a systematic investigation of these interactions. The model includes the generation of meteorological pseudo data, apple tree growth, leaf-level oviposition behavior, and insect population dynamics. APPLE-POPDYN distinguishes between “picky” insects that prefer vigorous leaves and “tolerant” insects that do not discriminate. Picky insects develop faster but spend more time searching for suitable leaves. As a result, they produce more generations per year but achieve lower population sizes and cause less overall damage than tolerant insects. Additionally, increasing infestation levels reduce leaf vigor, negatively feeding back on host attractiveness. Our findings suggest that adaptive insect behavior does not necessarily lead to higher population sizes and provide new insights into the ecological dynamics of plant–insect interactions.

Keywords plant vigor hypothesis · individual-based model · host plant selection · oviposition behavior · apple productivity · leaf miner

Introduction

Herbivorous insects account for an important part of worldwide crop losses. Van der Meijden (2015) estimates that up to 15% of crop yields are lost due to insect pests. Most research on plant-herbivore interactions focuses on the damage and resistance mechanisms of plants and their respective herbivores that feed on aboveground plant

structures, especially leaves (Schoonhoven et al. 2010). Because folivorous insects are confronted with highly heterogeneous environments, it is not surprising that they have evolved a number of selective behaviors to assess host quality (Awmack and Leather 2002). While it is evident that insects prefer favorable conditions in terms of nutritional value, feeding deterrents, thermal properties, and protection from predators, there is ongoing debate if insects prefer more vigorous or less vigorous leaves as feeding and oviposition sites (Price 1991; Cornelissen et al. 2008). Two opposite hypotheses are at the centre of this ongoing debate: the plant vigor hypothesis and the plant stress hypothesis (Price 1991). The plant vigor hypothesis states that insects prosper better on well grown, vigorous plants as hosts, while the plant stress hypothesis states that insects prosper better on weak, already susceptible leaves.

The two hypotheses received support depending on the plant-host association. Galway et al. (2004) reviewed

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201 studies, including five feeding guilds and 12 different plant stress types to show that wood, sap, and leaf feeding insects thrive better on stressed host plants, thus supporting the plant stress hypothesis. In contrast, leaf miners and gall formers performed better on non-stressed host plants, supporting the plant-vigor hypothesis. Inbar et al. (2001) showed that insects from three different feeding guilds (ectophagous, leaf mining, and root feeding) prefer vigorous plants when offered a choice of varying vigor levels. In any case, it is the individual behavior of insects which is responsible for the host selection choices, but this choice is modulated by the plant condition. However, the actual rearing success of the larvae depends on the contrasting effects of more nutritious feeding material but also higher defense potential of the more vigorous leaves.

Adult insect behavior in relation to host selectivity for oviposition influences the demographic structure of the next generation through its effects on larval instar duration and survival rates. While several experimental studies have provided evidence for both strategies—oviposition preference for vigorous versus stressed host leaves—little is known about the demographic consequences of these contrasting behaviors. This is related to the fact that demographic consequences based on insect behavior are very difficult to study experimentally. Thus, studies often rely on models that extrapolate the plant condition dependency of insect behavior. As biotic interactions are generally complex to model, especially in large populations and multi-trophic interactions, there are not many models that simulate insect behavior in the context of host selection choices. Most of the available models apply statistical modelling approaches that do not include those mechanisms mechanistically (Geng and Jung 2017a, b). There is a lack of process-based, mechanistic models that integrate demographic development and host selection choices of herbivorous insects.

The development of such models could also help to investigate yet another research question raised by Garcia-Robledo and Horvitz (2012): Does host selection lead to increased offspring performance? Garcia-Robledo and Horvitz (García-Robledo and Horvitz) condensed this question in two contrasting hypotheses: The “mother-knows-best” hypothesis states that oviposition choices of mothers (or survival probability) increase offspring longevity by finding optimal rearing sites. The “optimal-bad-motherhood” hypothesis states that oviposition choices of mothers increase their own longevity by investing less energy into finding optimal rearing sites, allowing them to lay more eggs in their lifetime. Within this context, the population size of the offspring is mainly driven by larval development and survival. These factors are often determined by the chemical composition and thermal properties of host leaves, as well as exposure to and protection from predation (Nawaz et

al. 2021; Lindstedt et al. 2019). Furthermore, host selection leads to intra- and interspecific competition between insects, which is density dependent (Wolf 1974).

Even though many of the factors that contribute to the individual leaf selection of herbivorous insects are known, there is a knowledge gap regarding the complex mechanistic interplay of those factors within a single plant and their consequences for insect demography. Here, we address this knowledge gap using an individual-based modelling approach. We developed APPLE-POPDYN, which captures a two-way interaction between plants and insects. It examines how insect infestation affects the physiological performance of plants and the feedback effects of plant leaf quality on insect behavior. This includes how individual insects select leaves and the consequences for insect population dynamics. The modelled insect-plant system of our study was inspired by the interaction between the spotted tentiform leaf miner *Phyllonorycter blancardella* (Lepidoptera: Gracillariidae) and its main host, the cultivated apple (*Malus domestica*). *Malus domestica* is an important economic tree species cultivated worldwide.

Phyllonorycter blancardella is a small leaf mining moth, for which larval feeding reduces photosynthetic rates and causes premature fruit drop on various fruit trees (Li et al. 2003; Reissig et al. 1982). Most studies to date rather focus either on phenological aspects of *P. blancardella* or on the impact of its feeding damage to the photosynthetic potential of its host (Pincebourde et al. 2006). To the best of our knowledge, no studies on the interaction between plant physiology and the population dynamics of *P. blancardella* exist so far. Here, we fill this gap using an individual-based simulation modelling approach. We develop a model focusing on the link between apple plant physiology and individual host selection of the leaf mining moth *P. blancardella*. This model simulates the growth of an individual apple tree by modelling the ecophysiological properties and growth of individual leaf clusters. Additionally, the host selection choices of individual insects as well as larval development within the leaves are modelled. While studying this interaction experimentally is difficult, a modelling approach provides a valuable tool for exploring the demographic consequences of varying plant and leaf-mining insect traits within the leaf miner–apple system. Based on observational data describing the reduction in photosynthesis as a function of leaf mining damage and the larval development rates in relation to leaf quality, the model allows us to investigate how different oviposition strategies of leaf miners influence the population size of the next generation—and consequently the extent of future leaf mining damage (Wolf 1974).

Our theoretical approach aims to identify the mutual impacts of host selection behavior, insect demographics,

and plant growth by artificially manipulating insect host searching mechanisms from a qualitative, conceptual perspective, rather than producing quantitative population dynamics predictions. Within this scope, we analyzed the temporal development of infestation and phenological patterns of a leaf mining moth (*P. blancardella*) as a function of its host searching and oviposition behavior. We investigated how certain behavioral patterns influence leaf-mining damage and plant growth. These behavioral patterns refer to individual host selection strategies of leaf-mining insects towards leaf attributes and are implemented as model rules.

To better understand the consequences of the plant vigor hypothesis, we contrasted two different behaviors (picky versus tolerant host leaf selection) and investigated how these behaviors influence the development of leaf miner populations. We hypothesized that host selection behaviors of leaf miners lead to different leaf miner demographics. More specifically, we hypothesized that a picky host selection behavior results in increased leaf miner populations by increasing nutritional importance of the leaf, reducing larval development and generation time.

Materials and methods

Biological system

Phyllonorycter blancardella is a small leaf-mining moth that overwinter as pupae in detached apple leaves and emerge as an adult during spring, shortly after budburst. Emerging leaf-mining insects fly from the ground to the young leaves of the lower crown (Ministry of Agriculture, Food, and Rural Affairs, Ontario 2022). As the growing season progresses, the moths gradually move upward in the tree crown to find leaves that are suitable for oviposition. Larval development includes five instars within the leaf tissue (mine), with developmental time highly dependent on the mine temperatures (Pincebourde et al. 2007; Geng and Jung 2017b). In the continental climate zone, this leaf miner can have two to three generations per growing season. However, the leaf miner *P. blancardella*, together with the bacterial symbiont *Wolbachia*, is able to manipulate leaf chemistry in order to keep infested leaves photosynthetically active until autumn and help generate a third or fourth generation (Kaiser et al. 2010). The last generation ends with pupated larvae in detaching leaves in the fall (Ministry of Agriculture, Food, and Rural Affairs, Ontario; 2022). Pincebourde et al. (2006) showed that photosynthesis of damaged leaves is only moderately reduced. About 20 mines per leaf account for a decrease in photosynthesis of about 30% (Pincebourde et al. 2006).

Interestingly, damaged leaves alter their stomatal activity in such a way that water use efficiency is increased compared to undamaged leaves, thereby compensating for the loss in carbon assimilation (Pincebourde et al. 2006). In addition, infestation increases the likelihood of premature fruit drop, but this varies widely among apple cultivars (Li et al. 2003; Reissig et al. 1982). Finally, there is an almost uniform distribution of leaf mines within tree canopies despite the presence of complex microclimatic patterns, indicative of a bet-hedging strategy in host leaf selection by leaf miners (Pincebourde et al. 2007). This strategy makes it very difficult to disentangle the interplay of individual mechanisms within the complex process of host selection, even though the phenology and damage patterns of this leaf miner are already well characterized.

Model overview

We developed the individual-based, spatially explicit APPLE-POPDYN model (APPLE LEaf miner POPulation DYNamics) in three spatial dimensions, which comprises plant physiology, plant growth and leaf miner phenology at the scale of a single apple tree. This specific model offers the advantage of studying the population development of leaf miners on relatively small spatial scales in a spherical tree crown while still implicitly considering immigration to and emigration from other trees. In addition, the model setup allows for the capture of decades of apple tree development, from young to mature trees, enabling long-term analysis of both growth, development, and insect demographics. The model was implemented in NetLogo 6.2.1 (Wilensky 1999). The model description below follows the ODD protocol (Grimm et al. 2020).

Purpose

The main purpose of the APPLE-POPDYN model is to better understand the interactive relationship between the growth dynamics of a single apple tree—represented by its main attributes, *net assimilation*, *leaf number*, and *fruit production*—and the population dynamics of the leaf miner insect *P. blancardella*, represented by the model attribute *adult population size*. More specifically, the model investigates how the size of adult leaf miner populations changes over time according to host leaf selection behaviors (picky versus tolerant leaf miners) related to the leaf-related attribute “*vigor*”. In addition, the influence of different forms of leaf miner behavior on population development, and thus infestation levels, was determined. Weather is an important driver of both apple tree growth and leaf miner dynamics. We implemented real weather data to validate the model in terms of apple net assimilation rates. Then, we used an

artificial weather regime to model leaf miner demographics to control for unwanted variability and stochasticity in weather patterns, allowing us to discriminate the effects of the interaction between weather, plant physiology and insect demography, from the effect of weather regime alone.

Entities, state variables and scales

In APPLE-POPDYN, leaves, fruits, and branches are the plant-related agents (or individual units) of *M. domestica* (Fig. 1). They are arranged to form the approximate shape of a round crown. The leaves are modelled as superindividuals (Scheffer et al. 1995), where one leaf represents a spatial cluster of 20 leaves. Leaf clusters have an *age* [years] and a *leaf area* [cm²], which is drawn from a normal distribution with a mean of 140 cm², and a standard deviation of 40 cm² (N.D. State University Tree Handbook, 2022). Mean *photosynthetically active radiation* varies between the half-weekly timesteps, and also between different positions of leaves within the crown.

Each leaf cluster has the state variable *plant vigor* [unitless fraction], which describes how fast the crown part, where the leaf cluster is located, grows relative to other parts. More vigorous crown parts produce a greater number of leaf clusters. For this, a number of leaf clusters is grouped into different crown sectors in dependence of their productivity.

Adult leaf miners are the insect entities in the model. In the adult stage, they have an *age* [in years for computational efficiency, even though they only live for several days] and

a memory of the attributes of the leaves they have visited. Only female insects were considered. The different larval stages are not modelled as individuals and thus do not have explicit state variables of their own, however their development time still differs throughout the crown depending on leaf attributes. More specifically, the *total larval development* time is linearly dependent on the *plant vigor* of the respective host leaf (see Appendix 1.3).

Time steps were chosen to be half a week long (3.5 days), which is sufficient to account for all necessary growth processes of a tree (Li et al. 2016). However, this temporal scale requires an aggregation of the host-searching behavior of leaf miners because this behavior occurs at the scale of minutes to hours. The chosen length of the time steps was a compromise between accuracy and computational feasibility, because the temporal extent of the model was 30 years. This allows for long-term growth development of apple trees and long-term monitoring of leaf miner population development. The spatial scale of this model represents the dimensions of a mature apple tree while still maintaining a sufficiently fine spatial resolution to distinguish individual leaf cluster positions. This resulted in a spatial grain of 12.5 cm × 12.5 cm × 12.5 cm (one so called patch) and a spatial extent of 4 m × 4 m × 4 m (Fig. 1).

Process overview and scheduling

All model processes are detailed in Appendix 1 as are the standard parameter values and their sources (see Appendix 9). The environmental conditions reflect the seasonality of

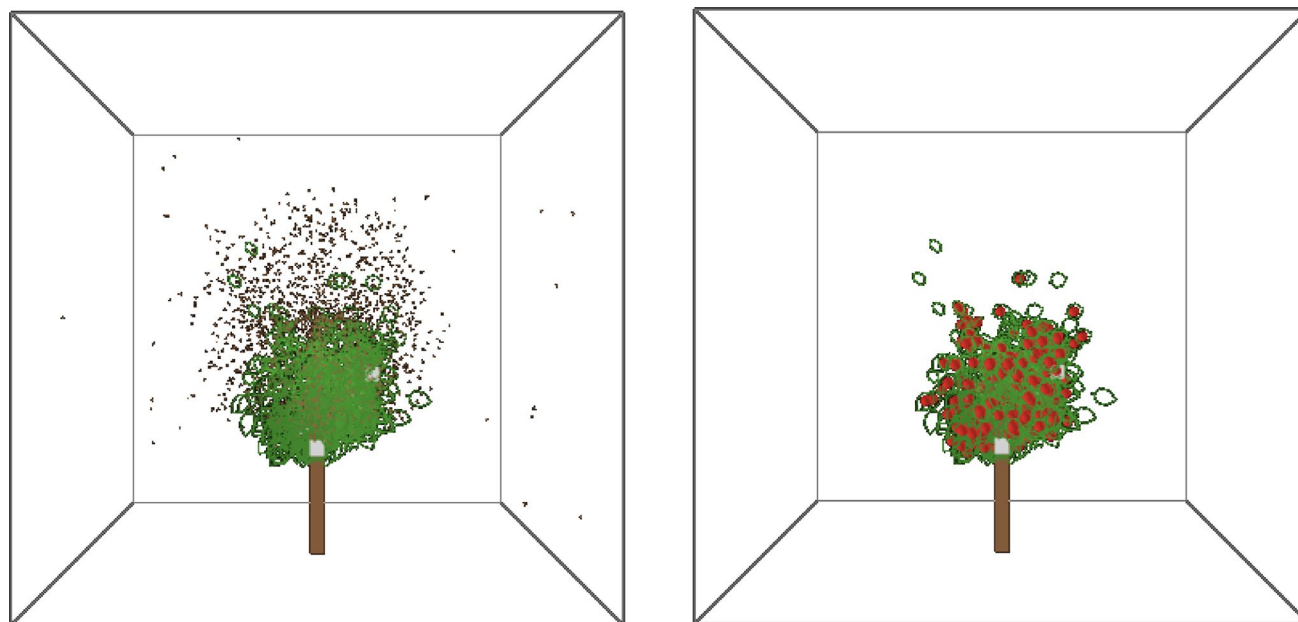


Fig. 1 Example images of the modelled NetLogo 3D interface with an apple tree in its 27th year of growth at the beginning (left image) and at the end of one growing season (right image). The green polygons

represent leaf clusters, the red items are for fruits, the white rectangles represent sticky traps for sampling, and the brown dots (left image) show the leaf mining insects searching for host leaves

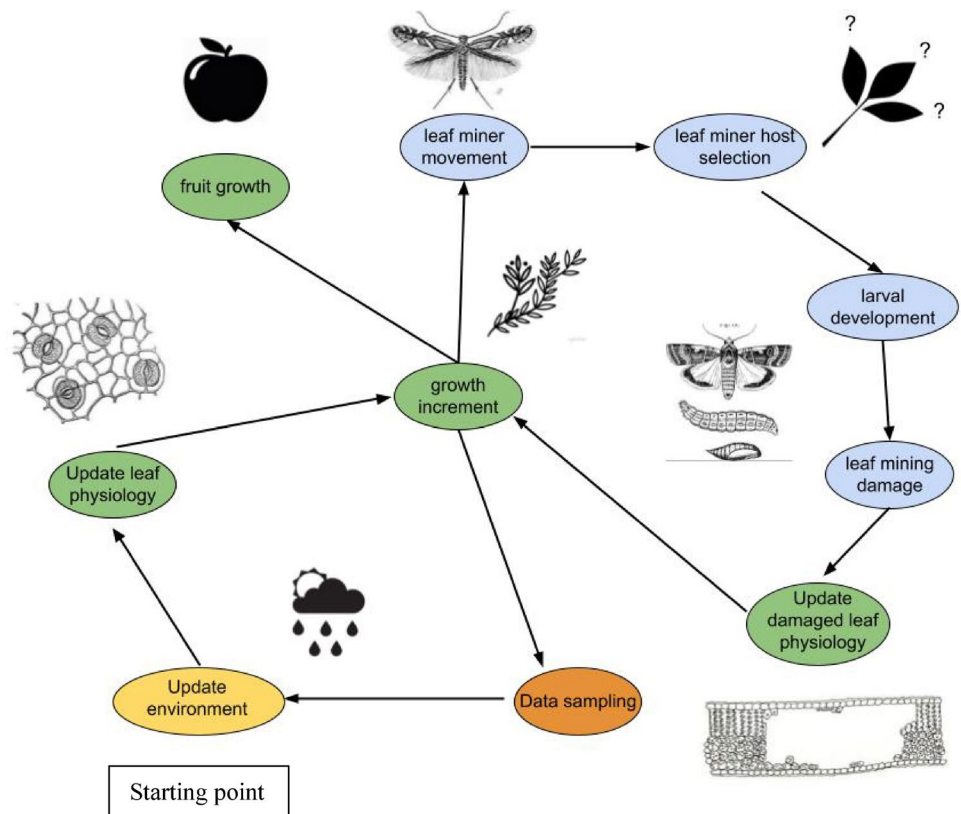
the temperate climate zone and are updated at the beginning of each time step (Fig. 2). This updating of the environment includes photosynthetically active solar radiation, ambient temperature, and soil water content. To update the incoming photosynthetically active solar radiation and ambient temperature, a function increases the respective value linearly until the year is half over, and then decreases the value again until the year is over. We implemented this simplification instead of using actual weather data for a specific location because the main purpose of the model is to foster a general understanding of the miner-plant relationship, not local site predictions. Soil water potential is calculated from soil water content via a polynomial function of third order from long-term observations (German drought monitor, Helmholtz-Centre for Environmental Research; 2021). For the sake of simplicity, wind speed and humidity are not considered in this model, because they are not the main drivers of the system (Pincebourde et al. 2006). Nevertheless, to demonstrate that the model is also able to reproduce the physiological variable of net assimilation under variable meteorological conditions, the model structure also allows for the input of real weather data, formatted as a single column with half-weekly temporal resolution.

Plant physiological processes are executed with leaf clusters being photosynthetically active during the whole growing season, from the beginning of week 16 until the end of week 38 (Peel et al. 2007). Plant physiological processes

include net assimilation, stomatal conductance, water use efficiency, growth-increment, plant-vigor, and fruit production (Fig. 3). Net assimilation is limited by photosynthetically active radiation and leaf water potential in a nonlinear relationship. For both factors, net assimilation can be modeled with a Ricker function (Bonan 2019; Appendix 1.1). The two theoretical values for net assimilation (one limited by photosynthetically active radiation and one limited by leaf water potential) are compared, and the minimum value is chosen to represent actual net assimilation. Stomatal conductance is inferred from a third order nonlinear polynomial relationship dependent on photosynthetically active radiation (Bonan 2019; Appendix 1.1). Water use efficiency is directly calculated as the ratio of carbon uptake (net assimilation) to water loss (stomatal conductance).

New leaf clusters are grown from the carbon assimilated by other leaf clusters in an age-dependent, individual-based manner. For this purpose, net assimilation is converted into biomass production per timestep [*new_biomass/old_biomass*]. Leaves must surpass a threshold of 1 g/g to produce their own biomass before they can contribute to the growth of new leaves. To make biomass production and energy requirements more realistic, approximately 85% of the surplus energy produced by a leaf is allocated to the growth of other tree parts (Lo Bianco et al. 2012). In addition, two neighboring leaf clusters produce one apple per year, independently of energy restrictions, to account for an estimated

Fig. 2 Flow diagram of the APPLE-POPDYN model with environmental procedure in yellow, plant procedures in green and leaf miner procedures in blue. Each time step starts with an update of the environment ("Update environment") and cycles through all procedures



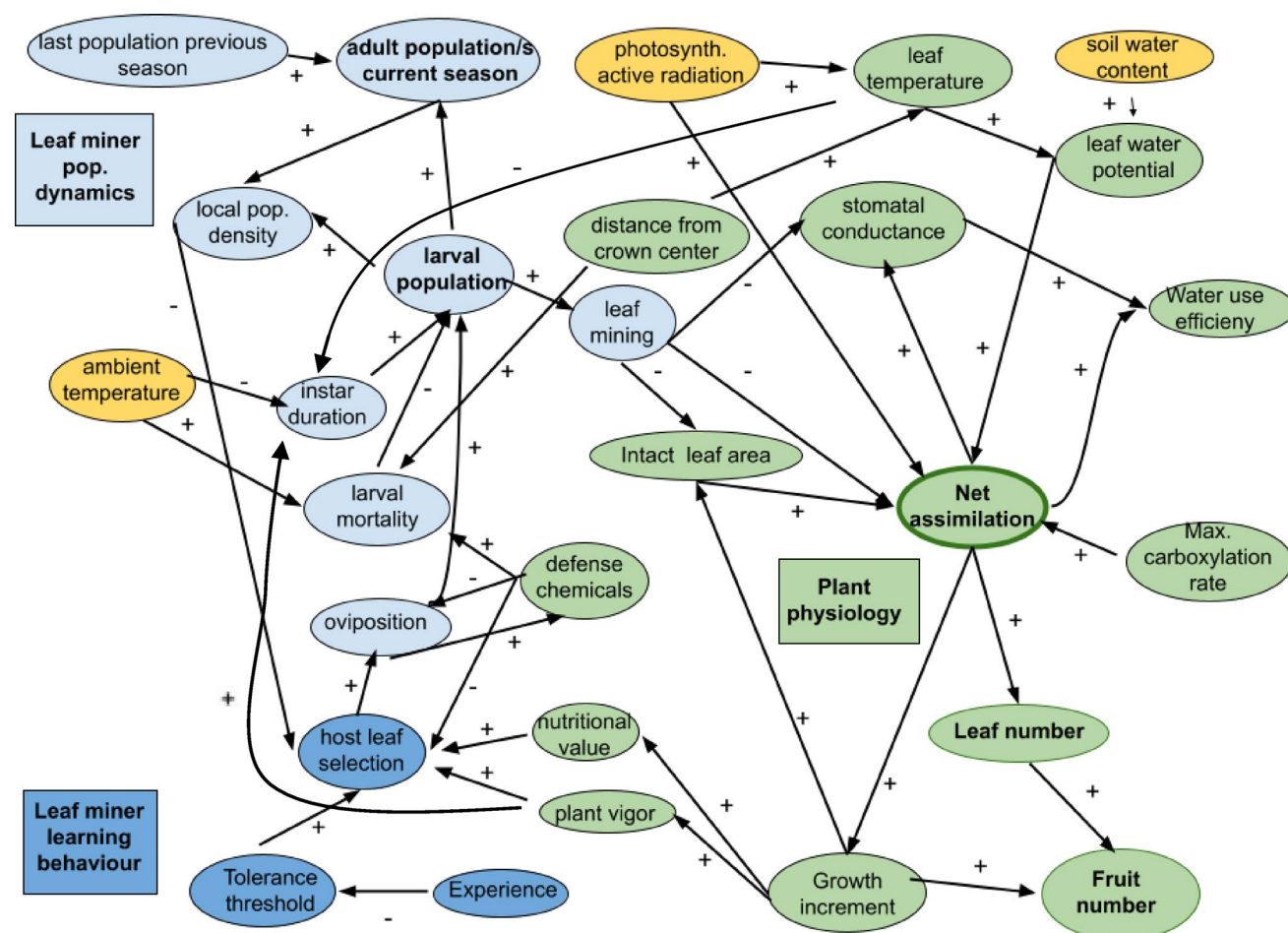


Fig. 3 Conceptual diagram of the APPLE-POPDYN model for simulating apple productivity and infestation dynamics of *P. blancardella* in a system of mutual influences. Plant physiological processes in green, leaf miner life cycle processes in blue and environmental processes in yellow. A plus (+) sign indicates that the upregulating of the originating process also leads to the upregulating of the consecutive process,

while a minus (-) sign indicates that the upregulating of the originating process results in the downregulating of the consecutive process. The boxes in bold represent the main functional categories of the model (in green – plant physiology and development, in blue – leaf miner population dynamics and leaf miner behavior, in yellow – environmental processes)

fruit production of one apple per 50 individual leaves based on a probability threshold. Leaf clusters are grouped according to *plant vigor*, depending on the productivity of their respective crown sector. For this purpose, the crown is separated into sectors determined by their distance from the crown center (Appendix 1.1).

Leaf miners emerge in spring, three weeks after the start of the growing season (i.e., week 19), and females are provided with a fixed number of eggs, dependent on ambient temperature (Geng and Jung 2017a, b; Geng et al. 2019). Most of the procedures determining the movement of leaf miners are implemented as biological estimates of individual behavior, and lack mathematical relationships, as movement and individual interaction are very difficult to implement mathematically (Grimm and Railsback 2005). Three weeks after the start of the growing season, leaf miners move from the ground upward with randomly assigned

x and *y* coordinates (process random-flight). This represents the early-season behavior of insects when they are still too far away from the tree crown to move directly towards leaves (direct-flight). If the distance of leaf miners to any leaf cluster is smaller than three grid cells (37.5 cm), the leaf miners move towards the closest leaf cluster. Once they have reached the crown, leaf miners identify a group of leaf clusters with high plant vigor and move to one of those leaf clusters within the group (move-through-crown). This is repeated each timestep throughout the life span (7 days) of all leaf miners until the end of the growing season. The preselection of several leaf clusters with high plant vigor accounts for the fact that leaf miners can visit more than one leaf cluster within half a week. It is assumed that the insects have already visited several leaves, and identified the better-grown ones.

Leaf miners memorize their position and use it in the next timestep to move to another leaf cluster (*next leaf cluster*) within this same group. The presence of other leaf miners also influences the behavior of females (assess-density). They can detect the number of leaf miners per grid cell. If this number exceeds a certain threshold (*mort_thresh-old*, parameter table Appendix 8) leaf miners move away from this location in a random direction. Each time a leaf miner visits a leaf cluster, the leaf attributes plant vigor and nutritional value of this leaf cluster are recorded in a list. A new item (new visited leaf cluster) is added to this list when the respective leaf miner visits another leaf cluster (miners-learning, update-learning). The mean value of all the attributes of visited leaf clusters determines a threshold used later for the oviposition procedure. In the oviposition procedure, each leaf miner can lay only one egg on a given leaf cluster within a single time step, and the same leaf cluster can receive several eggs from several leaf miners (oviposition). When new adult leaf miners emerge, they are provided with a fixed number of eggs. This egg number is temperature dependent and is inferred from a fourth-order polynomial approximation (parameter table in Appendix 8; Geng and Jung 2017b).

If oviposition had already occurred on any leaf cluster, the number of eggs transforms into immature mines in the next timestep (i.e., hatching is assumed to occur within 3.5 days). In addition, the leaf attribute (*larval_development_time*) is calculated as a linear relationship of leaf temperature (Geng and Jung, 2017 a), *plant vigor* (estimate based on Inbar et al. (2001)), and *nutritional value* (estimate based on Inbar et al. (2001)). When *larval_development_time* is exceeded, immature mines are transformed into mature mines, one leaf miner is created per mine, and mature mines are transformed to empty mines (larval-development). Larval mortality reduces the number of immature mines and is calculated via a negative linear relationship with the distance to the crown center (a proxy for seclusion within the crown).

Adult leaf miners leave the system due to either mortality or emigration (implemented in miners-die and over-winter). All adult leaf miners die naturally after a life span of 7 days (Geng et al. 2019). Additionally, the emigration process of leaf miners is determined by the distance to the crown center. A leaf miner is considered to have left the system if this distance is greater than 3 grid cells (37.5 cm) after the initial random-flight procedure. After the end of the growing season, the last generation of immature mines in the leaves creates an equal number of leaf miners, which are positioned on the bottom of the simulated world for overwintering.

Immigration and emigration from other trees are highly simplified. If all leaf miners in a tree leave the system, a tenth of the initial leaf miners are created as means for

immigration. Conversely, if the maximum density of leaf miners (50 individuals per grid cell) obtained from the procedure assess-density is reached, a tenth of the whole population size of leaf miners dies (as representation of emigration to other trees). Those values were retrieved from an internal model calibration (Appendix 8).

Although the model is deliberately general and the environmental parameters are quite coarse because of lack of data for this system, we compared the simulated temporal dynamics of infestation with actual field data to ensure that the model captures temporal fluctuations. A virtual insect trap was set up to sample insects at five points in the tree crown throughout the year (virtual-ecologist). Those points represent sticky traps, and count the number of insects present at the respective location (Puckett et al. 2013). The number of insects recorded per sticky trap were summed up over five modelled trees to compare the population development with field data from Gagne and Barrett (1994).

Design concepts

According to Grimm et al. (2020), eleven specific design concepts of agent-based models can be identified. Here we detail the six specific concepts that apply to our work.

Emergence: While the environmental conditions are imposed on the model system, the plant physiological variables *leaf water potential* and *net assimilation rates* are emergent properties, because they are determined by several other imposed leaf variables such as leaf temperatures. Also, tree growth emerges as a function of environmental conditions. Larval development is an emergent property, depending mainly on *plant vigor* and *leaf temperatures* and to a smaller extent also on air *temperatures*. Furthermore, the oviposition choice of leaf miners, as well as the population size of the following leaf miner generation are emergent properties. In addition, larval mortality is also emergent because it depends on the position of the respective leaf cluster within the crown.

Sensing: Leaves respond to air *temperature* and *photosynthetically active radiation*. Leaf miners also respond to air *temperature*, and to the leaf attributes *plant vigor*, *nutritional value*, and *defense* status. In addition, leaf miners are able to sense the number of other leaf miners per grid cell as a measure of leaf miner *density*.

Interaction: Leaf miners do not interact with each other directly, but high leaf miner densities per patch that exceed the patch's carrying capacity (50 individuals per patch, estimate) make individual leaf miners move away from those patches. Leaves and leaf miners interact with each other because leaf miners inflict damage on leaves and decrease their photosynthetic capacity.

Stochasticity: Stochasticity influences the initial tree architecture (positioning of initial leaves) and tree growth, determining whether the produced biomass per leaf is used to grow a new leaf or other parts of the tree. Stochasticity also affects fruit production, where a cluster of leaves has a certain probability to produce a fruit. This accounts for the cases when a fruit fails to develop before harvest time, such as early fruit fall or fruit herbivory.

For leaf miners, stochasticity plays a role for the initial positioning of pupae individuals on the floor of the simulated world, in the initial movement after emergence and in the host searching procedures. Mortality of adult leaf-mining insects is mainly due to predation, and this is more likely in the outer regions of the tree crown.

Collectives: Individual agents are not clustered into collectives per se, but the leaf agents are implemented as superindividuals (Scheffer et al. 1995), and thus each superindividual represents a cluster of 20 leaves.

Observation: Model outputs (leaf numbers, net assimilation, leaf water potential, plant vigor, leaf miner numbers) are observed via a virtual ecologist procedure (Zurell et al. 2010). Within this procedure, virtual insect traps at five different points in the crown are set up to sample insects throughout the year(s).

Initialization

The model was initialized with a number of randomly positioned leaves around the crown center where the center of the three-dimensional world lies in the center of the cartesian coordinate system. For processing power reasons, the leaves were implemented as superindividuals, where each superindividual represented a cluster of 20 leaves with similar attributes. The xyz coordinates of the initial leaves were allowed to vary from the crown center by drawing a number from a normal distribution with standard deviation 12.5 cm (obtained from model calibration). All parameters were initialized as stated in the parameter table of Appendix 8 in the supplementary material.

In APPLE-POPDYN, the input values photosynthetically active radiation [$\mu\text{mol m}^{-2} \text{s}^{-1}$] and soil water content [g/g] (as half weekly mean values) are fixed intrinsically and were chosen within the range of values observed for natural systems. In addition, they do not vary between years, however they vary seasonally. For the mathematical equations in use, parameters were directly inferred from the literature (see full parameter table in Appendix 8). This more conceptual approach is justified by the general purpose of the model to demonstrate and understand mechanisms rather than to make point predictions for a specific field location. Nevertheless, our approach aimed at the simulation of broadly

realistic values, which was checked during model validation (see section Model validation).

Input data

We have used measured data of photosynthetically active radiation from Heinicke and Childers (1937) to validate the simulated net assimilation rates.

Submodels

A detailed description of the mathematical relationships in the model and all model procedures is available in the supplementary material (Appendix 1).

Model validation

For our main simulations we used simulated environmental data as inputs, which are plausible but do not necessarily reflect the actual conditions of a specific geographical site. This allows us to propose a model with broad applicability, but it limits our ability to validate the quantitative model results. To demonstrate that the model is also able to reproduce in-situ conditions, we compared simulated net assimilation rates with observed values from Heinicke and Childers (1937), using real weather data and the modified model structure described in Sect. 2.5. Net assimilation was selected as the validation variable because it is directly influenced by meteorological conditions and thus provides a sensitive indicator of model performance under realistic environmental inputs. At the same time, to preserve the conceptual aspect of the model, we retained simulations using meteorological pseudodata to compare the seasonal population development and leaf-mining area of *P. blancardella* against observed data from Gagne and Barrett (1994). For this purpose, empirical data and model outputs were compared in terms of their seasonal dynamics and the range of values over two years, using the original model structure based on pseudodata.

Experimental design

Given the stochastic processes in APPLE-POPDYN, individual simulation results can be highly variable under identical parameter settings. To capture this variability and obtain reliable average results, each scenario was simulated multiple times, using the R package nlrx (Salecker et al. 2019). To determine the required number of replicates for robust results, APPLE-POPDYN was run a thousand times. The arithmetic mean and standard error of the main output, “leaf number”, were calculated. The dataset was subsampled to create datasets of varying sizes (1 to 1000 replicates)

and their means and standard errors were calculated. Based on this analysis, and balancing a small standard error with computational constraints, all model simulations presented here are based on 500 runs per parameter combination.

To investigate the effects of leaf miners on apple productivity and the behavior of leaf-mining insects on population dynamics, the APPLE-POPDYN model was run in three different scenarios: the first mode was a control treatment with undamaged plant growth and productivity and excluded leaf-mining damage on apple leaves. The second mode included leaf-mining damage on growth and productivity, with “tolerant” leaf-mining insects that show low selectivity regarding leaf attributes. The third mode also included leaf-mining damage but featured “pickier” leaf-mining insects that prefer vigorous leaves. In this mode, the leaf miners also display a simple form of learning behavior to account for dynamic host leaf selection.

Used software and statistical data analysis

For the mathematical equations, parameters were ideally inferred directly from the literature. If these values were not explicitly provided in the text or tables, we used WebPlot-Digitalizer 4.5 (PlotDigitizer, 2022) to extract the x and y-coordinates from the original published figures. From this inferred dataset, nonlinear models were built in RStudio using a variety of nonlinear functions. Statistical data analysis was performed in RStudio using R 4.2.2 (R foundation for statistical computing). Non-linear models for parametrisation of net assimilation rates versus irradiance and stomatal conductance versus irradiance were built with data from Pincebourde et al. (2006) using the nls package (Baty et al. 2015). The resulting nonlinear models were based on nonlinear weighted least-squares estimates of the parameters. All parameter and function values are provided in Appendix 8. To test for statistical significance of the effects of categorical variables (different behavioral modes of leaf-mining insects) on the APPLE-POPDYN model outputs, linear regression models were fitted and the normal distribution of the residuals was checked. If the residuals were not normally distributed, a log/exp transformation was performed, followed by ANOVA tests and Tukey’s range tests.

Results

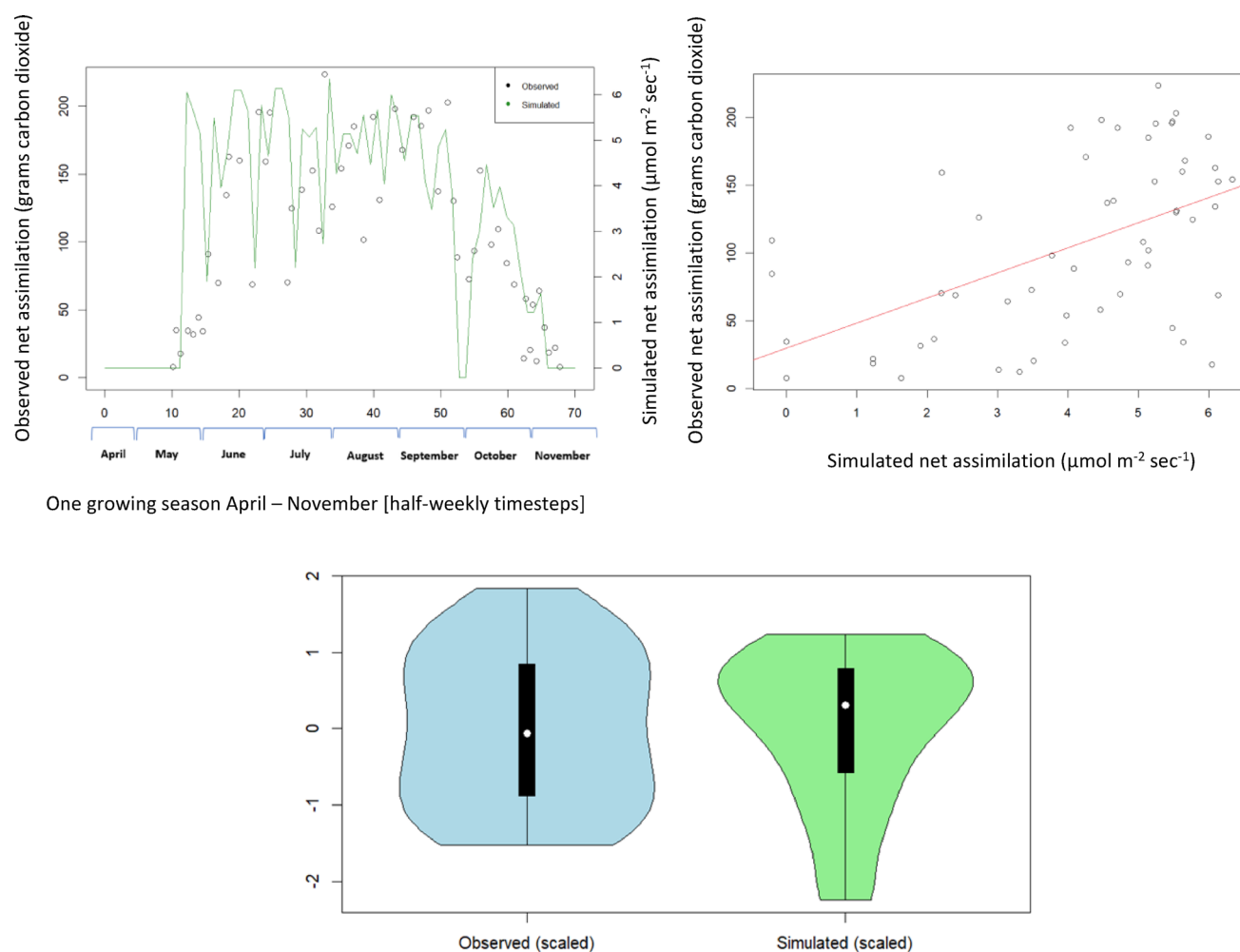
Validation of the APPLE-POPDYN simulation model

The observed net assimilation values reported by Heinicke and Childers (1937), expressed in grams of fixed CO₂, were not directly comparable to the simulated net assimilation rates in $\mu\text{mol m}^{-2} \text{s}^{-1}$, as total CO₂ fixation strongly depends

on the leaf area index and, consequently, on tree age. Therefore, the comparison in this study focused on the seasonal development of net assimilation throughout the growing season rather than on absolute magnitudes. When real weather data were used, both simulated and observed net assimilation rates exhibited similar seasonal patterns. At the beginning of the growing season, simulated rates increased more rapidly than observed rates, but this difference leveled off by the end of May. From early June onward, simulated and observed trends were closely aligned, including the decline in October and November. The respective local maxima and minima of both datasets also corresponded well (Fig. 4). Based on this comparison, a linear regression model was developed using simulated net assimilation rates as predictors of observed rates, resulting in an adjusted R² of 0.2607. The linear regression between simulated and observed net assimilation rates yielded an intercept that did not differ significantly from zero ($p=0.11$), indicating no systematic bias. However, the slope was significantly different from unity ($p<0.001$), suggesting that the model systematically underestimates observed values across the range of net assimilation rates. (Fig. 4).

The violin plots of standardized-centered data illustrate the distribution of observed and simulated net assimilation rates (Fig. 4). Both datasets show a roughly comparable overall spread. The observed data (left panel) display a broad range of values, suggesting considerable temporal variability in measured net assimilation. In contrast, the simulated values (right panel) exhibit a somewhat narrower and more symmetric distribution, indicating that the model captures the central tendency of observed rates but underrepresents extreme fluctuations. The median and interquartile ranges appear similar between datasets (bottom panel), though the differing units highlight that the simulated rates may not fully match the magnitude of observed carbon assimilation when expressed in absolute terms (Appendix 3) (Fig. 5).

The simulation results of the APPLE-POPDYN model showed temporal patterns that were similar to the observed leaf miner phenology data from Gagne and Barrett (1994). These patterns included the temporal dynamics across the season of both, leaf-mining insect population development and the number of leaf mines per sampled leaf. Characteristically, *P. blancardella* displays three to four distinct generations per year, where each generation can vary considerably in peak population size and timing of generation peaks between years and different locations (Figs. 6 and 7). The APPLE-POPDYN model outputs and field data were comparable in terms of leaf miner population size; however, the modelled leaf miner population was generally higher than the observed one. Between the two model modes with leaf-mining damage, peak population sizes of tolerant leaf miner generations (i.e., without selective behavior) were rising



One growing season April – November [half-weekly timesteps]

Fig. 4 Comparison between simulated mean net assimilation of all leaves from the modelled results of a 22-year-old tree (green line) and measured net assimilation rates from field observations (black dots; from Heinicke and Childers 1937; left panel). In the right panel observed net assimilation rates were plotted against simulated net assimilation rates (black dots) with the fitted regression line (in red)

from the resulting linear model (adj. $R^2=0.2607$). In addition, the histograms and the violin plot (bottom panel) show the distribution of values for the simulated net assimilation rates (in green) and the observed net assimilation rates (in blue). White dots represent the medians while black dots show the 25 and 75% quartile

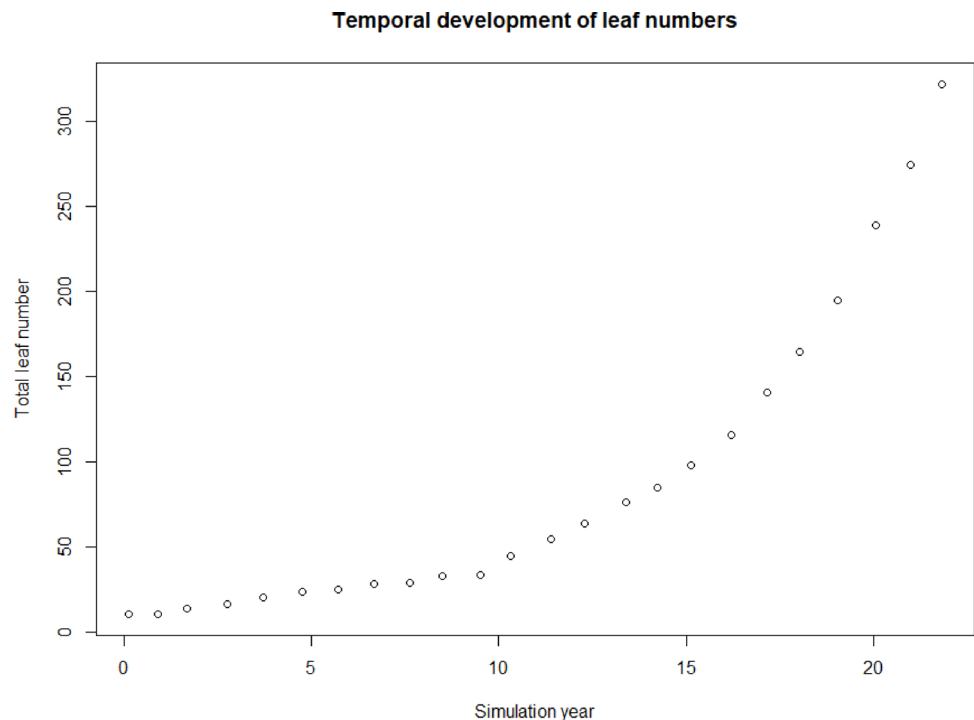
sharply over the course of one year, while peak population sizes of pickier leaf miner generations (i.e. with selective learning behavior) increased more moderately or remained at comparable numbers (Figs. 6 and 7). Model outputs showed three to four generations, visible as population size peaks, comparable with observed outputs. The number of leaf mines per leaf were similar in modelled and field data (Fig. 8).

Tree productivity in a 30-year time period

Leaf-mining insects caused damage to infested leaves, reducing their net assimilation rates. Number of leaf clusters varied significantly as a function of treatment (ANOVA: $F(2, 155997)=142.7$, $p<0.001$). Completely uninfested trees had the highest number of leaf clusters. Infested trees

had 5% fewer leaf clusters when insects displayed selective learning behavior, and 4% less leaf clusters when the insects did not display selective learning behavior and chose any visited leaf cluster for oviposition (Fig. 9A). The highest fruit numbers were observed in completely uninfested trees, followed by trees infested by insects with selective learning behavior (4% fewer fruits), and trees infested by insects without selective learning behavior (5% fewer fruits). Consequently, fruit numbers displayed a similar trend to leaf numbers (Fig. 9B). Mean net assimilation rates of uninfested trees were approximately 8% higher than those of severely infested trees (ANOVA: $F(2, 1964896)=54721$, $p<0.001$, Fig. 9C).

Fig. 5 Simulated total number of leaf clusters of one tree over 22 years of growth. The values refer to the total number of leaf clusters at the end of the annual growing season without considering leaf litter fall during autumn



Leaf miner populations displayed a relationship with leaf numbers which depended on behavior

Different behavioral modes of leaf miners (picky versus tolerant) resulted in different simulated annual population developments. The number of generations per year as well as the population size per generation differed between behavioral modes. Model runs with tolerant leaf miner behavior showed approximately twice the population size of model runs with picky leaf miner behavior. However, model runs with picky leaf miner behavior sometimes showed a higher number of generations per year (four compared to three, see Fig. 6). There was a clear relationship between mean final number of leaf clusters and mean final leaf miner population size for each year across all model runs (Fig. 10). For both of the model options “tolerant leaf miners” and “picky leaf miners”, the population size of leaf miners increased in relation to the number of leaves, however the slope of the curve was less steep in the case of “picky leaf miners”.

Selective behavior and distribution of damage

Leaf mining damage led to a small reduction in simulated number of leaf clusters (Fig. 10). Furthermore, the distribution of damage depended on the distribution of the plant vigor of each individual leaf cluster across the tree crown. When leaf miners displayed “tolerant” host selection thresholds, all crown parts were almost equally damaged. However, if leaf miners exhibited “picky” host selection thresholds, more vigorous crown parts showed higher leaf

mining damage (Table 1) because picky leaf miners chose more vigorous leaves for oviposition, as was imposed by the model structure. For both tolerant and picky model versions, leaf mining damage was an output variable with considerable variation within-crown variation. There was a higher determination coefficient for the model version with “picky” host selection thresholds ($R^2=0.26$) than for the model option with “tolerant” leaf miner host selection thresholds ($R^2=0.18$). This implies that the effect of leaf vigor on leaf miner selection choices were somewhat stronger in case of “picky” leaf miner host selection thresholds (Table 1). Overall the data of leaf mining damage across different plant vigor classes showed high variability (Appendix 6).

Discussion

The interactions between herbivore feeding behavior, plant responses and insect population dynamics remain under-explored. The impacts of such behaviors on insect population dynamics are almost impossible to test experimentally (Casas and Djemai 2002) and our modelling approach provides a tool for assessing these effects in arthropods feeding on plants. The APPLE-POPDYN model was used to investigate leaf mining damage and physiological development of trees for time periods as long as 30 years and represents to our knowledge the first approach to combine effects of leaf-mining insects on plant growth with feedbacks of plant growth on insect populations. By developing and applying

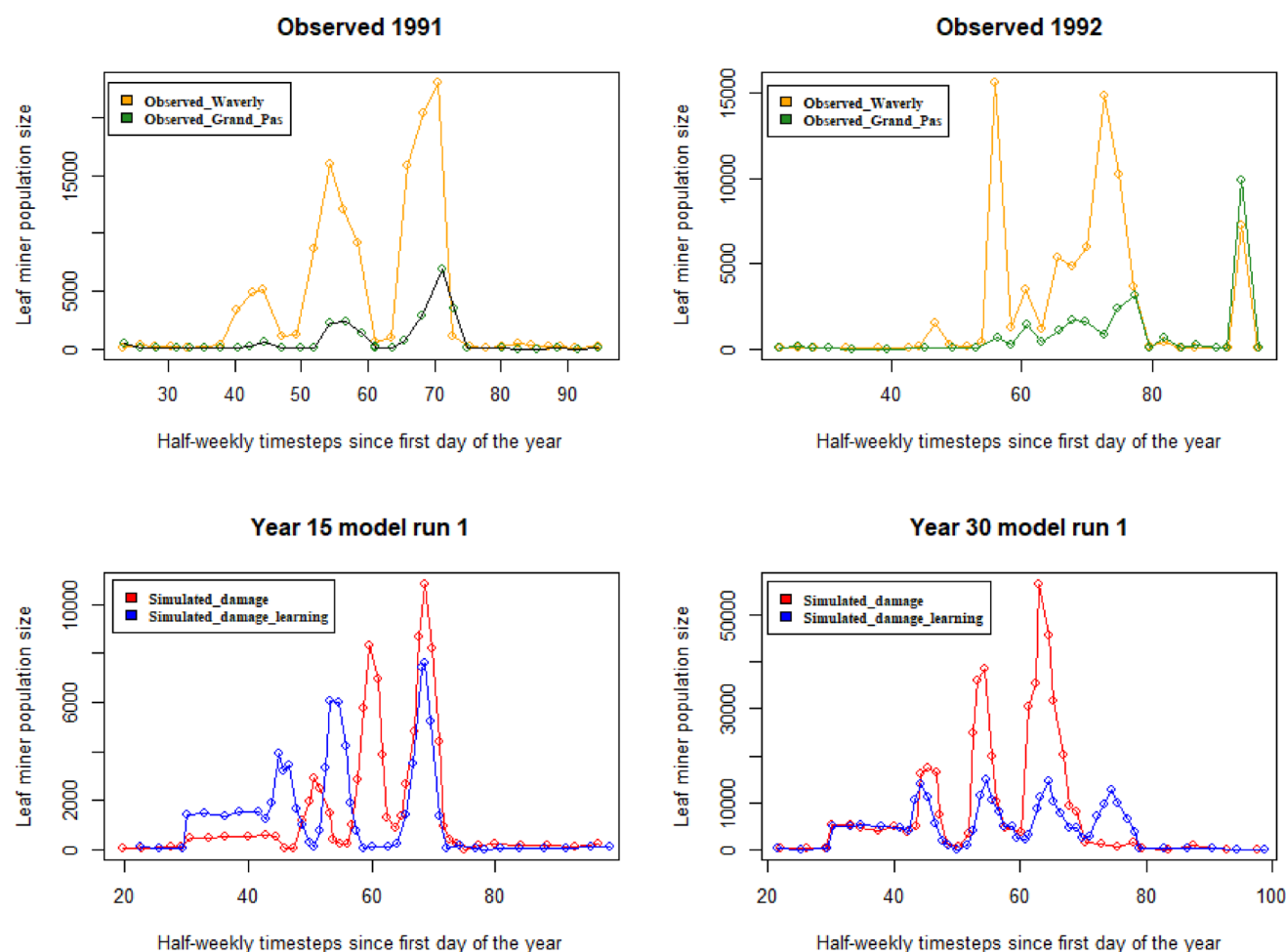


Fig. 6 Selected yearly population development of leaf miners from observations and from model outputs. The top panels show the total number of adult *Phyllonorycter* spp. trapped each week on white sticky traps located at the orchard sites of Grand Pass center (in green, both *P. blancardella* and *P. crataegella* present) and Waverly center (in orange, *P. blancardella* only) in 1991 and 1992. The bottom panels

show the total leaf miner population size of two different years from the same model run. The x-axis represents seasonal development in half-weekly timesteps. Red lines denote leaf miner behavior with “tolerant” host selection thresholds, blue lines denote leaf miner behavior with “picky” host selection thresholds

an individual based model to the case of apple tree productivity under leaf miner infestations, we show that long term productivity of the apple tree is not dramatically altered by the pest insect. Indeed, this species is often categorized as a secondary pest in apple orchards because it does not attack fruit directly and high densities are needed to alter fruit yield (Kappel and Proctor 1986; Barrett 1994). Our results are coherent with this observation, as leaf miner population sizes were large (in the tenths of thousands of adult insects per tree) and fruit yield losses were low (around 5%). We show that the selection behavior of the insect produces different dynamics with lower infestation and lower impact on plant physiology and yield when the insect selects only vigorous leaves.

Model trends mirrored empirical data

Generally, the model patterns that are relevant for the research question were validated successfully against real data. We found realistic levels of leaf mining infestation compared to Gagne and Barrett (1994), as well as realistic plant growth dynamics. The model reproduced reasonably well the general patterns of seasonal net assimilation rates from empirical data by Heinicke and Childers (1937), validating the use of APPLE-POPDYN for simulating the multi-annual growth development of a tree. However, simulated assimilation rates were higher than observed values at the beginning of the growing season. A likely explanation is that early-season physiological processes—particularly flowering and the associated carbon allocation costs—reduce net assimilation in real trees. These processes are not yet represented in APPLE-POPDYN, which assumes that

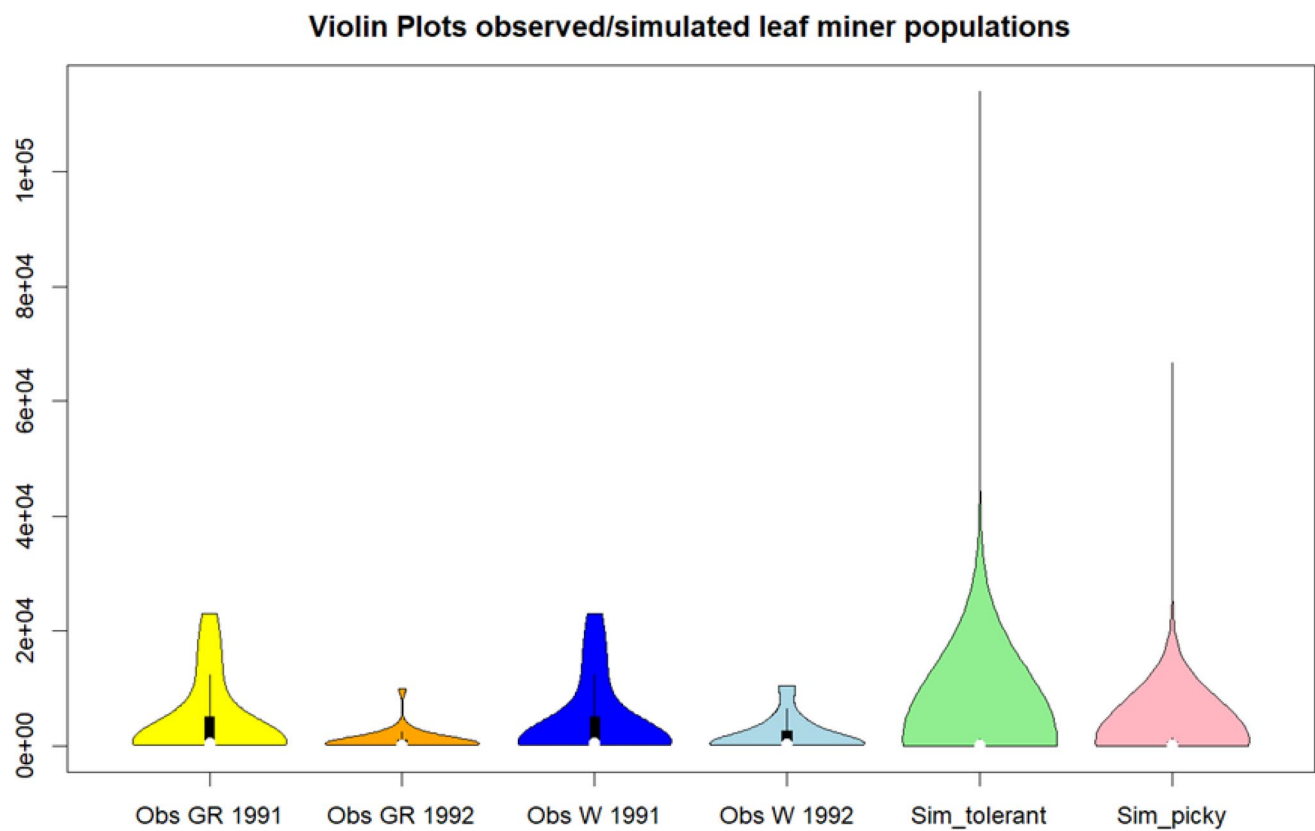


Fig. 7 Violin plots showing the distribution of values for observed and simulated data. Observed data are separated into different orchards (Grand Pass – GR, Waverley – W) and different years (1991, 1992).

Simulated data are separated into different leaf miner behavior (tolerant, picky). White dots represent the medians, black lines the 25 and 75% quartile respectively

developing leaves operate at full assimilation potential once expanded. As a result, modeled assimilation rises more rapidly in spring than indicated by empirical measurements.

The violin plots help illustrate these differences. Observed assimilation values show broader variability, reflecting short-term fluctuations driven by rapidly changing environmental conditions and by physiological transitions such as leaf expansion and flowering. In contrast, the simulated values display a narrower and more symmetric distribution, because the model smooths over fine-scale environmental variation and omits early-season sinks that temporarily suppress net assimilation in real trees. This leads to less variability and, in spring, to higher simulated rates relative to observations.

Overall, the comparison indicates that while APPLE-POPDYN captures the general seasonal course of net assimilation, improvements are needed to account for early-season phenology and short-term environmental dynamics. The APPLE-POPDYN model can be modified to feature the actual architecture of apple canopies, although this demands much higher computing times (Pincebourde et al. 2007; Woods et al. 2015). Apple tree architecture data are available in e.g. Sinoquet et al. (2009).

An interesting question related to the growth development of the tree is if a final leaf number of approximately 20,000 individual leaves (or 1000 superindividual leaf clusters) after 30 years of growth is realistic for *M. domestica*. This number is coherent with Bonan (2019). The modelled leaf miner population development, as well as the number of leaf mines per leaf were in agreement with empirical data from Gagne and Barrett (1994). However, the different leaf miner populations of modelled results could not simulate any leaf miner generation later than the end of September, a phenomenon which is imposed by the model structure. This threshold can be adjusted in future model versions if required by future research questions, for example to integrate the additional generation produced by the relationship with Wolbachia (Kaiser et al. 2010).

Leaf mining damage, plant growth and host selection: an interactive system

This study integrated the interactive effects of leaf mining damage on plant growth and the feedback effect of plant growth on population dynamics of leaf miners. Leaf mining damage negatively affected the net assimilation rates of

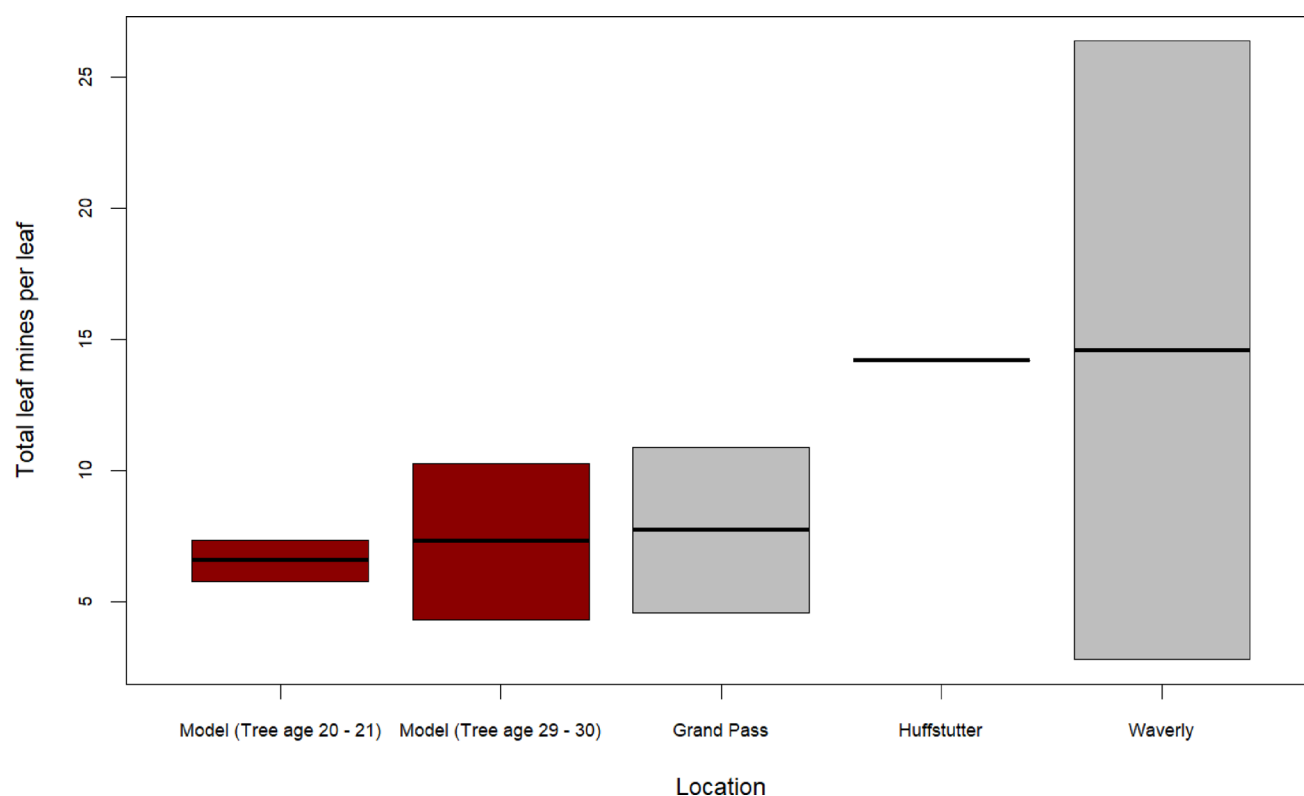


Fig. 8 Total number of leaf mines per leaf at the end of the growing season for different locations from the field study (Gagne and Barrett 1994) (grey) and model simulations (dark red). X-axis captions “Grand Pass”, “Huffstutter” and “Waverly” refer to the different orchards in Missouri where the field study was conducted. No direct climate data

from those sites were used for the simulations (see Appendix 1.1 for modelled climate). Field data were available from two consecutive years. The model outputs also integrate two consecutive years of one model run to account for an age development from 20–21 years and 29–30 years of the simulated tree

infested leaves. This fed back to reduced leaf miner population dynamics—especially in the model version with picky leaf miners—because the reduced net assimilation rates decreased leaf vigor, and picky leaf miners preferred more vital leaves. However, the APPLE-POPDYN model does not consider the additional influence of a change in nutritional quality of the leaf when it is already attacked by a leaf miner. This is important because leaves with leaf mines contain different amounts of nutrients and secondary compounds (Kaiser et al. 2010; Body et al. 2013). Therefore, our results may actually underestimate the density effect of larger leaf miner population sizes on leaf mining damage. Modelled leaf miner population sizes were also limited by the number of available leaves, and thus the size of the tree crown. Our simulations were bound to a single tree canopy, but in orchards the species can expand to several canopies surrounding the primary host tree (Barrett 1994). However, selective learning behavior of picky leaf miners also led to a saturation of population size, indicating that crown architecture might also limit leaf miner populations, as suggested for the relationship of leaf miner population size with temperature in previous studies (Pincebourde et al. 2007). Inbar et al. (2001) pointed out that leaf miners

can display selective behavior towards host leaves of higher nutritional quality in order to improve rearing conditions for the offspring (‘mother-knows-best’ scenario). Our study shows that selective behavior towards host leaves of higher quality greatly ameliorates the annual population dynamics of *P. blancardella*, e.g. in terms of a higher number of generations. Such performance-preference concept has been demonstrated in various taxa (Jones 2022), and is now integrated in pest population models, although without considering the feedbacks of pest infestation onto plant physiology (Garcia et al. 2020). Consequently, it is worthwhile considering feedback effects of leaf mining damage on pest insect population dynamics in future population models.

Leaf number and fruit production decreased under infestation

Leaf miner infestations caused reductions in leaf number and fruit production. Model results imply a reduction of photosynthetic rates by around 8%, and a reduction of around 5% of the number of leaves and fruits under severe leaf mining damage with tolerant leaf miners (low selective thresholds). This is in accordance with the hypothesis that

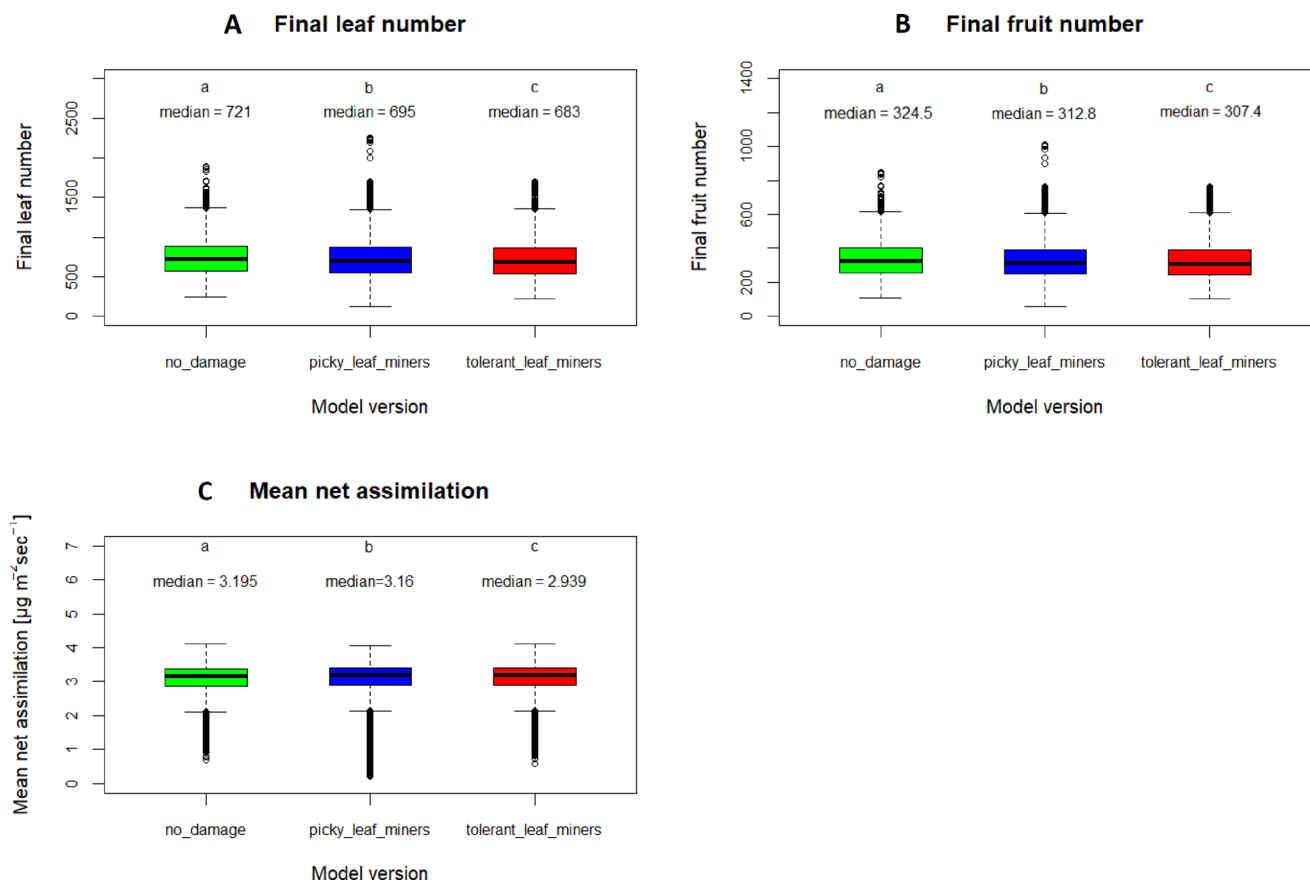


Fig. 9 Final leaf number (A), fruit number (B) and mean net assimilation (C) of *M. domestica* after 30 years of plant growth under different infestation scenarios. Uninfested trees are denoted as “no damage” in green, damaged trees with “picky” leaf miner host selection behavior in blue, damaged trees with “tolerant” leaf miner host selection behav-

ior in red. Data are shown as boxplots for 25th and 75th percentile. The horizontal line in the box indicates the median. Single data points represent outliers. Data were analyzed by One-way ANOVA followed by Tukey’s range test. Different letters above whiskers indicate significant difference at $p \leq 0.001$

leaf mining damage has a negative impact on leaf number and fruit production. Comparable reductions of 10–15% in photosynthetic rates are reported by Pincebourde et al. (2006). Previous studies (e.g., Reissig et al. 1982; Li et al. 2003) have shown that leaf-mining damage can vary considerably among apple varieties and locations, often leading to premature fruit drop and reduced fruit size. Reissig et al. (1982) reported, for instance, that in some years crop losses can reach around 25%, with a reduction in individual fruit weight of about 100 g. In this context, our model results—showing a simulated reduction in fruit number of about 5% under severe infestation—suggest that the APPLE-POPDYN model may underestimate fruit losses by a factor of two to four compared to the highest observed values. This discrepancy could reflect cultivar-specific differences or simplifications in the modeled fruit-drop mechanism.

From a practical perspective, our findings support the idea that pest management could benefit from selective treatment strategies within the tree crown, focusing greater control effort on areas with higher leaf miner selectivity,

while reducing interventions in less affected crown regions. Such spatially differentiated management could optimize control efficiency and minimize unnecessary pesticide use. This could be put into practice via hyperspectral imaging or other screening techniques to identify the respective crown areas (Knauer et al. 2024) and targeted spraying methods for a selective treatment (Xun et al. 2022).

Moreover, although the leaf miner reduces photosynthetic activity, it also allows the plant to increase its water use efficiency and therefore to save water (Pincebourde et al. 2006). This suggests that the plant may benefit from (moderate) leaf miner infestation during particular conditions such as drought, but this hypothesis remains to be challenged. More complex relationships between plant physiology, insect effects and climatic conditions can be implemented in the model in the future.

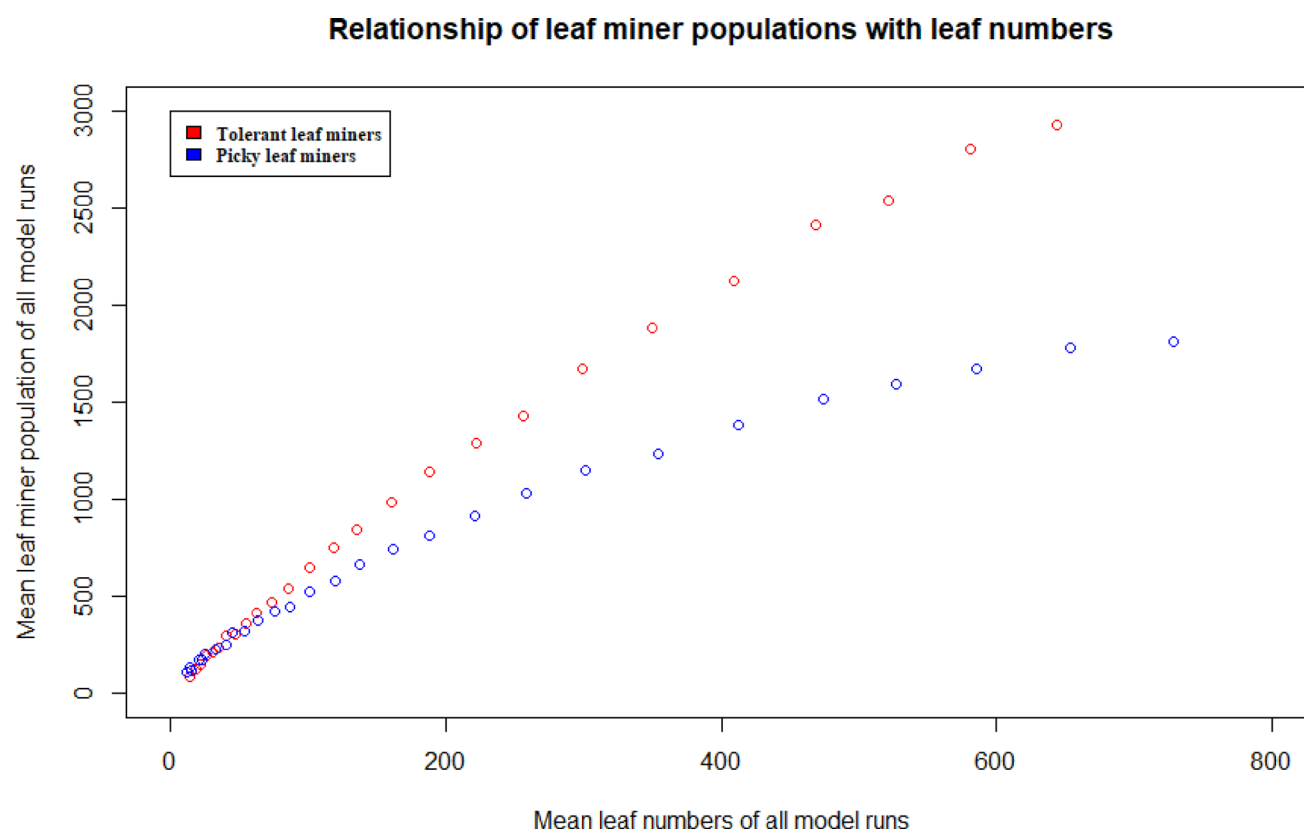


Fig. 10 Mean final yearly leaf miner population size plotted against mean final yearly number of leaf clusters over all model runs for different behavioral modes (tolerant (in red) and picky (in blue) host selection thresholds of leaf miners)

Table 1 Adjusted R-squared and p -values from linear models of damaged leaf area [cm^2] as a function of plant vigor [unitless fraction from 0–1] for simulated data from two versions of the APPLE-POPDYN model. Tolerant and picky leaf miners have low and high host selection thresholds, respectively

Model version	Leaf mine damage	Estimate	Standard error	t-statistics	p -value	Adj. R-squared
Tolerant leaf miners	Intercept	8.28	0.029	288.3	2×10^{-16}	0.18
	Slope	80.40	0.1	816.8	2×10^{-16}	
Picky leaf miners	Intercept	2.52	0.025	101.0	2×10^{-16}	0.26
	Slope	89.39	0.086	1044.0	2×10^{-16}	

The effects of selective behavior

Selective learning behavior of leaf miners produced smaller infestation-related decreases in number of fruits and number of leaves, lowering the number of leaf miners at any given number of leaves (or tree age), and decreasing the amount of mined area per leaf at any given plant vigor compared to scenarios without selective behavior. However, selective behavior in the oviposition choices should in theory result in more favorable conditions for the offspring, which may play out as increased population sizes and fitter offspring (Nieberding et al. 2018). The fact that this was not observed in the modelled results could be explained by the mechanics of the modelled selective behavior. The modelled leaf miners use their memory of previous leaves to decide whether a leaf is suitable for oviposition. If the modelled leaf miners

do not find a leaf suitable for oviposition, they do not oviposit at all rather than compromise—a strategy that seems to not prevail in nature (Thompson 1988). The finding that leaf miner populations did not increase in size any further when a certain number of leaves had been infested indicates that such an uncompromising host selection strategy is not very advantageous in a dynamically changing system. Another very important factor in this dynamic system is that, in reality, the leaf miner population size is not merely the result of oviposition success and larval development dependent on leaf temperatures (Davies 1988), as implemented in the model. In addition, larval survival rates and lifetime dynamics are highly dependent on leaf nutritional quality, chemical defenses and water content (Davies 1988). Those limitations are currently not included in the APPLE-POPDYN model, but clearly higher mortality rates are expected for

eggs laid on suboptimal leaves. Furthermore, this particular implementation of the plant vigor hypothesis—where leaf miners with selective behavior prefer more vigorous leaves but do not oviposit at all on sub-standard leaves—does not result in the predicted outcome of the hypothesis, namely an advantage for leaf miner populations due to faster larval development. Taken together, we suggest to continue to take advantage of agent-based modelling to explore individual behaviors such as host selection and learning, but expand the range of types of behaviors and host selection strategies that are explored in future modelling.

Model assumptions and limitations

The APPLE-POPDYN model considers only one level of heterogeneity within the tree crown, represented by the attribute plant vigor. However, other variables may vary considerably within a single mature apple tree canopy. These include leaf and mine temperature (Pincebourde et al. 2007) and leaf gas exchange, such as the assimilation rate as function of leaf age (Pincebourde and Ngao 2021). These additional levels of variation should impose further constraints on the host leaf selection behavior of the insect. Finally, these variations would be important for applying APPLE-POPDYN to fruit tree cultivars, especially because apple cultivars can differ in their gas exchange properties and leaf surface temperatures (Massonnet et al. 2008).

Leaf miners also take part in complex trophic interactions including parasitism, for example by parasitoid wasps. These trophic interactions were only considered as a stochastic factor in the model that depended on the distance to the outer crown layers and represented the probability of seclusion from parasitism. Field observations have shown that trophic interactions can fundamentally change leaf miner demographics (Gagne and Barrett 1994), which can be another explanatory factor for the discrepancies between observed and simulated leaf miner populations.

APPLE-POPDYN integrates environmental data in a rather simple way (average over 3.5 days). Daily variations, including daily maximum temperatures (T_{max}) also influence insect physiological rates and survival (Ma et al. 2021). Future model development could incorporate smaller-scale processes to improve the accuracy of model predictions. Furthermore, the model structure could be improved by enhancing the leaf miner's host searching mechanisms and flying behavior. The current host searching mechanisms are not very dynamic. They should account for a more flexible behavior (e.g. the willingness to oviposit on substandard leaves) of leaf miners when there are not many leaves of favorable quality present.

Additionally, the final leaf number and growth form of modelled trees from different model runs varied enormously.

This is most likely due to the stochastic processes in the growth-increment procedure, in which stochastic elements play a role in leaf generation and positioning. Having variable growth forms without management interventions is not unrealistic per se but can most often be explained by environmental variation. Given that environmental conditions were implemented similarly for each model year and model run, the high level of variation represents the effects of additional environmental factors that were not modelled, e.g. due to a lack of data.

In summary, each of these model limitations needs to be judged in light of the goals of model analysis, with additional detail being added only where it is critical to the conclusions drawn. A first step towards model improvement would be to conduct a thorough sensitivity analysis to identify options for model simplification, if any, and to guide improvements in the model parametrization. The next step would be to input real environmental data on incoming solar radiation, soil moisture, and ambient temperatures into the model, all at the half-weekly time steps used in the model. Those data could be taken from recorded time series but also from future climate simulations. This may improve predictions of fruit yields and leaf mining damage, which would be needed if the model purpose was to be shifted from demonstration and understanding more towards prediction.

Conclusion

The individual-based APPLE POP-DYN model realistically simulates fruit losses, physiology, and growth processes of *M. domestica* under infestation of the leaf miner *P. blattardella* and feedbacks on leaf miner host selection and population sizes. Severe infestation led to fruit losses of about 5%. To our knowledge it represents the first model that treats infestation as an interactive system where leaf mining damage due to infestation creates feedbacks on the population dynamics of insects. As expected, infestation by leaf miners decreased plant performance, which indirectly led to a reduced leaf miner performance via plant vigor and host selection mechanisms. Unexpectedly, a pickier host searching behavior of leaf miners resulted in lower leaf miner population sizes with more generations per growth period in comparison to leaf miners with a more tolerant host searching behavior. This calls for more agent-based modelling to explore more facets of this interactive feedback loop between plants and insect herbivores, with particular emphasis on different host selection and learning types, to further improve the mechanistic understanding of plant-insect interactions under changing environmental conditions.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11829-026-10233-w>.

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Code availability All model source code and metadata used in this study are openly available in the GitHub repository: <https://github.com/Felix738/APPLE-POPDYN-model>. This repository contains the simulation scripts, configuration files, and documentation required to reproduce the results of the study. Raw simulation output data supporting the findings are archived on Zenodo and accessible via the DOI: <https://doi.org/10.5281/zenodo.16027116>.

Declarations

Competing interests The authors declare no competing interests.

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