

INSTAR: An Agent-Based Model that integrates existing knowledge to simulate the population dynamics of a forest pest



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ABSTRACT

Pine plantations, very common in the Mediterranean basin, are recurrently affected by forest pests due to intrinsic characteristics (high density, low spatial heterogeneity) and external factors (consistent trend towards a warmer and drier climate). *INSTAR* is an Agent-Based Model aiming to simulate the population dynamics of the *Thaumetopoea pityocampa* forest pest. The model has been designed using a modular approach: several interconnected modules (submodels) facilitate the incorporation of new knowledge about the pest biology and can serve as template for the design of other similar models. The model is spatially and temporally explicit and allows its implementation under different climate and land use scenarios. *INSTAR* is described in detail in this manuscript using the standardized ODD (Overview, Design concepts and Details) protocol.

Temperature is known to be one of the main factors modulating the population dynamics of *T. pityocampa*. In order to be coherent and structurally realistic, *INSTAR* should faithfully reproduce the effect of this factor on the species' phenology. This requirement has been assessed here through a consistency test of the submodules responsible for species development. This assessment is constituted by a calibration analysis of the pest phenology and a stress test performed by exposing the model to extreme climate inputs. As a result of calibration, the model successfully reproduces the phenology of the species in the simulated study area. Moreover, the stress test confirmed that the model behaves as expected when exposed to extreme input values. The results presented in this manuscript constitute a first internal validation of the development submodels. After this, *INSTAR* is ready for a deeper analysis consisting on a sensitivity and uncertainty analysis.

1. Introduction

Pine plantations are very common in the Mediterranean basin, where they were used in the early decades of the 20th century as management tools to halt soil loss. In Spain alone, 2.5 million hectares were planted between 1940 and 1980 (Ministerio de Medio Ambiente, 2002). Currently, their intrinsic characteristics (mainly low diversity and high stand density), together with external factors (i.e. climate change) cause pests to be a recurrent problem within these forests.

Forest pests receive great attention due to their relevance in ecosystems functioning and the economic impacts they cause on managed

forests (see Wingfield et al., 2015). Numerous articles are published every year providing insights on species physiology, reporting outbreaks and first records of species and showing up-to-date occurrences (Higham et al., 2017; Valenta et al., 2017; Zanetti et al., 2017; Tanase et al., 2018). Researchers also highlight the potential impacts of forest pests under climate change scenarios, which are expected to be more acute in coniferous forests and the boreal biome (Seidl et al., 2017). In this regard, current knowledge confirms the lower resistance and thus higher vulnerability of single species forests to disturbances such as forest pests, among others (Fares et al., 2015).

The lack of integrative and synthetic knowledge makes it difficult to

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forecast pest behaviour under specific abiotic scenarios and landscape configurations. Although experiments are possible on a small scale (individuals, small areas), obvious restrictions exist when the goal is to understand the dynamics of large-scale systems, such as extensive plantations and/or long time periods. This situation reveals an important drawback when trying to design more effective and feasible management strategies that use up-to-date knowledge. Therefore, there is a need to generate tools that can help foresters to avoid or minimise pest damage and ensure sustainability among forest masses (Fares et al., 2015).

Modelling has demonstrated its usefulness when carrying out *in silico* experiments (Chowdhury and Stauffer, 2005) and synthesising information from different scales, thus helping with acquiring more comprehensive and holistic knowledge. Our aim is to improve the general understanding of forest pest dynamics by studying specific cases, as suggested by Fares et al. (2015). Thus, our approach is to create a model which explicitly simulates the concatenated linkages between the abiotic configuration of the landscape (topography, climate, meteorology, etc.) and the performance of the ecosystem components (pine plantations and forest pests) in a global change scenario. The pine processionary moth (*Thaumetopoea pityocampa*) is especially suited for modelling purposes for several reasons:

- i) The pine processionary moth lifecycle allows for simplification without neglecting crucial processes: its characteristic gregarious behaviour allows modelling into groups of individuals that behave as fully functional units which constitutes an advantage in terms of computing power needs. Nevertheless, the lifecycle of this species is influenced by interacting abiotic and biotic factors, and therefore modelling such a complex system constitutes an interesting challenge. Winter temperature and habitat (Démolin, 1969a; Masutti and Battisti, 1990; Hódar et al., 2002) are among the most important abiotic factors influencing these pest dynamics, while biotic factors such as parasitism or amount and quality of available pine biomass also play a key role in modulating *T. pityocampa* populations (Battisti, 1988; Hódar et al., 2002; Hódar et al., 2004; Charbonnier et al., 2014; Torres Muros, 2015).
- ii) The pine processionary moth lifecycle is representative of many forest pests: long defoliating larval stage followed by pupation and short non-feeding moth stage (Dajoz, 2000; Netherer and Schopf, 2010; Barbosa et al., 2012), thus simulating its population dynamics can serve as inspiration to model the behaviour of other forest pests. Similar to other species, *T. pityocampa* is experiencing an expansion process fostered by the spread of the above-mentioned pine plantations in which it feeds as well as climate change (Hódar and Zamora, 2004; Battisti et al., 2005; Petrucco Toffolo et al., 2006). Modelling the population dynamics of this species can help in understanding the potential impact of global change on the functioning of pine plantations in the Mediterranean area. This is of high importance given the extent of such forests and their potential growth decline due to the interaction between defoliation and drought stress (Linares et al., 2014; Sangüesa-Barreda et al., 2014). Besides, modelling the population dynamics of this species will also allow the study of the interaction between pests and land uses, therefore helping to improve management strategies in the long term (Régolini et al., 2014; Castagneyrol et al., 2014b).
- iii) The pine processionary moth constitutes a forestry, ecological and public health problem nowadays since affected trees reduce their growth and are more sensitive to other pests (Markalas, 1998; Kanat et al., 2005; Arnaldo et al., 2010; Jacquet et al., 2012). It also causes stinging and allergic reactions to humans and animals due to its urticating hairs (Rebollo et al., 2002; Vega et al., 2003; Battisti et al., 2017). Thus, simulating the population dynamics of *T. pityocampa* could help manage its outbreaks to minimise health and ecological impacts.

Some authors have modelled the distribution of *T. pityocampa* by means of equations-based models (Robinet et al., 2014) or statistical analysis (Seixas Arnaldo and Monteiro Torres, 2005; Régolini et al., 2014). Most authors interested in this species highlight the importance of climate on the impact of the pest, and some have even attempted to model the effects of climate change on it (Robinet et al., 2007; Robinet et al., 2014; Robinet et al., 2015; Seixas Arnaldo et al., 2011). However, no Agent-Based Model (ABM) model is available for *T. pityocampa*.

In this article, a spatial and temporally explicit ABM called *INSTAR* is presented. *INSTAR* has been designed to simulate the population dynamics of *T. pityocampa*. This manuscript firstly provides an overview about the ecological background of the target species. The structure and functioning of *INSTAR* are then described in detail according to the ODD protocol ("Overview, Design concepts and Details") proposed by Grimm et al. (2010). Finally, we present a consistency test of the sub-modules responsible for species development, constituted by a calibration analysis of the pest phenology and a stress test exploring the influence of extreme temperatures on the model.

2. Ecological background of the species

T. pityocampa is present in the entire Mediterranean Basin, from North Africa to the South of Europe and from the Atlantic Coast to the western part of Turkey, and it is especially present in afforested areas. It is a univoltine oligophagous species feeding on *Pinus* sp., and more rarely on *Cedrus* sp. and planted *Pseudotsuga* sp. (Battisti et al., 2015). A complete outline on the biology of *Thaumetopoea* species in general, and of *T. pityocampa* in particular, can be found in Roques (2015). However, the detailed features of the *T. pityocampa* cycle widely vary between sites and between years.

The biological cycle of *T. pityocampa* is shown in Fig. 1. After mating, **female** moths lay between 150–350 eggs around pine needles or, more rarely, twigs. Eggs are exposed to predation and parasitism mainly caused by *Ooencyrtus pitocampae* and *Baryscapus servadeii*. Parasites are temperature-limited, and therefore the parasitism rate shows an altitude gradient: the higher the altitude, the lower the parasitism rate (Torres Muros, 2015). Hatching occurs in early summer in northern (and higher) locations and late summer in southern (lower) ones, thus avoiding high temperatures which are lethal for the larvae (Démolin, 1969b; Seixas Arnaldo et al., 2011).

Larvae are mainly characterised by their gregarious behaviour. Just after hatching, larvae build silk nests or colonies, as protection against low temperatures and predators. Since *T. pityocampa* is a poikilothermic species, air temperature plays a key role during larval development (Démolin, 1969b; Huchon and Demolin, 1970; Robinet et al., 2007; Hoch et al., 2009), as well as in later stages. Moderately high temperatures (below 30 °C according to Démolin (1969b)) accelerate larval growth, while cold temperatures delay development and can cause mortality due to freezing or starvation. Thus, *T. pityocampa* has a higher affinity for trees situated at the edge of the stands or around clear areas, since nests there receive more light and therefore are in a more advantageous situation in terms of temperature (Démolin, 1969b). Moreover, larvae colonies can move within the tree to find the most exposed areas of the pines at each moment (Démolin, 1969b; Hoch et al., 2009; Pimentel et al., 2011). Normally, larvae feed during the night and digest during the day inside their nests. In contrast to other defoliator species, the larval phase of *T. pityocampa* takes place during winter. Therefore, increasing winter temperatures due to climate change are expected to favour this species (Netherer and Schopf, 2010; Battisti et al., 2005).

Larval development requires five larval stages or "instars". Growth and survival of early development stages depend on food quality (Hódar et al., 2002) and higher survival rates are observed for pine trees not affected by defoliation during previous years (Hódar et al., 2004). On the other hand, late stages are more limited by the amount of food available (Démolin, 1969b; Huchon and Demolin, 1970; Hódar

species biology, distribution and individuals' behaviour explains the population dynamics patterns observed in selected forests. Thus, in the short term, it aims to identify caveats and gaps in our knowledge about such dynamics, and promote research aiming to fill these gaps. The first steps in this process are presented in this study. It consists in the construction, documentation and initial testing of the model.

More specifically, and following Jakeman et al. (2006), the context of *INSTAR* refers to the following topics which help clarify our purpose. Firstly, it addresses questions such as: How well can *INSTAR* simulate the dynamics of the processionary moth forest pest in a spatially and temporally explicit way? Is it possible to obtain landscape level metrics (defoliation rate per year and watershed) modelling the behaviour of individual agents? Is *INSTAR* able to reproduce natural patterns of the *T. pityocampa* cycle such as density-dependent restrictions? Moreover, *INSTAR* has been designed to satisfy the needs of scientists interested in simulating ecological processes and, specifically, *T. pityocampa* population dynamics, who would find in *INSTAR* a modular tool to conduct *in silico* experiments.

3.1.2. Entities, state variables and scales

An overview of entities and state variables can be found in Table 1. *INSTAR* contains a simplified version of the biological cycle of *T. pityocampa*, represented by three entities: egg and larval colonies, clusters of pupae and moths; the pine trees on which larvae feed are represented by the entity hosts; and the environment is constituted by cells.

Each colony represents all surviving individuals from the same egg laying and its stage defines the phase of the lifecycle in which the colony is, namely: "egg", larvae 1 (L1, representing the first two instars: I and II) or larvae 2 (L2, representing the last three instars: III, IV and V). This entity is also defined by the state variables number of individuals (i.e. the number of eggs, larvae 1 or larvae 2 contained in the colony), days as egg, days as L1 and days as L2 (days remaining for the stage to be completed), and host (colonies develop on pine crowns, and therefore their location within the environment is described by the host they are linked to). Except for the host they are linked to, all colony variables values change throughout the simulation, i.e. they are dynamic state variables.

Table 1
Summary of entities and state variables within *INSTAR*.

ENTITY	STATE VARIABLE	DESCRIPTION	VALUES (units)
Colony	stage	Indicates in which phase the colony is.	"Egg", L1, L2
	number of individuals	Number of individuals within the colony	0 - ~ 200 (ind.)
	days as egg	Number of days remaining before the colony in instar "Egg" will change to instar L1.	0 - 30 (days)
	days as L1	Number of days remaining before the colony in instar L1 will change to instar L2.	0 - 30 (days)
	days as L2	Number of days remaining before the colony in instar L2 will transform into a cluster of pupae.	0 - 90 (days)
Cluster of pupae	host	Pine on which the colony is located, to which it is linked.	Host ID
	number of individuals	Number of individuals within each cluster.	0 - ~ 200 (ind.)
	days as pupae	Number of days remaining before the cluster of pupae will become moths.	0 - 215 (days)
Moth	location	Cell where it is located.	Cell coordinates
	sex	Sex of the moth.	Female, Male
	mated	Describes whether the moth is mated or not.	Boolean (true/false)
Host	location	Cell where it is located.	Cell coordinates
	height	Pine height.	1 - 20 (m)
	quantity	Relative amount of available biomass for larvae: 0% corresponds to a completely defoliated tree while 100 % corresponds to a tree in the best possible conditions.	0 - 100 (%)
Cells	quality	Indicates whether a tree was defoliated the previous year or not.	defoliated, not defoliated
	location	Position of the host in the world.	x and y coordinates
	elevation	Elevation above sea level.	0 - 8000 (m.a.s.l.)
	probability of emergence	Probability of emergence which defines the number of individuals from a cluster of pupae those survive and become moths. It is calculated based on the number of hosts per cell (see sections 3.3.1 and 3.3.3.1).	0 - 12 (%)
	maximum temperature	Maximum air temperature each day.	-50 - +50 (°C)
minimum temperature	Minimum air temperature each day.	-50 - +50 (°C)	

The entity **cluster of pupae** refers to all individuals from an egg laying that have reached the end of the larval stage and have successfully buried in the soil on a given cell. This entity is used to model the development of pupae and is defined by similar state variables as the colonies: number of individuals, days as pupae and the static variable location.

Finally, the entity **moth** represents an individual moth in the real world. It has a static assigned sex and can be mated or not. Thus, in the transformation from cluster of pupae into moths there is an individualisation process, which is explained in detail in section 3.3.3.

Host entity represents trees (*Pinus* sp.) on which the larvae develop. Hosts are characterised by their static variables location and height (as surrogate of tree size), which defines its carrying capacity, i.e. how many colonies can feed on it before it gets defoliated. Moreover, they also have the dynamic state variables quantity of available biomass, and quality, which indicates if the tree was defoliated in the previous season or not. *T. pityocampa* is an oligophagous species feeding on different *Pinus* species, with variable susceptibility depending on tree species and study site. In SE Spain *T. pityocampa* is found and thrive on *P. sylvestris*, *P. nigra*, *P. pinaster* and *P. halepensis*, as well as some others less frequent species. Thus, we assume that parameters from different host species are straightforward to use on *INSTAR* and that *INSTAR* can be applied to any *Pinus* spp. affected by *T. pityocampa*. Nevertheless, differences in development according to host species cannot be ignored and surely *INSTAR* performance can be improved by parameterising the state variables and submodels according to each species (see section 3.3).

INSTAR works with a 30 m spatial resolution at a temporal resolution of 1 day. The world in the model is constituted by cells, which represent 30 × 30 m, and have elevation associated as a static variable. Cells also have dynamic state variables referring to weather conditions, which change in every time step (1 day). These are the minimum and the maximum temperature. Moreover, cells also have an assigned integrated temperature, an internal variable referring to the temperature of a colony which is exposed to the cell air temperature and the number of insolation hours per day, according to Démolin (1969b). This variable is calculated as:

$$\text{integrated temperature} = \text{maximum temperature} + (1.5 \times \text{insolation hours})$$

3.1.3. Process overview and scheduling

Fig. 1 depicts a schematic overview of the submodels that take place in each time step as well as the entities which perform them. After initialisation (see section 3.3.1), every time step consists of:

- **Environment reading:** *cells minimum and maximum temperature* are updated to the current date and integrated temperature is calculated.
- **Colonies update:** *number of individuals* is updated following the “colony mortality” submodel and *stage* is updated following the “colony development”. Then, “procession” submodel is applied to **colonies** which have completed their development and will become a **cluster of pupae**.
- **Clusters of pupae update:** *number of individuals* is updated following the “pupae mortality” and the length of this phase is adjusted through the “pupae development” submodel. Once a **cluster** completes its development it results in a number of **moths**.
- **Moths update:** **moths** become *mated* following the “mating” submodel and choose a **host** on which to lay their eggs through the “oviposition” submodel.
- **Hosts update:** the available biomass, *quantity*, is updated every day based on growth and larvae consumption through the “host development” submodel.

These submodels are explained in detail in section 3.3.3. Besides that, from the observer perspective, in each time step several state variables values are stored. For a detailed explanation of how model outputs are structured see details regarding observation in the following section.

3.2. Design concepts

This section explains how some important concepts are implemented in *INSTAR*. These basic concepts describe characteristics of ABMs that are not common in other modelling approaches. Describing these concepts in a standard structured format can help transmit the key aspects of the model to others, either ABM experts or those not familiar with this approach (Railsback and Grimm, 2011).

The basic principle of *INSTAR* model is that *T. pityocampa* population dynamics are strongly influenced by the environmental (mainly climate) conditions and therefore these define the impact of the forest pest, the timing of its outbreaks and the areas where it has the highest incidence.

The spatial distribution of the pest as well as the forest state (amount and quality of available biomass) emerges from the simulation as a result of an individual's behaviour. On the one hand, the selection of burial spots and the pines on which moths lay their eggs define the spatial location of the newly created agents, and thus their impact on the pines. On the other hand, timing and scale of the pest outbreaks is regulated through mortality and development. Literature shows a higher incidence of the pest on areas with low pine density (Régolini et al., 2014) and shifts in phenology due to climate changes (Hóðar and Zamora, 2004).

Colonies in *stage L2* adapt to increase their success probability by selecting the burial site considering the number of **hosts** on the **cells** around them and choosing the one which optimises the probability of survival.

T. pityocampa development is dependent on environmental conditions and adjusts its biological cycle to keep it univoltine (Démolin, 1969b; Berardi et al., 2015). *INSTAR* implements this by indirect objective-seeking, constraining the total duration of the biological cycle to one year by shortening and lengthening the **colony** and **cluster of pupae** phases depending on the environmental conditions.

INSTAR entities are able to use information from their surroundings and themselves to define their behaviour, i.e. they *sense* (Railsback and Grimm, 2011). **Colonies** can sense the state variables of their **host** and

the **cell** where they are located. Moreover, **colonies** are also able to sense the number of **hosts** within a certain radius to select a spot where to bury (see “procession” submodel in section 3.3.3.3). Similarly to **colonies**, the **clusters of pupae** can also sense the state variables of the **cells** where they are, since it affects their mortality. Finally, at the end of the cycle, **female moths** can sense if there is a **male moth** within a certain distance and where the surrounding pines are (see “mating” and “oviposition” submodels in section 3.3.3.3). No prediction or learning mechanisms are implemented in *INSTAR*.

Agents interact with each other in an indirect way. **Colonies** within the same **host** compete with each other for their food. When the number of **colonies** on a **host** equals its carrying capacity, the biomass consumption will slowly lead to complete defoliation of the tree, and therefore to the death of larvae present on it (see “colony mortality” submodel in section 3.3.3.1). Moreover, there are intra- and inter-generational interactions. The intragenerational interaction appears when **colonies** turn into **clusters of pupae** and these into **moths** as development takes place, inheriting state variables values. The *number of individuals* of the **cluster of pupae** is inherited from the *number of individuals* of the **colony** it comes from, and the number of **moths** that emerge from the burial site is defined by the *number of individuals* within the parent **cluster of pupae**. Moreover, the location of each agent is defined based on the location of its predecessor. On the other hand, the intergenerational interaction comes from the defoliation of one season defining the *quality* state of the **host** in the coming season and thus affecting the probability of survival of the coming generation of larvae.

To simulate the intrinsic variability of natural processes, several stochastic processes are included during *INSTAR* initialisation: assigning *quantity* to **hosts**; assigning *number of individuals* to **colonies**; assigning *days as egg* to **colonies**; and selecting which are the initial infected **hosts**. Moreover, pseudorandom numbers are also used during the model running to: assign **moth sex** (1:1 ratio); decide whether a **female moth** becomes *mated* or not once it finds a **male moth** and choose the **hosts** where **moths** lay their eggs, following a weighted random selection based on distance to the **moth**. These functions are explained in details in the corresponding submodels descriptions (section 3.3.3).

The representation of *T. pityocampa* biological cycle in three agent types, responds to a necessity to simulate the behaviour and characteristics of each development phase. **Colonies** and **clusters of pupae** are, in a way, collectives since they represent a group of individuals. This assumption does not constitute an oversimplification of the real system considering the characteristic gregarious behaviour of this species, where **colonies** behave as fully functional units (Démolin, 1969b). Besides, defining them as collectives is an advantage since it reduces computing power needs, thus allowing the simulation of larger areas.

To observe the pest dynamics and **hosts** state, *INSTAR* provides several outputs. At system-level, average **hosts quantity**, percentage of infected pines and *number of individuals* of *T. pityocampa* at each life stage are stored for each day. Moreover, monthly averages of all these state variables are also stored at **cell** level. This allows the evaluation of the forest pest development over time for a whole landscape unit (i.e. a specific forest, a basin, etc.) as well as within the simulated area (stand edges, distribution and movement of each phase, most affected **hosts**, etc.).

3.3. Details

ABMs often require a high number of parameters and detailed information is needed to fully parameterise the model (Kelly (Letcher) et al., 2013). Thus, as any other ABM, *INSTAR* parameterisation requires an exhaustive review of literature as well as testing. During last 20 years we produced and recorded data on *T. pityocampa* in Sierra Nevada and surrounding areas (SE Spain) regarding phenology,

Table 2
INSTAR parameters.

PARAMETER	VALUE (units)	DESCRIPTION AND REFERENCES	More details in
Qt_{mean} Qt_{sd}	50, 20 (%)	Mean and standard deviation used to assign initial values of <i>quantity</i> to the hosts , following a normal distribution with such parameters. Reference: This study, assuming an intermediate health state of the simulated pine stand.	3.3.1
CS_{mean} CS_{sd}	193.2, 4.5 (ind.)	Mean and standard deviation used to assign initial values of <i>number of individuals</i> to the colonies , following a normal distribution with such parameters. Reference: Torres Muros (2015).	3.3.1
$Ql_{threshold}$	57.16 (%)	Threshold used to define the <i>quality</i> of the host based on their <i>quantity</i> at the end of the defoliating season. Reference: Muukkonen (2005).	3.3.1
Egg_{min}	30 (days)	Minimum time needed for colonies at stage “egg” to become L1 . Reference: Démolin (1969b).	3.3.1
$L1_{min}$	30 (days)	Minimum time needed for colonies at stage L1 to become L2 . Reference: Démolin (1969b).	3.3.1
$L2_{min}$	90 (days)	Minimum time needed for colonies at stage L2 to become cluster of pupae . Reference: Démolin (1969b).	3.3.1
$L1_{mort}$	10 (%)	Percentage of individuals which die in a colony at stage L1 if its <i>host</i> was defoliated the previous season. Reference: This study, to be parameterised with real data when available.	3.3.3.1
$L2_{mort}$	2 (%)	Percentage of individuals which die daily in a colony at stage L2 if its <i>host</i> has a <i>quantity</i> below $L2_{mort_threshold}$. Reference: This study, to be parameterised with real data when available.	3.3.3.1
$L2_{mort_threshold}$	20 (%)	Threshold defining the <i>quantity</i> of hosts below which individuals of colonies at stage L2 die due to food scarcity. Reference: This study, to be parameterised with real data when available.	3.3.3.1
T_{lethal_max}	32 °C	Maximum temperature above which colonies die. Reference: Démolin (1969b).	3.3.3.1
T_{lethal_min}	-12 °C	Minimum temperature below which colony die. Reference: Démolin (1969b).	3.3.3.1
NPP	28 (%)	Net Primary Production rate defining the daily increase of <i>quantity</i> in the hosts during the growing season. Reference: self-defined based on $Ql_{threshold}$, assuming constant growth rate and according to the growing season described by Alcaraz-Segura et al. (2016).	3.3.3.2
T_{egg_devel}	20 °C*	Maximum temperature above which colonies at stage “egg” develop. Reference: based on Démolin (1969b).	3.3.3.2
$T_{larvae_devel_high}$	25 °C*	Maximum temperature below which colonies at stage L1 or L2 develop. This parameter is used in combination with $T_{larvae_devel_internal}$ and $T_{larvae_devel_low}$. Reference: based on Démolin (1969b).	3.3.3.2
$T_{larvae_devel_internal}$	20 °C*	Minimum integrated temperature above which colonies at stage L1 or L2 develop. This parameter is used in combination with $T_{larvae_devel_high}$ and $T_{larvae_devel_low}$. Reference: based on Démolin (1969b).	3.3.3.2
$T_{larvae_devel_low}$	-10 °C*	Minimum temperature below which colonies at stage L1 or L2 stop their activity. This parameter is used in combination with $T_{larvae_devel_high}$ and $T_{larvae_devel_internal}$. Reference: based on Démolin (1969b).	3.3.3.2
$Pupae_{max}$	215 (days)	Maximum time needed for cluster of pupae to become moths . Reference: Démolin (1969b).	3.3.3.3
$Procession_{max_distance}$	1.23 (cells)	Maximum distance that colonies can processionate to find a suitable place to bury. Reference: Robredo (1963).	3.3.3.3
$Mating_{max_distance}$	3 (cells)	Maximum distance that moths can fly to find a suitable partner to mate. Reference: This study, see Appendix A for a detailed explanation.	3.3.3.3
$Mating_{prob}$	95 (%)	Probability for a female moth to become mated when a male moth is found within $Mating_{max_distance}$. Reference: Rhainds (2010).	3.3.3.3
$Flight_{max_distance}$	3 (cells)	Maximum distance that mated moths can fly to find a suitable host to lay their eggs. Reference: This study, see Appendix A for a detailed explanation.	3.3.3.3

* Parameter values before calibration analysis presented in section 4.

relationship with altitude, egg parasitoidism, or tree species selection, and therefore the model is based on these local data whenever possible. When unavailable, data were taken from scientific literature elsewhere. The parameters used by INSTAR are listed in Table 2 and decisions for parameter estimation are fully explained in Appendix A. In any case, INSTAR was built as a customisable model in which parameter values can be changed to fit biological information to local conditions as well as to incorporate new information when it becomes available, constituting one of its potential.

Some of INSTAR parameter values are well referenced pest traits (CS_{mean} , CS_{sd} , $Procession_{max_distance}$, $Mating_{prob}$) or have been based on best available knowledge considering certain assumptions (Egg_{min} , $L1_{min}$, $L2_{min}$, $Pupae_{max}$, **NPP**, $Ql_{threshold}$, see section 3.3.3.2 and Appendix A). Other parameters require calibration for each study area (T_{egg_devel} , $T_{larvae_devel_high}$, $T_{larvae_devel_internal}$, $T_{larvae_devel_low}$, as presented in this manuscript). Finally, another set of parameters are required for model functioning and can serve in the future for purposes such as scenario setting (Qt_{mean} , Qt_{sd} , $L1_{mort}$, $L2_{mort}$, $L2_{mort_threshold}$) or pest expansion experiments ($Mating_{max_distance}$, $Flight_{max_distance}$, T_{lethal_max} , T_{lethal_min}).

3.3.1. Initialisation

INSTAR is initialised by creating **cells** and **hosts** and assigning their state variables values for the simulated area. *Elevation*, **host location** and *height* are loaded as input data (see section 3.3.2). Moth *probability of emergence* is then calculated for each **cell** based on number of **hosts** on it as follows:

$$probability\ of\ emergence = \begin{cases} 0.12 & \text{if } h_i < 3 \\ 0.1636 - 0.0169h_i & \text{if } 3 \leq h_i \leq 10 \\ 0 & \text{if } h_i > 10 \end{cases}$$

where h_i is the number of **hosts** in **cell** *i*. This function assumes that the number of **hosts** per **cell** is a good surrogate of shaded surface, which affects soil moisture and temperature. These seem to be the main factors explaining the **cluster of pupae** emergence rate according to Torres-Muros et al. (2017), who reported mortality and emergence rates of **cluster of pupae** based on vegetation cover and soil moisture. Above 10 **hosts** per **cell**, full coverage was assumed and therefore cause the *probability of emergence* to be 0. Below 3 **hosts** per **cell**, no effect on surface coverage was considered, and therefore maximum *probability of emergence* was assigned, following data from Torres-Muros et al. (2017). A linear relationship was assumed between these two values, resulting in the above-mentioned function.

After this, *quantity* and *quality* values of **hosts** are assigned. The *quantity* assigned to each **host** is based on a normal distribution with mean Qt_{mean} and standard deviation Qt_{sd} , therefore allowing the user to setup the initial state of the pine stand. *Quality* is defined as **defoliated** or **not defoliated** according to a threshold value $Ql_{threshold}$. Three extra internal variables are calculated for **hosts**:

- The carrying capacity (*cc*) of each **host**: the number of **colonies** that a pine can host. It is calculated based on observations relating the number of **colonies** on highly **defoliated** trees and tree *height*. Briefly, the number of winter colonies in trees suffering a severe (~90%) defoliation was related to the height of the tree for 20 pines

of a pine plantation near Sierra Nevada Protected Area (unpublished data from J.A. Hódar, see Appendix A for details). In this way, estimate of how many colonies are needed to completely defoliate a tree depending on its size (*height*) is obtained:

$$cc = 11.63 \times \ln(\text{height}) - 4.60 \quad (R^2 = 0.65)$$

- The daily consumption per colony (*consumption*): the relative amount of biomass consumed per day by one **colony** in **L2 stage**, given the carrying capacity (*cc*) of the **host** on which it is feeding. It is calculated by assuming that all **colonies** consume the same amount of biomass per day, regardless of the number of individuals in it; it also assumes that **colonies** feed during the minimum number of days needed for a **colony** in **L2 stage** to develop into a **cluster of pupae** (i.e. 90 days) and considering full consumption a defoliation of 90%, in agreement with observations used for the carrying capacity calculations which are as follows:

$$\text{consumption} = 90 / ((cc \times 90)) = 1 / cc$$

- and moth suitability (*mu*) of each **host**, which is calculated as:

$$\mu_i = \sum(\text{count} \times \text{coefficient})_i$$

Where *i* corresponds to the cardinal and intercardinal directions (i.e. north, northeast, east, etc.), the count is the number of trees in each direction *i* at a radius of 1 **cell** (30 m) and each coefficient provides a weighting (see Appendix B) for the influence on each direction of the suitability of a tree for the **moth**. This weighting creates an initial distribution of **colonies** in which there are more colonies on more exposed trees, which is what happens in the real world since burials occur in clear spots and moths choose a host based on the distance to their emergence point.

Afterwards, **colonies** are initialised. The number of **colonies** to be created is defined by the percentage of infected pines, which can be set by the user as a model input. In this study, real data from a defoliation monitoring programme within the Andalusia region (southern Spain) are used. This programme assigns a defoliation value from 0 (no defoliation) to 5 (complete defoliation) to each forest plot at the end of every defoliating season. These data are used to define the percentage of infected pines and thus the number of **colonies** present in the landscape. **Colonies** are then distributed among the **hosts** by weighted random selection based on moth suitability: the higher the moth suitability, the less probability for the **host** to be infected (i.e. to have colonies on it). **Colonies** are initialised as “egg” stage with days as egg corresponding to a random number between 0 and Egg_{min} .

3.3.2. Input data

INSTAR uses a set of input data as follows:

- Map of elevation for the simulated area, obtained from the Andalusian Network of Environmental Information (REDIAM) in a raster format and 30 × 30 m resolution.
- Daily maps of meteorological variables (maximum and minimum temperature) for the simulated area and period. These maps are raster files generated by a hydrometeorological model interpolating data from weather stations at 30 × 30 m resolution (Herrero et al., 2007, see Appendix C for more details). In this study, the meteorological dataset corresponds to years 2008–2013 (see section 4 for more details).
- Map of the pines present in the simulated forest. This map is a vector file derived from Airborne Laser Scanning data, which contains the location and height of trees (more details about this processing in Appendix D). All identified trees are considered to be pines (i.e. **hosts**).
- Initial percentage of infested pines. In this study, this percentage

was based on defoliation data from Andalusian defoliation monitoring programme. This dataset provides an infestation rate based on observed defoliation for each plot within the region, on a 0–5 scale. The initial percentage of infested pines is calculated based on the defoliation assigned by the monitoring programme to the plot where the simulated area is located. This dataset is fully documented by Ros-Candeira et al. (2019).

3.3.3. Submodels

INSTAR uses a series of submodels to simulate the development of the pest, as well as its interactions with the **hosts** and the **cells** (Fig. 1). These submodels make use of best available current knowledge about *T. pityocampa*, but have been built in such a way that will allow an easy integration of new information as knowledge on this pest increases. As an example, if new information on pupae distribution is found, the “procession” submodel could be adjusted to follow such distribution by including a kernel function. These submodels can be classified into three types: mortality, development and movement.

3.3.3.1. Mortality submodels. Mortality submodels simulate the death of organisms due to abiotic or biotic conditions. Since some of *INSTAR* agents represent groups of organisms, some mortality factors apply to the agent as a whole (i.e. they cause the death of a whole **colony**), while others apply to a portion of the individuals that the agent represents (i.e. they cause the reduction in the number of individuals of a **colony**). *INSTAR* applies mortality submodels to **colonies** and **clusters of pupae**, while **moth** mortality is already included in pupae mortality and **hosts** do not have an associated mortality submodel since *T. pityocampa* rarely causes pine death.

The submodel “colony mortality” can reduce the number of individuals of the **colonies** or kill whole **colonies** to simulate mortality rates due to different abiotic and biotic factors. Such mortality rates differ between each *stage*. At the beginning of *stage* “egg”, when the **colony** is created, a mortality factor due to parasitism is applied. Mortality is calculated based on Torres Muros (2015). It considers *elevation* to be a proxy for egg parasitism and causes the original number of individuals to be reduced as follows:

$$\text{number of individuals}_{\text{after mortality}} = \text{number of individuals}_{\text{original}} * p_i$$

where

$$p_i = e^{-n_i} / (1 + e^{-n_i})$$

and

$$n_i = 0.2082 + (0.0006 * \text{elevation})$$

where p_i is the percentage of individuals which survive at a **cell** *i*.

At *stage* **L1**, two mortality factors are applied. The first one is related to *quality* of the **host** and is applied at the beginning of this *stage*, when “eggs” become **L1**. If *quality* is **defoliated**, number of individuals is reduced by a certain percentage $L1_{mort}$. The second factor is due to lethal temperatures and is applied every day: the whole **colony** dies if *maximum temperature* is higher than $T_{lethal,max}$ or *minimum temperature* is below $T_{lethal,min}$.

At *stage* **L2**, two mortality factors are also applied every day. The first one is related to scarcity of food: if *quantity* of the **host** is below a certain threshold $L2_{mort,threshold}$, number of individuals is reduced by a certain percentage $L2_{mort}$. The second factor is the same as for *stage* **L1**: the whole **colony** dies if *maximum temperature* is higher than $T_{lethal,max}$ or *minimum temperature* is below $T_{lethal,min}$.

The submodel “pupae mortality” affects the variable number of individuals of the **cluster of pupae** to simulate mortality rates due to shading (Torres-Muros et al., 2017), which is assumed to be related to the number of **hosts** on a **cell**. A mortality factor is applied at the beginning of this phase, when **colonies** in *stage* **L2** become a **cluster of pupae**. The state variable

probability of emergence defines the percentage of *number of individuals* which survive and result in the number of **moths** which are created (see “pupae development” submodel, section 3.3.3.2):

$$\text{number of individuals}_{\text{after mortality}} = \text{number of individuals}_{\text{original}} * \text{probability of emergence}$$

No mortality submodel is applied to **moth** agents, since it has been included in the *probability of emergence* of “pupae mortality” submodel.

3.3.3.2. Development submodels. Development submodels are used to simulate how an organism increases its biomass over time or how it changes to the next stage of its life-cycle. These submodels are depicted in Fig. 1. In *INSTAR*, **hosts**, **colonies** and **clusters of pupae** have an associated development submodel, while a **moths’** development submodel is not required based on the assumption that all **moths** live one day.

The submodel “hosts development” defines how *quantity* and *quality* state variables change over time. The *quantity* of a **host** on a given day is defined as:

$$\text{quantity}_{(t)} = \text{quantity}_{(t-1)} - \text{consumption} + \text{growth}, \text{ where}$$

$$\text{consumption} = \text{daily consumption per colony} * \text{number of L2 colonies on the host}$$

$$\text{growth} = \text{NPP between April and August and 0\% the rest of the year}$$

Regarding *quality*, this variable is assessed before the growing season starts (i.e. on the 31 st March). *Quality* will be defined as **defoliated** if *quantity* at that moment is below $Q_{l_{\text{threshold}}}$, and **not defoliated** otherwise.

The submodel “colonies development” sets the time that is needed for a **colony** to change its *stage* and eventually become a **cluster of pupae** through “procession submodel”. Each colony *stage* has a counter as state variable (*days as egg*, *days as L1* and *days as L2*, respectively), which defines the length of each *stage* in number of days. When the counter of each *stage* reaches 0, the following *stage* starts (from “egg” to **L1** and from **L1** to **L2**). Finally, **colonies** in *stage L2* will perform the “procession” submodel when *days as L2* become 0. These counters are initially set to the minimum length of each phase based on literature ($E_{\text{gg}_{\text{min}}}$, $L1_{\text{min}}$, $L2_{\text{min}}$) but they will be extended under certain conditions:

- If *maximum temperature* is below $T_{\text{egg}_{\text{devel}}}$ “egg” *stage* will be extended by one day, i.e. *INSTAR* halts the development of eggs on those days where temperature is lower than the threshold ($T_{\text{egg}_{\text{devel}}}$).
- If *maximum temperature* is above $T_{\text{larvae}_{\text{devel}_{\text{high}}}}$ and the integrated temperature is below $T_{\text{larvae}_{\text{devel}_{\text{internal}}}}$ **L1** *stage* will be extended by one day. Moreover, if *minimum temperature* is below $T_{\text{larvae}_{\text{devel}_{\text{low}}}}$, **L1** *stage* will be further extended by one day. Same rules apply to **L2** *stage*. In other words, *INSTAR* halts larval development when temperatures are not high enough for larvae to digest the biomass they have ingested, but, in addition, also when temperatures are too low for larvae to leave their nests to feed.

Extension in **colony** stages causes the following pupae phase to decrease in the same length (see “pupae development” submodel, section 3.3.3.2), in order to maintain a univoltine cycle as literature refers (Berardi et al., 2015).

The submodel “pupae development” sets the length of the phase **cluster of pupae** within the lifecycle of the processionary by adjusting the *days as pupae* state variable, similar to “colony development” submodel. *Days as pupae* are decreased by 1 in every time step. When it becomes 0, the **cluster of pupae** disappears and becomes a certain number of **moths**. The number of **moths** which are then created is

defined by *number of individuals*. For the sake of simplicity, *INSTAR* does not consider extended diapause, as our study area is located in the Mediterranean area, where *T. pityocampa* rarely engage in extended diapause (see Section 2). Nevertheless, a submodel implementing this phenomenon could be easily integrated.

3.3.3.3. Movement submodels. Movement submodels are used to describe processes where an agent selects a place to move to based on information from its surroundings. Three movement submodels are defined in *INSTAR*: “procession”, which simulates the search for a burial spot, performed by **colonies** in **L2** *stage*; “mating”, which simulates the search of a **male moth**, performed by **female moths**; and “oviposition”, which simulates the selection of a **host** to lay the eggs on (i.e. creation of a new **colony**), and is performed by mated **female moths**.

The “procession” submodel defines the place where **colonies** at *stage L2* and *days as L2* equal to 0 become a **cluster of pupae**. Agents performing this submodel search among the surrounding **cells** within $Procession_{\text{max}_{\text{distance}}}$ and select the ones with the lowest pine density (i.e. number of pines in **cell**). If several **cells** have the smallest pine density, they choose the closest one among them. A **cluster of pupae** is created in that **cell** and the **colony** disappears. The state variables of the newly created **cluster of pupae** are inherited from the parent **colony**: *number of individuals* corresponds to the *number of individuals* of the parent **colony** and *days as pupae* equals $Pupae_{\text{max}}$ minus the number of days that the parent **colony** was extended (see “colony development” submodel description).

The “mating” submodel defines which **moths** will become *mated* and where they will be located after mating. **Female moths** become mated with a probability $Mating_{\text{prob}}$ if there is at least one **male moth** within $Mating_{\text{max}_{\text{distance}}}$. When this happens, *mated moths* move halfway towards their partner.

The submodel “oviposition” selects the **host** on which a new **colony** will be created (i.e. the **host** to which the new **colony** will be linked to). After “mating”, *mated moths* choose a **host** to lay their eggs within $Flight_{\text{max}_{\text{distance}}}$. Weighted random selection is used to define which will be the selected **host**. This selection gives a higher probability of being chosen the closer the **host** is to the **moth**. If no **host** is found, no **colony** is created. The state variables of the newly created **colony** are defined as: *number of individuals* corresponds to a random number within a normal distribution with mean CS_{mean} and standard deviation CS_{sd} , *stage* is “egg” and *days as egg* equals $E_{\text{gg}_{\text{min}}}$. The other state variables are set to 0.

4. Model consistency test

INSTAR has been written in NetLogo language (Wilensky, 1999) and reviewed in an iterative process by a multidisciplinary team consisting of computer scientists, modellers and ecologists. An independent implementation of each individual submodel has been used to check that the model agrees with the conceptual model initially proposed by Torres Muros (2015) or, in other words, for model verification in the sense of Findeisen et al. (1978). The last *INSTAR* stable version can be freely downloaded from GitHub (http://sl.ugr.es/github_instar) and run under a NetLogo free licence (<https://ccl.northwestern.edu/netlogo>). Besides this, a demo execution of *INSTAR* can be run at <https://vlab.geodab.eu>, a virtual laboratory promoted by ECOPOTENTIAL project (<https://ecopotential-project.eu>).

4.1. Methodology

Pattern-oriented modelling led *INSTAR* design and helped to decide which processes should be included in the model, as recommended by Wiegand et al. (2003). The most important pattern regarding pine processionary population dynamics corresponds to phenology, which is mainly driven by temperature. Thus, in order to be coherent and

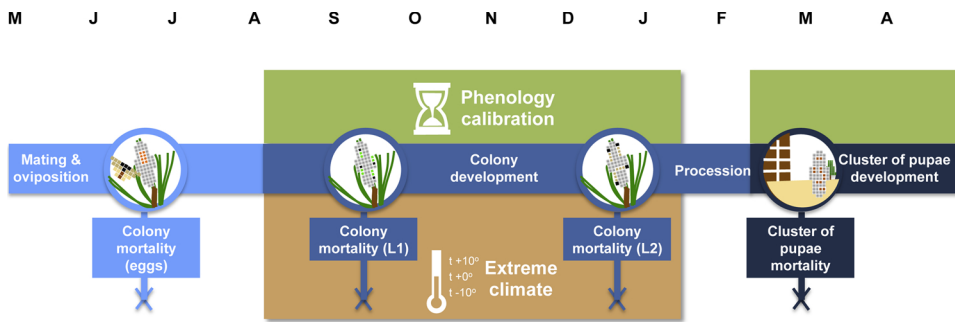


Fig. 2. Diagram showing the submodels within *INSTAR* that are analysed in the consistency tests. Green box corresponds to phenology calibration experiment, while orange box refers to extreme climate experiment (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

structurally realistic, *INSTAR* should faithfully reproduce the effect of this factor on the species’ phenology. The submodels involved in this process are development submodels (section 3.3.3.2) and therefore, a calibration of the parameters involved in these submodels has been performed. Besides this, a stress test was simulated by defining extreme climate scenarios as input data. Stress tests often help to identify unexpected behaviours which cannot be detected when the model is run under normal conditions and therefore extreme unrealistic inputs are used in these tests (Railsback and Grimm, 2011). These experiments constitute a first internal validation of the development submodels (Fig. 2), since they can help with confirming hypothesis and observing unexpected model behaviours. After these tests, parameterisation and sensitivity analysis are needed before the model can be fully applied.

A virtual experimental area was created for this analysis by using a combination of real and built-in datasets (see Appendix E for more details). This virtual area is 15 × 12 cells large, covering an area of 450 × 360 m² (16.2 ha). The location is real: Sierra Nevada Protected Area (south-eastern Spain) at an elevation of 1706 ± 34 m.a.s.l. and contains 1128 pine trees, which have been extracted using an existing LIDAR dataset (see section 3.3.2). Finally, the climatic data needed to conduct the consistency analysis were generated by WiMMED hydrological model (see section 3.3.2) and correspond to years 2008–2013.

4.1.1. Phenology calibration

Each phase in *T. pityocampa*’s life-cycle shows a characteristic phenology, which shifts each year within certain limits depending on climate conditions. Thus, testing whether *INSTAR* reproduces a realistic phenology constitute one of the first steps to validate the model. In order to test whether the phenology of the model reproduces field observations, a calibration of the “colonies development” submodel was performed. The parameters involved in this submodel are the temperature thresholds regulating the length of each phase and the minimum lengths of each stage (see Table 2). This calibration analysis aims to find the values of the parameters T_{egg_devel} , $T_{larvae_devel_high}$, $T_{larvae_devel_low}$ and $T_{larvae_devel_internal}$ that best reproduce the species phenology in the study area.

INSTAR results were calibrated against field observations provided by the Sierra Nevada Global Change Observatory (Bollullos and Aspizua, 2014). The observations consist on a dataset reporting hatching, procession and egg laying dates recorded for several plots within the Sierra Nevada mountain range during years 2009, 2010 and

2011. A summary of this dataset can be observed in Table 3.

Calibration was performed following a stepwise approach: egg development calibration followed by larvae development calibration. In the first step, the parameter T_{egg_devel} , which modulates how long the stage “egg” takes by adjusting *days as egg*, was calibrated in order to obtain simulated hatching dates within the range of the above-mentioned observations. For this analysis, a systematic execution of the model was performed with values of T_{egg_devel} ranging from 15 to 25 °C in 1 °C steps. Every simulation was run in triplicate, lasted 4 months and was initialised at Julian day 210 of the corresponding year (2009, 2010 and 2011). For each simulation, the hatching date of each colony was recorded and the difference between observed and simulated average hatching date was calculated as a metric of model fit.

Once the parameter T_{egg_devel} was calibrated, the second step of the calibration took place. The parameters $T_{larvae_devel_high}$, $T_{larvae_devel_low}$ and $T_{larvae_devel_internal}$ were calibrated to obtain procession dates within the range of the above-mentioned observations. These parameters affect how long the stages *L1* and *L2* take by adjusting *days as L1* and *days as L2* (see section 3.3.3.2). For this analysis, a new systematic execution of the model was performed. A range of values for each parameter was tested: 20–30 °C for $T_{larvae_devel_high}$, 15–25 °C for $T_{larvae_devel_internal}$ and –15 to –5 °C for $T_{larvae_devel_low}$, in 1 °C step, resulting in 1331 combinations of parameter values. Simulations were initialised with colonies at stage *L1*, to avoid noise coming from the previous stage. Each simulation was started on Julian day 226 of the corresponding year and lasted 9 months, therefore extending to the beginning of next year. Thus, input datasets correspond to years 2008/2009, 2009/2010 and 2010/2011. The initialisation date corresponds to the average hatching date derived from the previous experiment. For each combination of parameter values and input dataset, five replicates were run. Finally, to avoid noise coming from other submodels, mortality submodels based on host quality and quantity were disabled and the procession submodel was unconstrained (colonies could bury in all cells around them). In this case, the procession date of each colony was recorded in each simulation and the difference between observed and simulated average procession date was calculated as a measure of model fit.

The above described stepwise calibration was based on hatching and procession dates within 1-cycle runs. Once the involved parameters are calibrated, it becomes necessary to test whether the selected parameter values reproduce the phenology pattern over the years. To test these criteria, *INSTAR* was run for the period 2008–2011

Table 3

Average, earliest and latest hatching, procession and egg laying dates for *Thaumetopoea pityocampa* observed in Sierra Nevada during years 2009, 2010 and 2011. Data from Sierra Nevada Global Change Observatory (Bollullos and Aspizua, 2014).

	Hatching date			Procession date			Laying date		
	Earliest	Average ± SD	Latest	Earliest	Average ± SD	Latest	Earliest	Average ± SD	Latest
2009	23 rd July	12 th August ± 10 days	4 th Sept.	4 th March	26 th March ± 13 days	12 th May	22 nd June	27 th July ± 20 days	31 st August
2010	28 th July	22 nd August ± 11 days	28 th Sept.	28 th November 2009 ^a	8 th February ± 47 days	19 th May	2 nd July	3 rd August ± 20 days	23 rd Sept.
2011	28 th July	21 st August ± 10 days	12 th Sept.	24 th January	23 rd March ± 25 days	19 th May	9 th April	28 th July ± 22 days	12 th Sept.

^a Note the year difference: earliest procession date occurred in 2009.

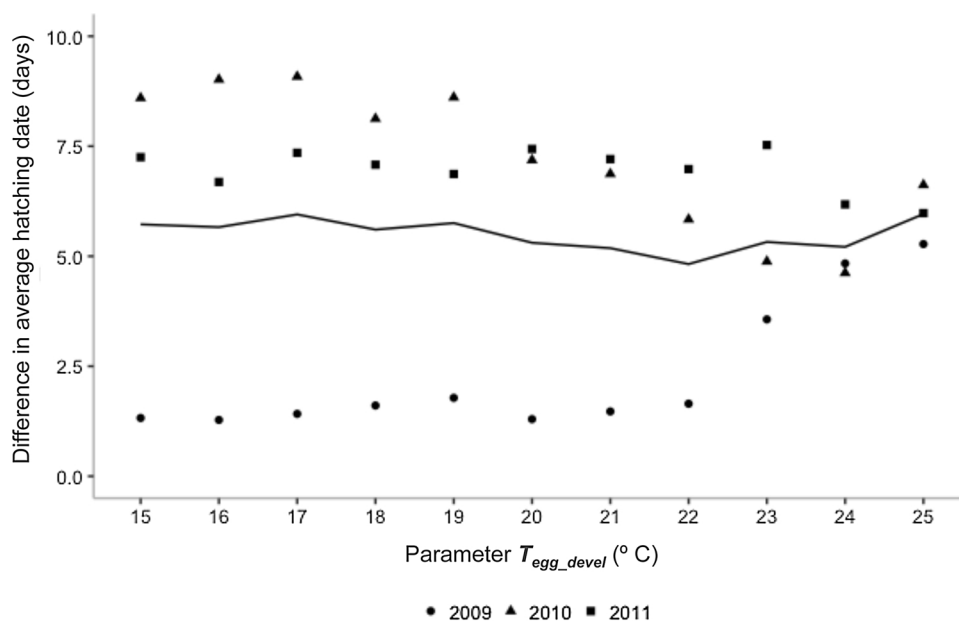


Fig. 3. Difference in observed and simulated average hatching date for years 2009, 2010 and 2011 along T_{egg_devel} tested values. Line shows the mean among years.

using the selected values for parameters T_{egg_devel} , $T_{larvae_devel_high}$, $T_{larvae_devel_internal}$ and $T_{larvae_devel_low}$.

4.1.2. Extreme climate stress test

By exposing the model to extreme climate, we aim to test the model consistency in relation to temperature influence on pest development. As mentioned at the beginning of this section, extreme unrealistic inputs are used in these tests in order to observe divergent behaviours in the model against normal input data. Thus, three input scenarios were used in this experiment: NORMAL, corresponding to the daily maps obtained from measured temperatures, MINUS10 and PLUS10. Scenarios MINUS10 and PLUS10 were generated by respectively subtracting and adding an offset (10 °C) to the measured temperatures, in order to reach lethal temperatures for the processionary moth and test whether *INSTAR* simulates development and mortality due to extreme temperatures as expected. The offset was applied equally to maximum and minimum temperatures, therefore maintaining the thermal range. Simulations were run in triplicate for the period 2008–2013. Considering these scenarios, larval development is expected to be accelerated when temperatures are high and delayed when they are low. Moreover, larvae mortality rates are expected to increase, even causing pest annihilation, due to the higher occurrence of extreme temperatures above or below the species survivability thresholds.

4.2. Results

4.2.1. Phenology calibration

Results from the egg development calibration can be observed in Fig. 3, which shows the difference between observed and simulated average hatching date for each year along the T_{egg_devel} tested gradient. The line indicates the mean of the difference among all three years. Data from year 2009 show differences of less than 2 days between simulated and observed mean hatching date for T_{egg_devel} values 15–22 °C. Data from years 2010 and 2011 show higher differences, above 5 days for T_{egg_devel} values 15–22 °C. For T_{egg_devel} values 23–25 °C, the trend changes and all differences range between 3.5 and 7.5 days. When the mean difference among all years is analysed, small fluctuations are observed. The minimum value is found for 4.8 days, corresponding to T_{egg_devel} equal to 22 °C and the maximum value, 6.0 days, is reached for T_{egg_devel} equal to 25 °C. Considering these results, the selected value for

T_{egg_devel} corresponds to 22 °C.

Once the egg phase was calibrated, larvae development calibration was carried out. Difference in average procession date between observations and simulations, which has been considered as the calibration metric for larvae development phase, was calculated for each combination of parameter values and seasons. The minimum difference across years corresponds to 2.5 days and is found for $T_{larvae_devel_high}$ equal to 27 °C, $T_{larvae_devel_internal}$ equal to 25 °C, and $T_{larvae_devel_low}$ equal to -8 °C, followed by all other $T_{larvae_devel_low}$ tested values except for -5 °C (data not shown). Fig. 4 shows the mean difference for the three years along the tested values for parameters $T_{larvae_devel_high}$ and $T_{larvae_devel_intern}$ ($T_{larvae_devel_low}$ fixed to -8 °C). A local minimum can also be observed for $T_{larvae_devel_high}$ equal to 22 °C $T_{larvae_devel_intern}$ equal to 23 °C. This local minimum, however, is not so clearly observed for data regarding each year separately (see Fig. 11A-C in Appendix F).

The influence of parameter $T_{larvae_devel_low}$ can be observed in Fig. 5. Differences generally remain below 10 days for all years and parameter values. Small differences are obtained for year 2008/2009 for most parameter values, except for $T_{larvae_devel_low}$ equal to -5 °C. Year 2009/2010 shows the highest differences for values below -9 °C, while year 2010/2011 shows fluctuating differences. If the mean across years is considered, a consistent increase can be noticed for values -7 °C to -5 °C. As mentioned above, the minimum difference is found at -8 °C. The influence of parameter $T_{larvae_devel_low}$ when the local minima of $T_{larvae_devel_high}$ equals 22 °C $T_{larvae_devel_intern}$ equals 23 °C can be observed in Fig. 12 in the Appendix F, resulting in higher differences for most values and years. It should be noted that parameter $T_{larvae_devel_low}$ is evaluated only when maximum daily temperature is above $T_{larvae_devel_high}$ and/or integrated daily temperature is below $T_{larvae_devel_intern}$ (see section 3.3.3.2), which could explain the seemingly erratic behaviour of this parameter.

Once the above described parameters were calibrated, results of the simulation regarding species phenology using the selected values for parameters T_{egg_devel} , $T_{larvae_devel_high}$, $T_{larvae_devel_internal}$ and $T_{larvae_devel_low}$ (22 °C, 27 °C, 25 °C and -8 °C, respectively), are shown in Fig. 6, which also shows the observed phenology. Egg layings fall within the observed ranges for years 2009 and 2011, but tend towards earlier dates for year 2010 in comparison to observations. Hatchings and processions occur within the observed range for all three years.

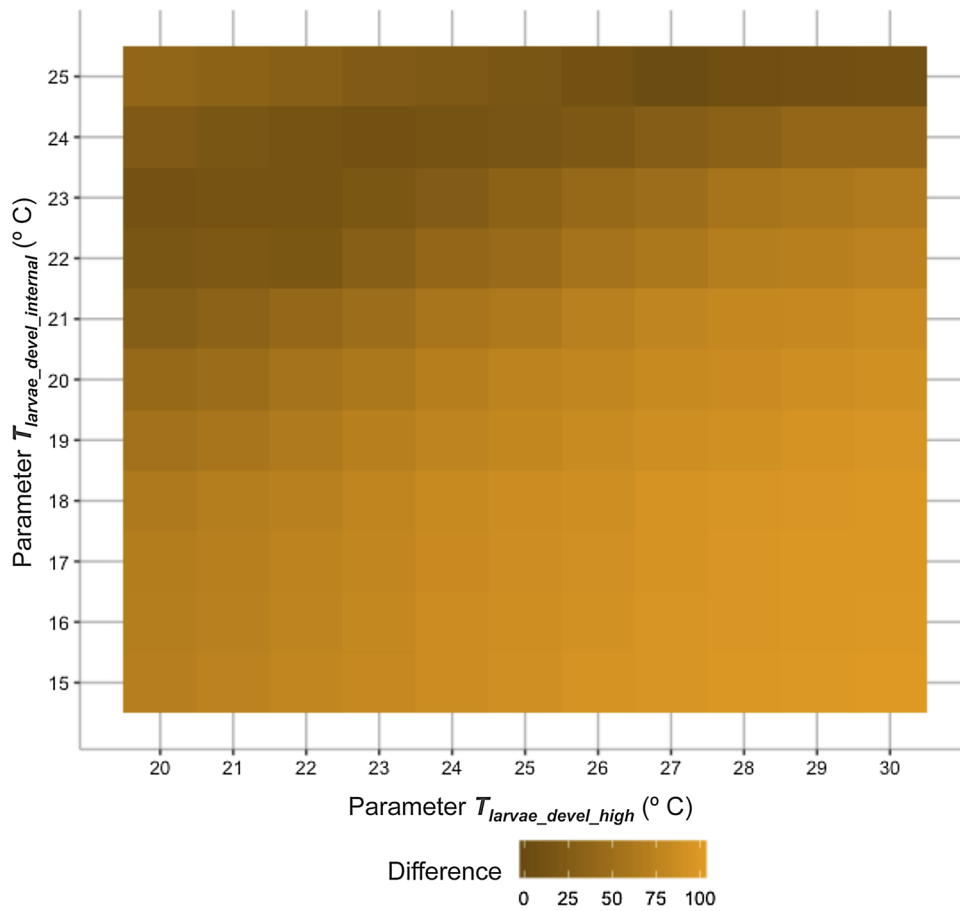


Fig. 4. Difference between observed and simulated average procession date, in number of days. Data refer to the mean across years 2008/2009, 2009/2010 and 2010/2011 for each combination of parameters $T_{larvae_devel_high}$ and $T_{larvae_devel_internal}$. The value for parameter $T_{larvae_devel_low}$ is fixed to -8 °C.

4.2.2. Extreme climate stress test

Pest dynamics for each scenario are shown in Fig. 7. As expected, high larvae mortality rates resulted in a reduced number of individuals in both MINUS10 and PLUS10 scenarios compared to the NORMAL

scenario. In the MINUS10 scenario, the population was greatly limited (Fig. 7A). Under the PLUS10 scenario, however, larvae mortality due to high temperatures was as high as to cause full annihilation of the pest before the first cycle was completed (Fig. 7B).

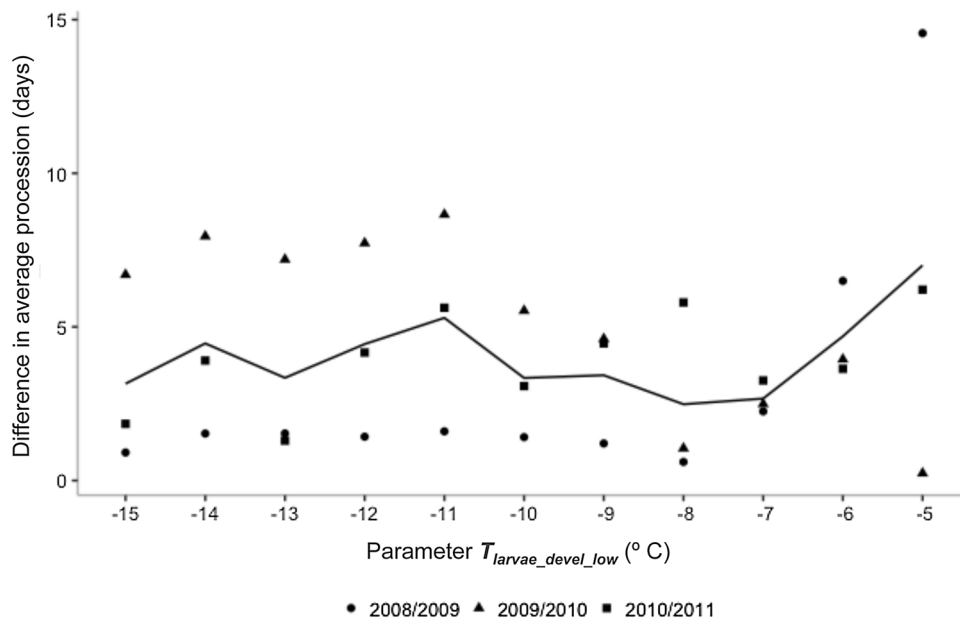


Fig. 5. Difference between observed and simulated average procession date, in number of days along $T_{larvae_devel_low}$ gradient. Data for each year (points) and across years (line) for parameter $T_{larvae_devel_high}$ fixed to 27 °C and parameter $T_{larvae_devel_internal}$ fixed to 25 °C.

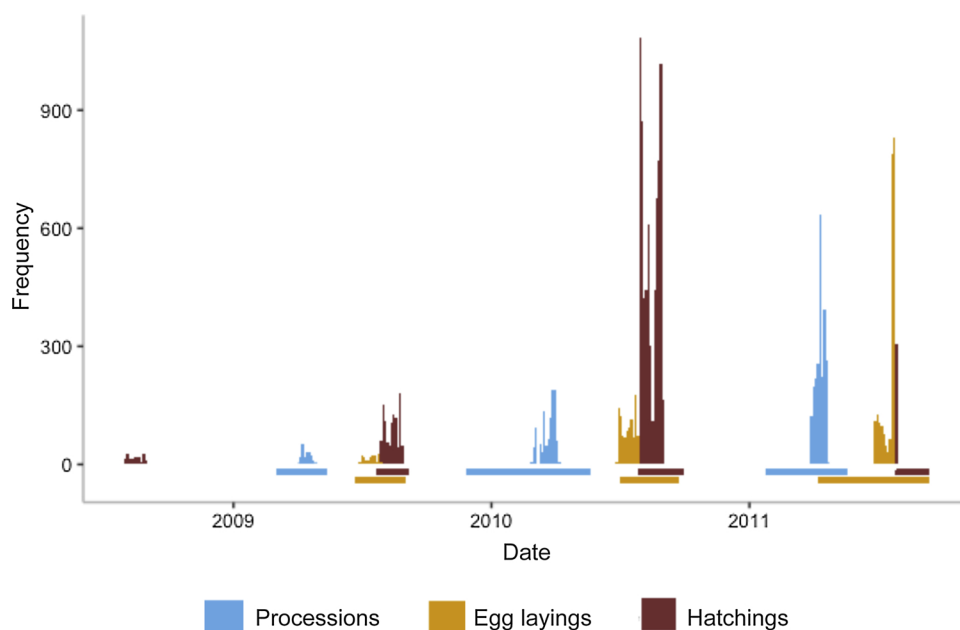


Fig. 6. Histograms showing the frequency of simulated egg layings (orange), hatchings (red) and processions (blue) along the simulation period (29/07/2001-20/07/2008). Field observations (2009–2011) are depicted in the plot as horizontal bars below the histogram (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

5. Discussion

To the best of our knowledge, *INSTAR* is the first ABM simulating the population dynamics of the pine processionary moth. This is a spatially-explicit model, which constitutes an advantage in comparison to other published models such as Robinet et al. (2014); Seixas Arnaldo and Monteiro Torres (2005) or Régolini et al. (2014). The model aims to improve our understanding of the pest's population dynamics and identify gaps in our knowledge. The design and implementation of *INSTAR* constitutes an effort to synthesize the available knowledge about the target species, while it allows an easy integration of newly produced knowledge. Under a structural point of view, *INSTAR* has been built considering all the ontological stages of the target species: eggs, larvae, pupae and moths. The concepts of colony and cluster as an agent types are used to represent groups of eggs, larvae or pupae, while moths are represented as individual agents. The model is built following a modular structure with three submodel classes: development, mortality and movement. The classification of submodels into a reduced number of classes helps to overcome some of the most common critics to ABMs: the difficulties of reproducing them, standardising their structures and defining guidelines to design, calibrate and evaluate them (DeAngelis and Grimm, 2014). Thus, the modular structure of *INSTAR* eases the exchange of information among modellers as well as the comparison between models. Such a structure improves the understanding of the model and facilitates communication with non-modellers. Moreover, it could constitute a framework to build models simulating other forest pests in a wide variety of ecological systems, since it summarises the key biological processes that take place in them. As an example, movement submodels could be adjusted to simulate the dispersal and establishment of mistletoe, another common pest in pine plantations, by following Mellado and Zamora (2016).

T. pityocampa is a poikilotherm species, and therefore air temperature plays a key role in its performance. Moreover, the distribution and density of pine plantation stands has been demonstrated to be another important factor explaining the population dynamics of the species (Dulaurent et al., 2011; Li et al., 2015; Torres-Muros et al., 2017). Thus, *INSTAR* considers climate and land use as the main forcing variables or drivers. In this manuscript, the role of temperature in *INSTAR* has been calibrated and analysed. Parameters involved in development submodels have been calibrated using phenology observations from Sierra Nevada (Spain) and the difference between observed and simulated

average hatching and procession date as a measure of model fit. The egg phase showed small differences (maximum 9 days) for all tested parameter values and years. The parameter value selected corresponds to the one which minimises the difference in observed and simulated average hatching date for all three years (T_{egg_devel} 22 °C). Larvae phase shows important differences for different parameter values and years. This implies that larvae phase is the main responsible for the phenology within *INSTAR*. The parameter set selected for larvae development corresponds to the one which minimises the difference for all years ($T_{larvae_devel_high}$ 27 °C, $T_{larvae_devel_intern}$ 25 °C and $T_{larvae_devel_low}$ -8 °C). This set also resulted in small differences for each year separately and causes the model to successfully reproduce the species phenology through a multiple-year simulation.

Besides this, *INSTAR* behaviour when exposed to extreme climate has also been analysed. Extremely low temperatures (MINUS10 scenario) have a severe impact on the number of larvae but not on the eggs. This is explained by the fact that the egg mortality implemented in the model is only due to parasitism which is not linked with temperature. The model could be improved in this regard by also including egg mortality due to lethal temperature (following Rocha et al. (2017)) and the effect of temperature on parasitism rates (following Tiberi et al. (2015)). When exposed to extremely high temperatures (PLUS10 scenario), the behaviour is quite different. This scenario causes a total annihilation of the pest during the first year of the execution. In other words, an extreme increase in temperature such as the one caused by PLUS10 scenario seem to cause most cells in the landscape to reach maximum lethal temperatures. Our simulated area represents a warm region of the distribution area of the pest. Therefore, the population is probably closer to its high temperature threshold than to its lower one, resulting in this scenario causing the population collapse which cannot be observed under the MINUS10 scenario (i.e. a change of the same scale towards low temperatures does not cause as many cells to reach minimum lethal temperatures). Nevertheless, these statements should be taken cautiously. The parameter values have been taken from literature, they refer to air temperatures and represent the general knowledge of *T. pityocampa*. The actual lethal values may differ for different populations and been influenced by other factors (e.g. wind speed, shading) which can modulate the actual temperature to which larvae are exposed. Another reason for the difference between scenarios can be that at higher temperatures, eggs develop faster and hatching is anticipated, causing the larvae to be exposed to the high summer

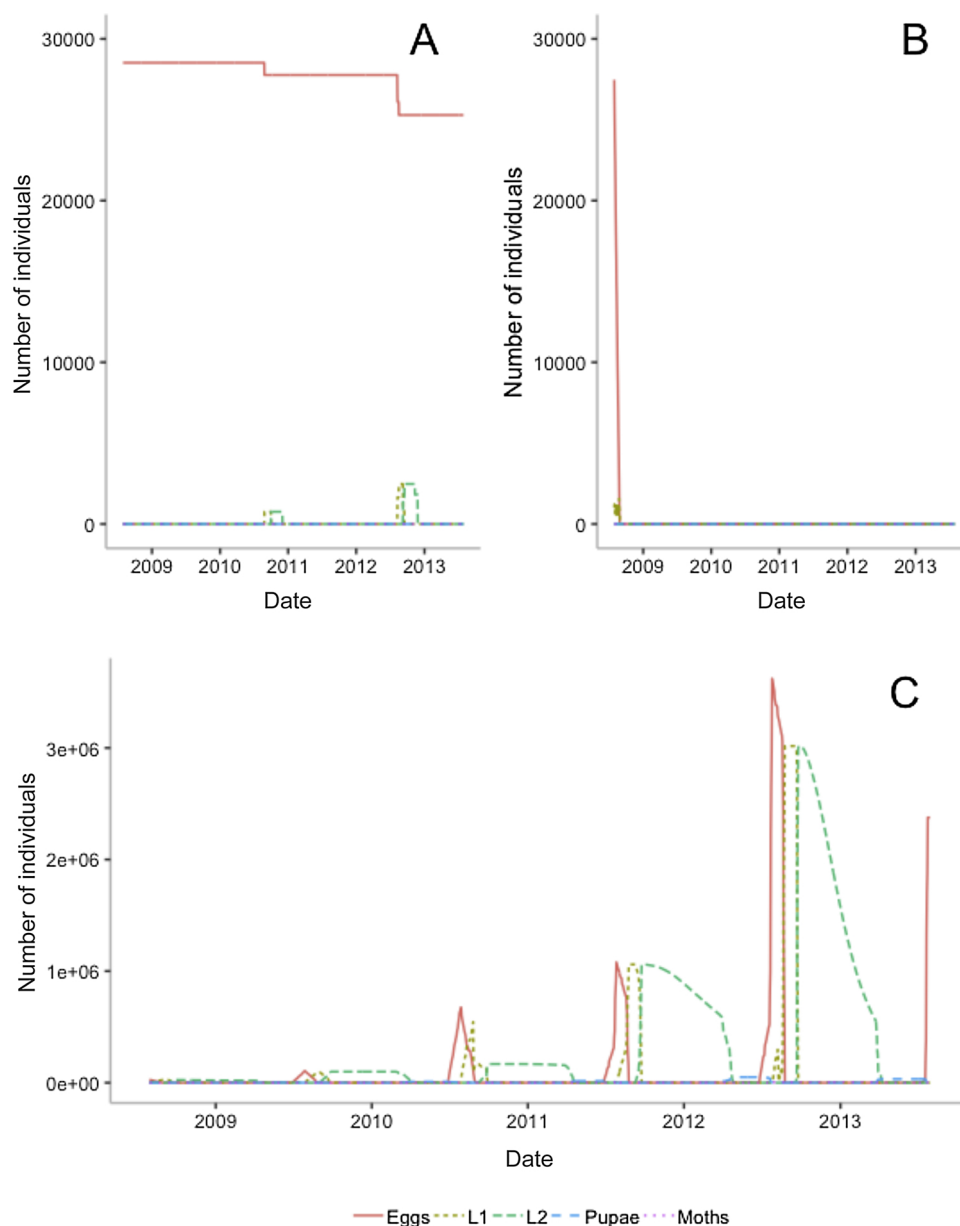


Fig. 7. Plots showing the pest development as number of eggs (red continuous line), larvae *L1* (light brown pointed line), larvae *L2* (green short-dashed line), pupae (blue long-dashed line) and moths (pink pointed line) under three different scenarios: MINUS10 (A), PLUS10 (B) and NORMAL (C), for the period 2008–2013 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

temperatures. Literature suggests that *T. pityocampa* adapts to areas with warm summers by delaying the egg phase to late summer, thus avoiding lethal temperatures (Chapter 2 in Roques (2015)). At the moment, *INSTAR* does not possess a mechanism simulating this process, since initialisation is fixed at a certain date as it is commonly done in processes which deal with seasonal and annual patterns (such as hydrological models). This limitation, however, can be overcome by calibrating the initialisation date for the area to be simulated based on field data. To sum up, phenology has been calibrated successfully according to the field observations. However, more knowledge about the drivers modulating the biological cycle of the species would be required for a more realistic modelling.

This article is focused on the phenological aspects of the processionary moth. Although this is a very important process, in order to correctly simulate the population dynamics of the pest, its spatial distribution should be addressed by calibrating and parameterising

movement submodels. However, data on movements by the pine processionary moth are difficult to obtain and literature often refers to non-natural conditions, such as flight distance measured under laboratory conditions (Sauvard and Yart in Battisti et al., 2015), or extreme values (Robredo, 1963).

Moreover, assessing the impact of the pest at a landscape scale requires high resolution data, such as quantifying per-larvae biomass consumption. Although larvae weight gain has been studied (Avtzis, 1986), no reference for biomass consumption has been found. This has avoided a more realistic modelisation of the host-pest interaction. Due to the interest on forest health, pests are commonly monitored by assessing their impact as defoliation or other stress signals on the host (Trumbore et al., 2015). In the case of the pine processionary moth, the number of colonies is also often monitored and reported. *INSTAR* uses this type of information for the calculation of the trees carrying capacity (see section 3.3.1 and Appendix A). However, data at a higher

resolution (i.e. number of larvae per colony at different stages) is not available and such information would be particularly valuable to improve how the host-pest interaction is modelled and to calibrate the mortality submodels. In general terms, information and field observations about movement and mortality parameters are scarce and therefore an important gap of knowledge exists in this respect.

INSTAR is focused on the processionary moth, and therefore host development is modelled in a very simple way. This submodel could be further improved by considering more a complex relationship of pine activity with climate, differences among pine species or linkages between primary production and topographic-soil features. This could be done by coupling *INSTAR* with independent models (such as the ones proposed by [Faías et al. \(2012\)](#)) simulating stand growth and development.

Due to the inherent characteristics of ABMs, there is a high degree of uncertainty in the model and a high number of parameters, which will require calibration and parameterisation ([Kelly \(Letcher\) et al., 2013](#)). Thus, further work should focus on determining the parameters which have the strongest impact on model outputs (i.e. sensitivity analysis) and identifying model uncertainty sources. Once the model is fully calibrated and validated, simulations can be considered as *in silico* performed experiments that are not feasible in the real world. *INSTAR* could then help to forecast the probability of occurrence and intensity of the pest outbreaks on pine plantations under different climate and land use scenarios. Thus, in the long term, *INSTAR* could be useful for the environmental decision makers in charge of managing the large area covered by pine plantations affected by this pest.

population. Further work should focus on testing and calibration of pest spatial distribution, as well as overall sensitivity and uncertainty analysis.

Author contributions

María Suárez-Muñoz led the manuscript writing process as well as the *INSTAR* code review and testing. She also designed the experiments showed in the text. Francisco Bonet-García contributed to the initial conception of the model and to write the manuscript. He supervised the whole process and contributed to the funding acquisition. José A. Hódar contributed to the conceptual model and provided basic data and knowledge regarding pine processionary moth natural history and ecology. He also participated in the model implementation phase, writing of the manuscript and the funding acquisition. Javier Herrero designed and executed the hydrometeorological model and contributed to the manuscript. He also produced and provided the meteorological data from Guadalfeo Projec network. Mihai Tanase pre-processed the LiDAR dataset and produced the LiDAR based metrics used in this study. He also contributed to the manuscript with the description of the LiDAR data analysis. Lucía Torres-Muros developed the initial conceptual model as well as to the collection of data needed to calibrate some *INSTAR* functions. The table shown below describes with more detail the specific contributions of each author. The authors' contribution to each parameter is depicted using a quantitative range from 0 (no contribution) to 5 (full responsibility)

Author name	Study conception	Methods	Computation	Formal analysis	Perform the experiments	Data collection	Data curation	Writing the manuscript	Data presentation	Supervision	Funding acquisition / project admin
María Suárez-Muñoz	3	3	4	3	4	1	5	5	4	0	0
Francisco J. Bonet-García	4	2	2	3	2	2	3	4	4	5	5
José Antonio Hódar	4	2	0	2	3	3	1	3	1	2	2
Javier Herrero-Lantarón	0	2	2	2	1	0	2	1	2	1	0
Mihai Tanase	0	2	2	2	1	0	1	1	2	0	0
Lucía Torres Muros	4	2	0	2	2	3	3	1	0	0	0

6. Conclusions

Current available knowledge on *T. pityocampa* has been synthesized and integrated into *INSTAR*, an ABM aiming to simulate the population dynamics of this species. In this article, we present *INSTAR* model structure according to a standard protocol, specifically designed to document ABMs, increasing its usability and reproducibility. Moreover, we have conducted a consistency test which constitutes a first internal validation of the model. The experiments presented here assess how the model simulates the development of the pest driven by temperature. Once the model has been calibrated, it successfully reproduces the phenology observed for a given area. This means that the submodels responsible for the development within *INSTAR* are well designed and implemented. Moreover, the model behaves as expected when exposed to extreme input values through a climate stress test. Extreme high temperatures cause full annihilation of the pest before the first cycle is completed and extreme low temperatures greatly limit the pest

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: <https://doi.org/10.1016/j.ecolmodel.2019.108764>.

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