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Laura Poitou[1], Christelle Robinet[1], Christelle Suppo[2], Jérôme Rousselet[1], Mathieu Laparie[1], Sylvain Pincebourde[2*]

[1]INRAE, URZF, 45075, Orléans, France

[2]Institut de Recherche sur la Biologie de l'Insecte, UMR 7261, CNRS - Université de Tours, 37200 Tours, France.

***Corresponding author:** Sylvain Pincebourde (sylvain.pincebourde@univ-tours.fr)

Journal: Journal of Thermal Biology

Type of paper: Original paper

Abstract

Temperature strongly drives physiological and ecological processes in ectotherms. While many species rely on behavioural thermoregulation to avoid thermal extremes, others build structures (nests) that confer a shelter against climate variability and extremes. However, the microclimate inside nests remains unknown for most insects. We investigated the thermal environment inside the nest of a temperate winter-developing insect species, the pine processionary moth (PPM), *Thaumetopoea pityocampa*. Gregarious larvae collectively build a silken nest at the beginning of the cold season. We tested the hypothesis that it provides a warmer microenvironment to larvae. First, we monitored temperature inside different types of nests varying in the number of larvae inside. Overall, nest temperature was positively correlated to global radiation and air temperature. At noon, when global radiation was maximal, nest temperature exceeded air temperature by up to 11.2-16.5°C depending on nest type. In addition, thermal gradients of amplitude from 6.85 to 15.5°C were observed within nests, the upper part being the warmest. Second, we developed a biophysical model to predict temperature inside PPM nests based on heat transfer equations and to explain this important temperature excess. A simple model version accurately predicted experimental measurements, confirming that nest temperature is driven mainly by radiation load. Finally, the model showed that nest temperature increases at the same rate as air temperature change. We conclude that some pest insects already live in warm microclimates by building their own sheltering nest. This effect should be considered when studying the impact of climate change on phenology and distribution.

Keywords: Microclimate, pine processionary moth, biophysical ecology, heat gain, nest, thermal niche.

1. Introduction

Temperature is the most impactful environmental variable for organisms since it drives virtually all biochemical processes and physiological rates (Walther et al., 2002). Temperature influences ectotherms at all levels from their physiology (Chown and Nicolson, 2004) to their geographic distributions (Menéndez, 2007). The vast majority of studies attempting to relate temperature and ecological or physiological processes in ectotherms uses ambient air or atmospheric temperature, often taken at relatively coarse spatial scale, as a proxy of the temperature experienced by organisms in their microhabitat (Kearney and Porter, 2009; Potter et al., 2013). Small ectotherms like insects, however, live in thermal habitats that can deviate substantially from ambient air temperature and that can vary according to patterns that differ from environmental fluctuations (Pincebourde et al., 2016; Pincebourde and Woods, 2020). For example, tropical ants can be confined to superheated plant surfaces in the canopy, thereby experiencing temperatures up to 25°C above ambient air temperature (Kaspari et al., 2015). Temperate aphids or spider mites also experience temperatures up to 20°C above ambient temperature at the surface of leaves exposed to solar radiation (Caillon et al., 2014; Saudreau et al., 2017; Cahon et al., 2018). Therefore, the temperature of the microclimate should be considered to better comprehend the global response of insects to environmental temperature variations. Yet, the microclimatic temperature to which most animals and plants are exposed remains to be quantified (Lembrechts et al., 2020; Pincebourde and Sallé, 2020; Pincebourde and Woods, 2020).

Some species build structures for diverse functions during part or all of their life cycle. These animal constructions can generate novel microclimates with specific temperature patterns that ameliorate their survival or fitness (concept of extended phenotype; (Dawkins, 1982)). A well-known example is the large termite mound in Africa, which greatly buffers the extreme environmental temperatures thereby improving survival in otherwise quite challenging thermal environments (Joseph et al., 2016). Many other insects build or induce more cryptic structures (Hansell, 2007) such as leaf mines, plant galls, or tunnels across the wood. Despite their small size, the microclimate temperature within these structures can deviate strongly from ambient air temperature (Pincebourde and Casas, 2016). For example, the temperature inside leaf mines can be up to ~15°C warmer than ambient air (Pincebourde and Casas, 2006, 2015). The nest of social insects including bees and wasps also generates particular thermal environments, mostly due to the ability of social insects to thermoregulate the atmosphere inside the nest (Hozumi et al., 2010; Stabentheiner et al., 2010). Finally, gregarious insects complete

part of their larval development by building nests often made of silk produced by individuals. This is the case of some Lepidopteran species whose communal nests generate microclimate temperatures that can deviate by up to 2-5°C from ambient air (Knapp and Casey, 1986; Ruf and Fiedler, 2000; Fitzgerald et al., 2012). In all those structures, heat is exchanged with the environment through i) conduction across the boundary layer of the structure, ii) convection in the ambient air, iii) absorption and emission of radiative energy, and iv) possibly also during evapotranspiration (Gates and Schmerl, 1980; Monteith and Reifsnyder, 2008). The relative rate of heat exchanged via those four processes depends on environmental properties like air temperature, wind speed and amount of solar radiation received, but also on the structure properties like its size, shape and color. For most insect structures, the convection is the main source of heat losses, whereas solar radiation constitutes the main heat source (May, 1979). Nevertheless, these mechanisms are rarely considered to characterize the microclimate of structures developed by insect pests.

Insect constructions not only generate novel microclimates but also sometimes provide insects with heterogeneous micro-environments inside which they can thermoregulate. Behavioural thermoregulation is an important process that allows insects to stabilize their body temperature or at least to buffer extremes (May, 1979; Woods et al., 2015). Both the architecture and the position within the structure are important components of this process. For example, the codling moth *Cydia pomonella*, develops within apple fruit (although this is not a structure built by the insect) and, under normal conditions, they select the warmer apple hemisphere, *i.e.* the one that receives solar radiation (Kührt et al., 2005). The fall webworm *Hyphantria cunea* constructs a colonial web which is heated by solar radiation, thereby generating a thermal gradient across the web (Rehnberg, 2002). Sometimes, the behavioural thermoregulation is combined with a form of intermittent endothermy (Heinrich, 1999). This process consists in the production of metabolic heat inside the structure that contributes to warming the nest. For example, the aggregation of social caterpillars of *Eriogaster lanestris* inside their nest results in a temperature increase of up to 3°C caused by metabolic heat-production (Ruf and Fiedler, 2000). This process is combined with the properties of the silken nest they build to generate a favourable microclimate for larval development (Ruf and Fiedler, 2002a). To understand the effects of structure microclimate on body temperature and insect development, few researchers built biophysical models of heat exchanges. For example, the phenology of *Ips typographus* was simulated by integrating, into a development model, the bark temperature predictions derived from solar radiation as a model input (Baier et al., 2007). The thermal environment of

the leaf miner *Phyllonorycter blancardella* was described mechanistically by using a biophysical model which revealed high heat excess inside so small structures (Pincebourde and Casas, 2006). This biophysical approach, however, is rarely applied to insect pests, despite its potential to quantify the temperature patterns actually experienced by these pests.

Our objective was to characterize the microclimate in the nest of an important Mediterranean forest pest, the winter pine processionary moth (PPM), *Thaumetopoea pityocampa* (Denis & Schiffermüller). PPM defoliation influences the growth and vulnerability of its host plants (pine and cedar species) (Hódar et al., 2003; Carus, 2004; Parlak et al., 2019). Most importantly, urticating setae produced by late instars larvae and blown in the air or accumulated in their habitats cause sanitary problems to humans and animals due to rashes or more intense allergic reactions (Moneo et al., 2015; Battisti et al., 2017). Because periods with risk exposure and environmentally friendly solutions to manage PPM populations are life-stage dependent, the knowledge about its phenological cycle has to be improved specifically the timing of target instars depending on temperature. Furthermore, the PPM has become a model to understand the ecological impacts of climate change because its spatial distribution has readily expanded in relation to the increase of winter temperature which facilitated larval feeding and survival (Battisti et al., 2005; IPCC, 2015). Information about the thermal environment of the PPM within its nest is crucial to better understand its past and future range expansion, and to improve predictions by identifying potential invaded areas. The larvae of this species are gregarious and make their development during the cold season in a silken nest, which they leave only for feeding. We tested the hypothesis that the silken nest generates a microclimate warmer than surrounding conditions. First, we measured directly the temperature at several locations inside the nest under contrasting environmental conditions to characterize the microclimate temperature patterns experienced by larvae. We surveyed both wild nests found *in natura* and nests built by larvae previously translocated into a pine nursery. The latter approach in a nursery allowed minimizing any variance associated with individual trees, their surroundings, or the position of the nests on trees. Moreover, translocating larvae onto those experimental trees allowed manipulating and standardizing larval colony size and nest weaving effort. We expected a significant thermal heterogeneity inside the nest due to its architecture (see below). Second, we developed a biophysical model to predict the temperature inside typical PPM nests. This model should improve our understanding of the actual thermal experience of larvae as well as the mechanisms responsible for the variations of nest temperature. It is a

critical step towards a toolbox for realistically predicting PPM larval development rates, phenology, spread, and for forecasting sanitary risks to humans, animals and trees.

2. Materials & methods

2.1 Study species

The PPM is a univoltine species native to Southern Europe and North Africa where it occurs on evergreen trees (pines and cedars) from Mediterranean lowlands with hot summers and mild winters to mountainous areas with mild summers and cold winters. Adult emergence generally occurs during summer and larval development from summer, to next spring, both depending on weather and bioclimatic region (Battisti et al., 2015). Larvae are gregarious and go through five stages before pupation. PPM fecundity increases with latitude suggesting that larger colony size could confer an advantage for nest building at higher latitudes (Pimentel et al., 2010). Moreover, colonies are often composed of siblings issued from one egg mass. An egg mass is composed of 70 to 300 eggs (Huchon and Demolin, 1970) with an average of 200 eggs (Martin, 2005). However, a given colony can merge with other colonies feeding on the same tree, especially at high population densities when the encounter rate increases. First instar larvae feed on needles near the egg mass where they build successive temporary nests, usually until temperatures start to decrease in fall. At this point, colonies often settle in higher branches well exposed to sunshine, where they build a durable and structured winter nest thanks to an increasing weaving effort at the third and fourth instars. Throughout their development, these larvae keep weaving silk to maintain, thicken or expand the winter nest. They stay in during the day and get out during the night to feed on needles when conditions are favourable (Huchon and Démolin, 1970; Battisti et al., 2005). At the end of larval development, they permanently leave the nest and crawl down the tree to seek a suitable pupation site in the ground, in so-called processions.

The PPM winter nest is a silk network with two superimposed layers. During winter, larvae continuously maintain the structural integrity of the nest. The density of the spinning increases from the external to the internal layers (Huchon and Demolin, 1970; Martin, 2005). Local climates may affect silk production: nests tend to be thicker towards northern regions and higher altitudes (Abgrall, 2001). The nest architecture creates a heterogeneous environment inside which larvae can thermoregulate behaviourally (Breuer and Devkota, 1990). Previous studies showed that temperature in the PPM nest can be higher than the environmental temperature

during the day (Breuer et al., 1989; Breuer and Devkota, 1990; Martin, 2005), but these studies did not provide mechanistic understanding of this temperature excess, and more detailed field measurements are needed. The hypothesis about the potential sources of this heat gain include the factors related to exposure to solar radiation (i.e., time of the day, nest localisation in tree and its orientation according to solar radiation) (Breuer and Devkota, 1990; Joos et al., 1988; Ruf and Fiedler, 2000). PPM nests are usually at the end of the main branches or at the top of the trees where they are exposed to intense solar radiation, especially at noon. Since larvae keep the same nest throughout winter, high quantities of excreta can accumulate in the lower part, but biogenic production of heat by bacteria therein was suggested to have less influence on internal nest temperature than solar radiation (Breuer and Devkota, 1990).

2.2 Field sites, nest selection and nest translocation

We measured the temperatures inside PPM nests in the Southern Paris Basin (France) under two conditions differing in the level of control of environmental variables that may influence the nest temperature. First, we surveyed four inhabited PPM nests selected randomly in the field in a private property at Mézières-Lez-Cléry (47.787255 N, 1.826399 E). These nests were equipped with temperature sensors (see below) but otherwise left untouched. The number of larvae inside these nests was retrospectively estimated using collar traps (Ecopiège®) to catch fifth instar larvae when they left the pine for pupation in the spring following measurements. This approach may under-estimate the number of individuals in a nest during measurements because the mortality before larvae migrated to pupate remains unknown. The number of larvae captured in collar traps ranged from 20 to 100 larvae (mean 44 larvae among the four nests). Second, we experimented on colonies collected in the field and translocated to the tree nursery of INRAE Centre Val de Loire at Orléans, France (47.832226 N, 1.911060 E). The tree nursery is in an open field zone, at the edge of a forested area, in a semi-urban area (Fig. S1). For this purpose, natural nests were collected (October 3rd, 2018) at Chaon, France (47.595665 N, 2.138123 E) on black pines and translocated (October 4th, 2018) in the experimental black pine nursery. Eight days later, each nest was collected to count larvae and create eight colonies of 200 caterpillars each from the overall pool of caterpillars (they were at the third and fourth larval stages). Each colony was then placed in a ventilated plastic box with fresh branches of black pine, and transferred to a climatic chamber at 12°C to promote silk weaving and the construction of a new slack nest. Ten days later (October 14th, 2019), the new nests were attached to distinct black pines at breast height (lower branches) in the tree nursery (each tree

was about 6 m high and 10 years). As expected, the colonies moved during the following days and built thicker winter nests at the top of the trees (N=8 trees). These winter nests were then equipped with temperature sensors (N=8 nests). This manipulation allowed standardizing the number of larvae inside each nest, the number of larvae contributing to the construction, and to control partially for the position of the nest inside trees (at the top of the canopy). Both experiments were conducted on black pines, *Pinus nigra*, which is among the most preferred host plant of the PPM distribution area.

Larvae may influence the temperature inside the nest by producing metabolic heat collectively (as observed on other tent caterpillar species; Ruf and Fiedler 2000). Therefore, in the tree nursery, we also deployed empty nests (but already 'mature', i.e. with dense silk layers) to be used as controls for the effect of larval presence. To remove larvae from natural nests without altering its structure, we put nests in plastic boxes and placed them in a climatic chamber at 30°C for one week. Larvae left the nests naturally and the resulting empty nests were then translocated in the tree nursery, and equipped with temperature sensors (N=3 nests) from February 1st to March 20th, 2019.

2.3 Temperature measurements

We determined the temperature inside the PPM nests and calculated the difference between this temperature and air temperature, i.e. the nest temperature excess (*Texcess* = Nest temperature (T_n) – Air temperature (T_a)), in each nest at the two sites. In November 2018, five thermocouples (Copper-Constantan, type T, 0.2mm in diameter, TCSA, Dardilly, France) were installed in each nest. Three thermocouples were positioned at different locations inside the nest (top, middle and lower parts, respectively) and two others were fixed in the external layer of silk, at the surface, on northern and southern sides of the nest. The fifth thermocouple was deployed on the same branch as the nest to measure air temperature in the shade near the nest. The thermocouples (5 m length) were connected to two weather stations (CR1000, Campbell Scientific Ltd, Leicestershire, UK) equipped with a multiplexer (AM25T, Campbell Scientific Ltd) allowing to connect up to 25 thermocouples each. The temperature sensors were set to record temperatures every 5 minutes over winter, between November 2018 and May 2019. To record the timing of larval processions, a collar trap (Ecopiège®) was installed on each tree trunk to intercept larvae on their way down for pupation (see Colacci et al., 2018 for more details on this method). These collar traps were checked every two weeks between February

2019 and May 2019. In addition, global radiation ($W.m^{-2}$) and wind velocity ($m.s^{-1}$) were recorded throughout the experiments from a weather station located less than 500 m away from the INRAE tree nursery.

2.4 Metabolic heat estimation

The production of metabolic heat by PPM larvae was estimated indirectly by measuring temperature in small containers containing a given number of caterpillars depending on ambient temperature and larval density. This method allowed estimating the influence of larval presence on air temperature inside a small volume, especially under cold conditions. Larvae were collected in the Orléans surrounding and randomly placed in 150 mL plastic containers to test two ambient temperatures (5 and 25°C) and six larval densities (0, 1, 5, 25, 50 and 100 larvae) under controlled conditions. All containers were closed. A datalogger (TidbiT V2, HOBO) programmed to sample temperature every minute for one hour was placed at the bottom of each container, in contact with the larvae.

2.5 Biophysical modelling

We developed a simple biophysical model to predict the PPM nest temperature from environmental variables and nest properties (Table 1). Assuming that nest temperature is determined by heat transfer between the nest and its surrounding (all the equations were derived from Gates and Schmerl, 1980), the energetic balance can be described by:

$$R_{abs} + (C + G) + IR + \lambda E + M = 0 \quad (1)$$

Here, R_{abs} is the amount of radiation absorbed by the surface of the nest ($W.m^{-2}$); C and G are heat transfers by convection and conduction, respectively ($W.m^{-2}$); IR is the radiation emitted by the nest surface ($W.m^{-2}$); is the transfer by evaporation or condensation of humidity ($W.m^{-2}$); M is the metabolic heat ($W.m^{-2}$). Those fluxes can be positive or negative depending on the direction of the heat transfer (gained or lost by the nest, respectively) (Fig. 1). In the model, evaporation was neglected because insect water reserves are too small to compensate overheating by evaporation (May, 1979), and we considered the nest as a dry structure. The production of metabolic heat was low in our experiment (see results), and therefore this production was neglected in our model ($M = 0$). Below, we provide the details for each term of the equation (1).

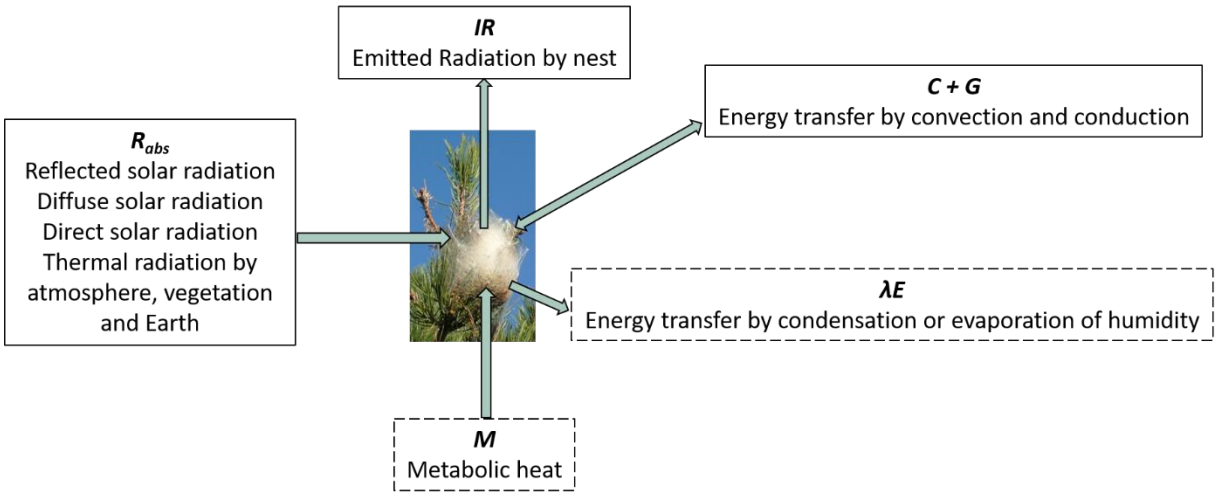

Figure 1. Schematic representation of heat fluxes involved in the energetic budget of a PPM nest. Arrows: direction of heat fluxes. Dashed boxes: fluxes that were neglected in our model.

The nest emits long wave infrared radiation according to the Stefan-Boltzmann law:

$$IR = \varepsilon_n \, \sigma \, T_n^4 \qquad (2)$$

where is the emissivity of the nest's surface, σ the Stefan-Boltzmann radiation constant (σ = 5.673 10^{-8} W.m^{-20}.K^4), and T_n the absolute temperature of the nest. The nest emissivity was estimated using an infrared camera (FLIR Systems B335; Wilsonville, OR) and a thermocouple (copper-constantan type T) at the same time. A piece of silk was placed on a metallic plate heated by a bowl of hot water. The thermocouple was applied against the silk layer. The emissivity value was adjusted in the settings of the camera until the temperature recorded by the camera reached the value recorded by the thermocouple. The silk emissivity (0.5) was found when the two temperatures were equal.

The PPM nest absorbs direct, reflected and scattered solar radiation plus long wave infrared radiation from the atmosphere, the vegetation and the ground. The nest absorbs in the visible and near infrared as follows:

$$R_{abs} = a^{VIS} \, 0.48 \, R_{ad} + a^{NIR} \, 0.52 \, R_{ad} + \varepsilon_a \, \sigma \, T_a^4 \qquad (3)$$

where R_{ad} is the global radiation (W.m^{-2}); corresponds to the emissivity of the atmosphere, and T_a is the absolute air temperature. a^{VIS} and a^{NIR} represent the nest absorbance in the visible (0.60) and near infrared (0.25), respectively, that we estimated from absorbance measurements

made on the natural silk fibers of insects like *Bombyx mori* (Balčytis et al., 2017). We hereby assume that all the elements in the environment of the nest have the same temperature than ambient air.

The heat transfer from the nest to atmosphere by conduction and convection is:

$$C + G = C_p\, g_h\, (T_a - T_n) \quad (4)$$

C_p is the specific heat of the air (C_p = 29.3 J.mol^{-1}.°C^{-1}), g_h is the nest boundary layer conductance, calculated as follows:

$$g_h = 0.135 \sqrt{\frac{\mu}{d}} \quad (5)$$

which depends on wind velocity μ and on nest characteristic dimension d. The factor 0.135 is obtained after integrating the values of air viscosity, air density and air diffusivity (Campbell and Norman, 1998). The PPM nest can be assimilated to an ellipsoid, giving for the characteristic dimension:

$$d = 0.7\, L \quad (6)$$

where L is the higher axis of the ellipsoid. In this model, the thermal inertia of the nest was considered negligible, allowing us to provide a simple version that considers the nest as a surface element (but see discussion for potential limitations).

2.6 Model simulations and validation

This model was coded in the R language (R Core Team 2018) and is provided in the supplemental material S1. Temperature inside the nest was simulated based on air temperature and global radiation recorded from November 2018 to May 2019. Then, the deviation between simulated and observed nest temperatures was calculated based on the Mean Absolute Error (MAE), as a measure of accuracy of the biophysical model.

The influence of air temperature and global radiation was quantified by running a simple sensitivity analysis of the model. To evaluate the effect of air temperature, the nest temperature predicted by the model was calculated for constant air temperatures 5, 10, 15, 20, 25 and 30°C with a fixed global radiation at either high level (750 W.m^{-2}) or low level (158.3 W/m^2). To assess global radiation effect, the nest temperature was predicted using constant global radiation

329 at 125, 250, 375, 500, 625 and 750 W.m^{-2} and setting air temperature to either 0 or 25°C. These
330 radiation levels reflect common values in our geographical area (Pincebourde and Casas 2006).

331 Finally, we assessed the effect of climate warming on nest temperature to test if the amplitude
332 of nest warming corresponds to the amplitude of climate warming. We ran the biophysical
333 model by adding 2 and then 5°C to the air temperature pattern recorded with the weather station
334 at our study site (Orléans) during the experiment. The other parameters and variables were not
335 changed.

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337 *2.7 Statistical analyses*

338 A non-parametric test of Mann-Kendall was used to analyse the difference between air and nest
339 temperatures, and the positive correlation between global radiation and nest temperature. To
340 test the effects of caterpillars' presence inside the nest (i.e., empty versus occupied nest), the
341 thermocouple position (i.e., within nest thermal heterogeneity), and the interaction between
342 those two factors, we used a repeated measure ANOVA with the nest temperature excess as
343 response variable. A non-parametric test of Kruskal-Wallis was used to analyse the effect of
344 thermocouple position on the recorded nest temperature. We quantified the accuracy of the
345 biophysical model by calculating the Mean Absolute Error (MAE) with the *mae* function of the
346 R package *Metrics.* R 3.5.1 was used for statistical analyses (R Core Team 2018).

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357 **Table 1**: List of the parameters involved in the biophysical model.

Parameters	*Symbol in equations*	*Values (units)*	*Sources*
Nest emissivity	ε_n	0.5	Field measurement
Atmosphere emissivity	ε_a	0.77	Campbell and Norman, 1998
Nest characteristic dimension	d	0.06 m	Field measurement
VIS nest absorbance	a^{VIS}	0.60	Balčytis et al., 2017
NIR nest absorbance	a^{NIR}	0.25	Balčytis et al., 2017
Global radiation	R_{ad}	20 to 577.78 $W.m^{-2}$	Field measurement
Air temperature	T_a	-2.45 to 31.74°C	Field measurement
Wind velocity	μ	0 to 6 $m.s^{-1}$	Field measurement
Nest temperature	T_n	-6.5 to 44.5°C	Field measurement
Stefan-Boltzmann radiation constant	σ	5.673 10^{-8} $W.m^{-20}.K^4$	Campbell and Norman, 1998
Specific heat of the air	C_p	29.3 $J.mol^{-1}.°C^{-1}$	Campbell and Norman, 1998

3. Results

3.1 Observed deviations between air and nest temperatures

In all nests (whether they are occupied by larvae or empty), temperature varied greatly according to the time of the day (Fig. 2a and 2c). Globally, regardless of the thermocouple position, nest temperature exceeded air temperature at noon but was very similar and sometimes lower than air temperature during night (Fig. 2b and 2d). For wild nests, maximal air temperature and maximal nest temperature (considering all nests and thermocouple positions) were 31.74°C and 44.5°C, respectively (Fig. 2a). For translocated nests, maximal temperatures were marginally higher, at 32.25°C for air and 44.98°C for nests (Fig. 2c). The nest temperature was positively correlated to the air temperature (Mann-Kendall p-value < 0.001, Rho = 0.67 for wild nests and p-value < 0.001, Rho = 0.76 for translocated nest). As expected, the nest temperature was positively correlated to global radiation (Mann-Kendall p-value < 0.001, Rho = 0.31 for wild nests and p-value < 0.001, Rho = 0.19 for translocated nests).

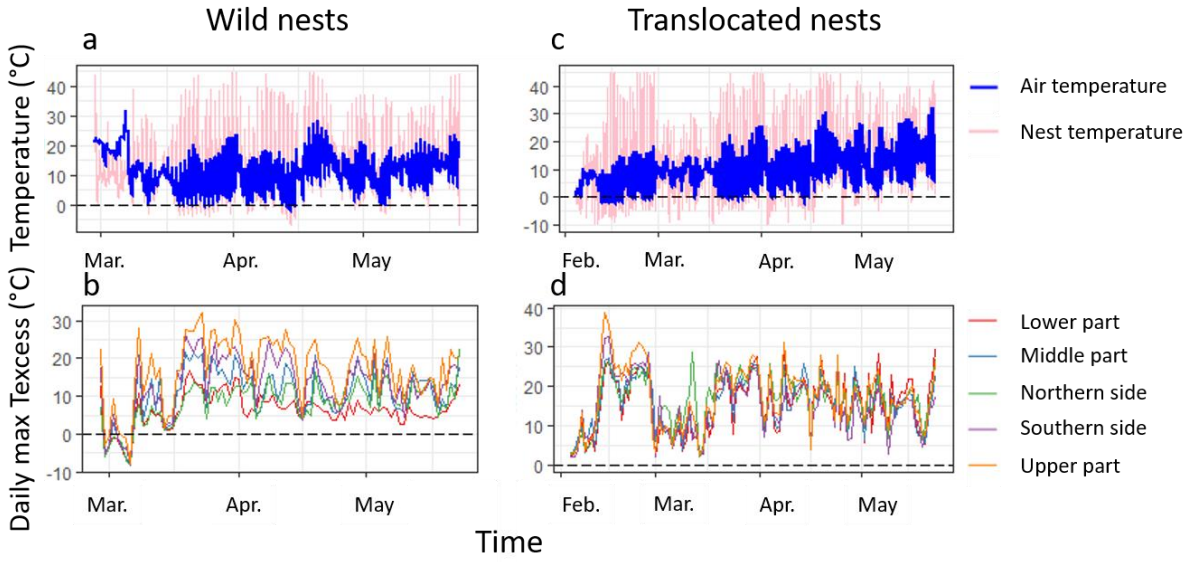

Figure 2. Air and nest temperatures when considering all thermocouple positions (°C) recorded in wild (a) and translocated nests (c). Daily maximal Texcess (°C) for each thermocouple position in wild (b) and translocated (d) nests.

Temperature was not homogeneous inside nests, neither for wild nor translocated nests (Fig. 2b and 2d). The temperature gradient inside nests, as inferred according to the position of thermocouples, was significant (RM ANOVA p-value < 0.001). For all wild nests, temperature

was higher in the upper part of the nest (mean daily maximal Texcess = 17.12°C) than in the middle (11.03°C) and in the lower part (6.39°C) (Kruskal-Wallis p-value < 0.01) (Fig. 2b). A similar pattern was observed in translocated nests (17.53, 15.48 and 15.30°C for upper, middle and lower parts, respectively; Fig. 2d), although the spatial gradient was less marked. Empty nests also displayed a significant internal temperature heterogeneity (Fig. S2). On average and globally (all thermocouples considered), the maximal Texcess was higher in translocated nests than in wild and empty nests (16.47, 11.23, and 14.75°C, respectively; overall mean of 16°C). The internal temperature (averaged from all thermocouples) significantly differed between nest types (translocated, wild, empty; Kruskal Wallis, p-value < 0.001). Air temperature recorded at the two sites (i.e. the site with translocated nests and the one with wild nests) was similar (Mann-Kendall p-value < 0.001, Rho = 0.66, average of 9.28°C and 11.26°C respectively) and therefore does not explain the temperature difference among nest types.

3.2 Estimating heat production by larvae

Heat production by larvae was found to be relatively negligible at all colony densities and ambient temperatures tested. Overall, the mean thermal difference between containers with larvae and empty containers (i.e., temperature in occupied containers minus temperature in empty containers) was very low (-0.02°C), ranging from -1.57°C (container with density 50 larvae in the warm treatment was 1.57°C colder than the control) to 0.99°C (density 100 larvae in the cold treatment, almost 1°C warmer than the control). These deviations were small and the sign of the difference was relatively erratic among the density treatments, potentially due to the lack of control of the contact point between the logger and the caterpillar(s) or of the humidity within the containers. Therefore, larval presence barely influenced the temperature within small volumes. These deviations (between 1 and 2°C) were deemed negligible compared to the amplitude of the nest temperature excess (see Fig. 2).

3.3 Model validation

The nest temperature predicted by the model was positively correlated with the nest temperature recorded in the field (Pearson's r > 0.9, p.value < 0.001) (Fig. 3 and 4). Our model does not predict temperature inside distinct nest parts with the same accuracy. The MAE were 4.31, 4.86, 5.25, 5.20 and 5.00°C for the lower part, middle part, northern surface, upper part, and southern

surface, respectively. Overall, the error of the model can be both positive (over-estimate) and negative (under-estimate), although there is a tendency to overestimate the nest temperature more often (Fig. 4).

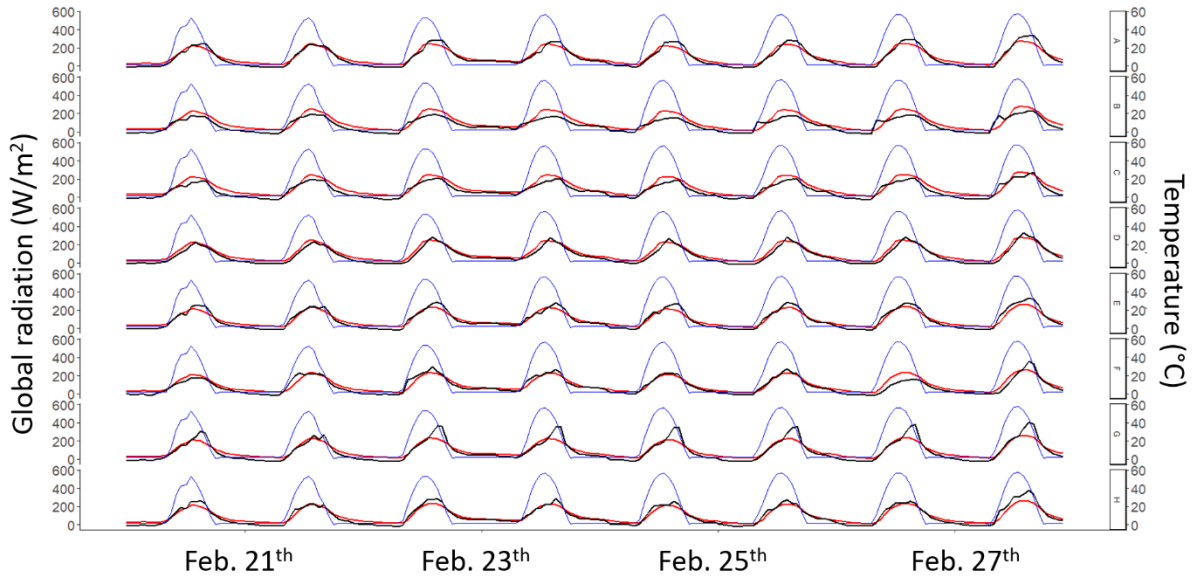

Figure 3. Temperature predicted inside nests by the biophysical model (red) and temperature recorded at the lower part of these nests (black) for a one-week period with clear sky (cloudless). Blue: Global Radiation (W/m^2). Letters: Nest IDs.

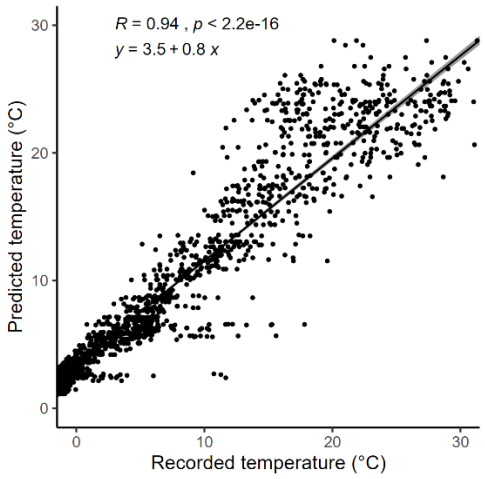

Figure 4. Performance of the biophysical model when combining all nest types. Pearson's correlation between predicted nest temperature and recorded temperature at the lower part of the nest, for the week from February 20th to February 28th.

3.4 Role of air temperature and global radiation: sensitivity analysis

Air temperature was the most influential variable on nest temperature predicted by the model. When air temperature increased from 5 to 30°C, the nest temperature estimated by the model increased linearly from 16.2 to 42°C at high global radiation of 750 $W.m^{-2}$, and from 9.38 to 35.31°C for a low global radiation level of 158.3 $W.m^{-2}$ (Fig. S3, slope = 1.03 for both radiation levels). By contrast, when air temperature was fixed at 25°C and the global radiation increased from 125 to 750 $W.m^{-2}$, the predicted nest temperature increased linearly but more slowly from 29.73 to 36.82°C (from 3.88 to 11.07°C when air temperature was fixed at 0°C) (Fig. S4, slope = 0.01 for both air temperatures).

3.5 Simulation of warming

The model was used to predict the nest temperature response to an increase in air temperature. With an increase of air temperature by 2°C (Tair + 2°C) and 5°C (Tair + 5°C) in the natural air temperature trace measured at our study site (Tair) from February 20th to February 28th, the mean temperature of the lower part predicted by the model was respectively 12.31°C and 15.42°C (Fig. 5a) for the period. The nest temperature excess during an increase of air temperature by 2°C and 5°C (4.47 and 4.57°C, respectively) was similar to the actual temperature excess recording for the same period (4.40°C) (Fig. 5b).

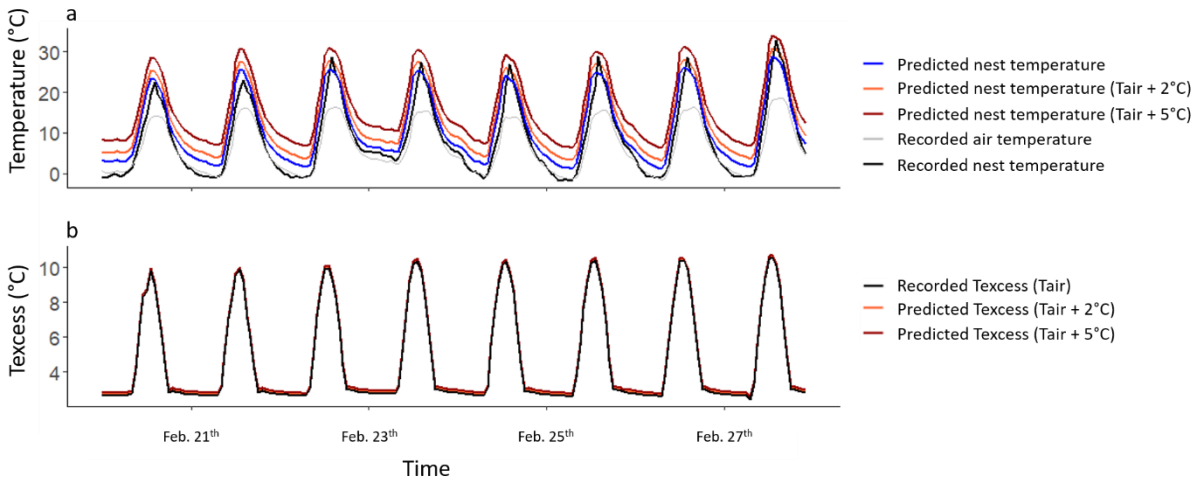

Figure 5. Model simulations for temperature in the lower part of the nest during one week of the experiment (a). Predicted nest temperature excess based on actual air temperature recordings (Tair) for the same period and for air temperature + 2°C and + 5°C (b).

4. Discussion

Ectotherms live in microhabitats that often provide particular thermal environments (Willmer, 1982). The thermal heterogeneity at very fine spatial scale can be exploited by arthropods to increase their survival and fitness (e.g., Pike et al., 2012; Caillon et al., 2014). We quantified the microclimatic temperature of the winter nest of the PPM, an increasing forest and human health concern in the context of global changes. We show that during winter, temperature within the nest can be much higher than ambient air temperature, by 16°C on average, when exposed to intense solar radiation on a cloudless day. Therefore, the winter nest may provide benefits in terms of development by exposing larvae to higher temperatures during the cold season that generally slows down development rates of insects (Sinclair et al., 2016), and by decreasing the frequency of experienced temperatures below developmental or feeding thresholds (Battisti et al., 2005; Robinet et al., 2007). Nevertheless, our results indicate that the hot nest of the PPM cannot help the caterpillars to overcome the cold challenge imposed by winter during night time, which is the daily period with lowest temperatures, for two reasons: metabolic heat production may be insignificant and the nest warms up only when exposed to radiation (combined with a low thermal inertia). In areas where the climate is not close to the limits of the species, the net advantage or disadvantage of living in a warm nest during winter remains to be determined as it is unknown if the resulting phenological changes would be beneficial, maladaptive, or buffered in this univoltine species.

The temperature inside the silken nest differs from air temperature, thereby confirming a previous study in Mont Ventoux (Southeast of France) during which the temperature excess reached 21°C in four nests taken in the wild (Martin, 2005). Breuer *et al.* (1989) measured temperature inside 28 nests in Greece according to their volume and thickness. The highest temperature excess was obtained at noon and was >15°C (Breuer et al., 1989). This phenomenon is also observed in other lepidopteran species like in the small eggar, *Eriogaster lanestris* (Ruf and Fiedler, 2000). Larvae inside the nest experience conditions warmer than surrounding temperature, mostly due to the production of collective metabolic heat in this particular case (Ruf and Fiedler, 2000). Indeed, the nests of the PPM and other tent caterpillars

like *E. lanestris* differ in their main function. The nest of *E. lanestris* is made of silk that reflects incoming radiation so that the nest does not absorb much radiative energy, and the metabolic heat produced by larvae (Ruf and Fiedler, 2002a) mainly adjusts the temperature excess inside the nest. By contrast, we showed that temperature in the PPM nest depends mostly on global radiation received. We found little support for the production of metabolic heat by larvae. This difference can be explained by the activity rhythms and the season: during summer, *E. lanestris* are active and exit the nest during the day, and they rely on metabolic heat during the night to keep it warm (Ruf and Fiedler, 2002a). By contrast, the PPM remains in the winter nest during the day, even when temperatures inside the nest reach >40°C (Breuer et al., 1989), and leaves it to feed during nighttime. This indicate that nest temperature may induce thermal stress during the winter due to elevated nest temperatures (e.g. we measured nest temperatures up to 40°C), but the thermal biology of this species remained poorly documented. We report nest temperature excess of >10°C relative to ambient air during day-time. Interestingly, this temperature excess is similar to that of a much smaller insect structure, such as leaf mines which also partly rely on incoming solar radiation that warms up the structure (Pincebourde and Casas, 2006). This temperature excess has profound influence on the development rate and survival of these leaf miners (Pincebourde et al., 2007). This demonstrates that the microclimate created by the nest during winter has to be considered to understand PPM larval development. PPM feeding activity was shown to occur if a daytime nest temperature exceeds 9°C and air temperature exceeds 0°C during the following night (Battisti et al., 2005). We hypothesize that the exposure to warmth during daytime in the winter nest optimizes assimilation rates, allocation of nutrients to somatic growth, and therefore overall growth rate.

Nest temperature is higher than ambient air, especially around noon when the global radiation is maximal. In dense forest stands, nest number is known to be much higher at south-orientated stand edges (Samalens and Rossi, 2011; Jactel et al., 2015). Moreover, a study on the position of the PPM winter nest in a tree demonstrated that PPM larvae prefer building the nest at the top of trees where exposure to solar radiation is high (Breuer et al., 1989). As in this study, we found a positive correlation between the PPM nest temperature and the global radiation. In the eastern tent caterpillar (*Malacosoma americanum*), one of the mechanisms involved in the heat gain is also related to absorption of global radiation (solar radiation and radiation emitted by the nest) (Fitzgerald et al., 2012). Again, this absorption of incident global radiation is probably even more important for the PPM, whose larval development is slowed

down by winter conditions. The silk of the PPM nest seems to absorb solar radiation. However, the properties of the silk nest to absorb visible and near infrared radiation remain to be detailed.

On average, the translocated nests reached higher temperatures than the wild nests. The greater mean of daily maximal temperature excess recorded in translocated nests may be due to their position in the trees. During the experiment, translocated nests with caterpillars were all at the top of the trees, whereas empty and wild nests were slightly lower in the canopy. Furthermore, empty nests were slightly warmer than wild nests, which refuted our hypothesis that larval metabolic heat could be involved in the heat excess of the nest. It is possible that empty nests were less exposed to wind than wild nests because they were in the middle of a pine nursery whereas wild nest were located at the periphery of the forest stand. The wind speed is known to influence the loss of heat by convection (Breuer et al., 1989; Joos et al., 1988; Ronnås et al., 2010). The number of caterpillars within the nest can affect nest temperature (Joos et al., 1988; Ruf and Fiedler, 2002a). Indeed, we found that the temperature excess in wild nests (20-100 individuals) was lower than in the translocated nests (200 individuals). The net increase in nest temperature during the day under solar radiation may be an alternative to heat up the nest without losing energy to produce metabolic heat.

Our model underestimated nest temperature for some of the nests we followed, indicating a potential effect of metabolic heat. However, we did not detect metabolic heat production from our temperature measurement in the nursery when comparing empty and occupied nests. Collective metabolic heat may exist in the PPM but its impact on the nest temperature is certainly buffered by the other components of the heat budget. Supportingly, a previous study indirectly inferred that the presence of larvae in the nest influences internal temperature by less than 1.5°C (Breuer and Devkota, 1990), a different order of magnitude compared to the influence we found for other factors. Our model overestimated nest temperature for other nests we followed. This tendency could suggest an effect of evaporation, since our model simulated a dry nest. However, evaporation was shown to have a minimal influence compared to global radiation and convection (Breuer et al., 1989). Other factors like the thickness of the silk can influence the temperature pattern (Breuer et al., 1989; Fitzgerald et al., 2012). Thickness changes over winter as the larvae continuously develop the nest – a dynamics that is not included into the biophysical model. In addition, the accumulation of faeces at the bottom of the nest may play a role in the nest temperature increase by capturing some of the incoming radiation and/or by favouring bacterial development and the production of heat (Battisti et al., 2005). Finally, winter precipitations may also interact on the nest heat budget

by adding water to the structure, thereby permitting evapotranspiration following rain events, but this effect was never tested. Thus, to improve the predictions of nest temperature by the biophysical model, the effect of those factors should be considered. Our model should be seen as a simulator of an average and static nest, but nest properties are quite variable in the field and they may be adjusted in the field according to season and weather conditions.

A significant thermal gradient was found in the PPM nest, generally from the bottom to the top. Deviations of >15°C were often recorded among the different locations inside the same nest. This gradient can be explained by the major impact of solar radiation at the top of the nest and by the position of caterpillars (generally in the upper part of the nest) (Joos et al., 1988; Ruf and Fiedler, 2000). We found that translocated nests were less thermally heterogeneous than wild nests, probably because they were more exposed to direct solar radiation, thereby homogenizing somehow the temperature at the scale of the nest and they contained more larvae to maintain nest structure thereby limiting heat loss. Therefore, the caterpillars can potentially move across the nest to thermoregulate behaviourally, but we currently lack evidence of such behaviour at the scale of the nest. Behavioural thermoregulation across very fine spatial scales was demonstrated for spider mites moving across single leaf surfaces that display thermal range of up to 10°C (Caillon et al., 2014). A similar process was found for flat rock spiders in challenging environments in Australia, with the female and its offspring using a gradient of 15°C across only few centimeters (Pike et al., 2012). In other tent caterpillars, the larvae were observed to leave their nest and use the temperature heterogeneity of the silk surface to regulate their body temperature (Ruf and Fiedler, 2002). Some observations were made indicating that PPM larvae exit the nest during hot days, but more detailed observations of caterpillar behaviour are needed to test this hypothesis. We propose that the PPM larvae could benefit from this nest thermal heterogeneity by moving up (warmer spots) during cold periods and down (cooler spots) during heat wave events.

5. Conclusion

Environmental warming is expected to influence the PPM nest microclimate. Our simple approach using the biophysical model allows inferring that the amplitude of warming inside the nest will likely follow the amplitude of warming in the atmosphere, assuming that global radiation and the nest properties remain unchanged. This result contrasts with other studies reporting that the microhabitat of some species (e.g., leaf miners, mussels on rocky

shores) allow them to buffer partially the amplitude of warming in the air – i.e., the temperature excess in the structure diminishes slightly with air temperature increasing (Pincebourde and Casas 2006; Gilman et al. 2006). This buffering is often linked to the evapotranspiration process, which was considered to be negligible in the PPM biophysical model, although we cannot exclude that evaporation can occur after precipitation events and also due to the presence of needles in the nest. Environmental warming will therefore be transferred into the PPM winter nest. The thermal tolerance thresholds of PPM caterpillars are not known, but given that they inhabit the permanent nest during the cold season, we propose that the microclimate warming will benefit to larval development rate and alleviate to some extent the cold stress constraint, especially near elevational and north range fronts. Many insect pest species build structures or develop inside particular microhabitats such as plant tissues (fruits, wood, and leaf tissues). The PPM nest creates a novel thermal niche, by producing a warm microclimate that could promote larval development during unusually cold years and facilitate survival in otherwise too challenging areas near the northern or altitude fronts of this range-expanding species.

Our results can help to generalize on the functions of silk nests in gregarious Lepidopteran species. Most species of the Thaumetopoeinae subfamily build more or less structured nests (Battisti et al. 2017) despite varied phenologies and climates, and other species within the *Thaumetopoea* genus weave silken nests during the cold season, such as *Thaumetopoea wilkinsoni* (Roques, 2015). The potential functions of the nest range include protection against natural enemies and/or dislodgment and promoting the maintenance of gregarious behaviours which may be important in the ecology of the species (de Boer and Harvey, 2020), such as feeding activity or dispersal. In the PPM, several observations suggest that the microclimatic function of the winter nest can be plastic. First, silk density and PPM nest thickness tend to decrease from harsh bioclimatic regions (North, more continental) to less stringent bioclimatic regions (South, oceanic), despite higher enemy pressures in historic compared to neocolonized regions (Démolin, 1965; Martin, 2005; Georgiev et al. 2020). Second, in a unique Portuguese population of *T. pitocampa* known for its atypical summer development, larvae were found to invest less energy in silk production than larvae from surrounding typical winter populations, resulting in loose and unstitched nests (Démolin, 1965; Santos et al., 2007). Loose silk nests are also observed in other closely related species completing their larval development between spring and summer, such as *Thaumetopoea ispartaensis*. Other species with larval development in spring do not build any silken nest, like *Thaumetopoea pinivora*. To avoid overheating, these spring larvae shuttle around the tree trunk

between shade and sunny places (Roques, 2015). Although a correlation between climate and tendency to build a silk nest remains to be explored, we propose that the hot microclimate is a fundamental nest function in species with winter larval development to enhance development and survival. By contrast, other functions such as protection against parasitoids and some predators may be more likely for species with spring and summer larval development. Additional thermal ecology studies are needed to test this hypothesis.

As PPM nests can shelter other arthropod species, this novel thermal niche may also play a role for some of them (concept of ecosystem engineers), especially for some non-web-building spiders (Branco et al., 2008). A similar thermal mechanism may hold for all insects developing within fruits like *Drosophila suzukii* or the codling moth. The temperature within fruits can be higher than ambient air (Saudreau et al., 2009) and some pests on apple exploit this thermal heterogeneity. Nevertheless, insect pest management programs only rarely consider the thermal environment actually experienced by those insects in the field. Identifying the microclimatic temperature that insect pests actually experience would help resolving the influence of atmospheric temperature changes on their development rate, their phenology, and ultimately on their demography and distribution with climate change.

Acknowledgements

We greatly acknowledge Walter Lapertot for the authorization to use his pine plot and Patrick Pineau for his technical assistance. We thank Météo-France and the AgroClim unit from INRAE for providing hourly global radiation and wind speed data. The study was made possible thanks to the financial support from the Centre Val de Loire Region (L.P.'s PhD grant), and the French National Research Agency (ANR) in the frame of the project called PHENEC.

Funding

Centre Val de Loire Region for thesis funding and ANR PHENEC [grant number19-CE32-0007-04].

Conflicts of interest

The authors declare no conflicts of interest.

Availability of data and material

The datasets collected and used to build the biophysical model of the nest are available from the corresponding author on request.

Code availability

In supplemental materials.

Authors' contributions

Conceptualization and experimental design: LP, ML, SP, CR, JR, CS. Sampling, experiments and monitoring: LP, SP. Data and statistical analyses: LP, SP. Original draft writing and preparation: LP, SP. Review and final editing: LP, ML, SP, CR, JR, CS. All authors have read and agreed to the final version of the manuscript.

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