Journal of Stored Products Research 109 (2024) 102466

Contents lists available at ScienceDirect

Journal of Stored Products Research

journal homepage: www.elsevier.com/locate/jspr

Development of *Idaea inquinata* (Lepidoptera Geometridae) at different constant temperatures and relative humidities under controlled conditions

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ARTICLE INFO

Handling Editor: Dr Raul Guedes

Keywords:
Life tables
Development rates
Integrated pest management
Warehouse
Dried herbs

ABSTRACT

The rusty wave moth *Idaea inquinata* is an insect pest that infests dried herbs, above all when stored in warehouses. Infestations were historically localised, but the recent climatic change might increase the incidence of this pest in many areas of north Italy. The artificial regulation of the environmental conditions of warehouses is one of the most common techniques to control pests, often combined with thermal treatments just after the introduction of the stocks. The optimisation of the warehouse conditions, however, requires a deep knowledge on how the species react to variations in temperature and relative humidities. This information is to date missing for *I. inquinata* and this work aimed to fill this gap in knowledge. The life tables at 35% and 70% RH, and at different constant temperatures were obtained for the egg, larval, and pupal stages by combining datasets provided by 20 years of continuous rearing of this species. A second part of the study, instead, concerned the estimation of the parameters of the temperature-dependent development rate functions, laying the foundations for further formulations of mathematical models to be applied in decision support systems. Life tables showed that conditions of low relative humidities and low temperatures are a good compromise that slows down the development time of the preimaginal stages. The upper thermal limit for the development of this species, instead, is around 40 °C, a threshold that can be considered for further thermal treatments to disinfest warehouses before the introduction of pest-free stocks or as a controlling action in case of infestations.

1. Introduction

Dried herbs are an important component of the agrifood industry, as they are widely used for both cooking and herbal medicine (Thamkaew et al., 2021). As with many crops worldwide, they are subject to phytosanitary issues due to infestations by insect pests and infection by pathogenic agents (i.e., fungi and bacteria). Those adversities can affect the plantations in different stages, from the sowing to the storage of the final product in *ad hoc* sites (Chomchalow, 2002; Edde et al., 2012; Vitullo et al., 2011).

Infestations in warehouses are a serious threat that can lead to conspicuous economic losses even in the case of dried herbs (Flinn et al., 2007). In the luckiest cases, the infested stored products can be sold at a lower price because of the reduced organoleptic properties or modifications in the shape due to pest damages (Fleurat-Lessard, 2011; Flinn et al., 2007; Sode et al., 1995), but in the worst cases infestations can raise potential issues for customers consuming infested products, leading the producers to remove the stock from the market (Atanda, 2011; El-Sayed et al., 2022; Fleurat-Lessard, 2011; Pisuttu et al., 2023). Many insect pests, belonging to different orders, infest dried herbs in storage sites of the Mediterranean basin. Some examples at hand are the Coleoptera *Lasioderma serricorne, Stegobium paniceum* (Anobiidae), *Oryzaephilus* spp. (Sylvanidae), *Tribolium* spp. (Tenebrionidae), and Lepidoptera *Plodia interpunctella*, *Ephestia elutella*, and *Cadra* spp. (Pyralidae) (Abdelfattah and Sayed, 2022; Adler, 2010; Guarino et al., 2020; Mohapatra et al., 2015; Pandir and Baş, 2016; Stejskal et al., 2015; Teke and Mutlu, 2021; Yaman and Şimşek, 2021).

Idaea inquinata (Scopoli, 1763), commonly known as the rusty wave moth (RWM), is an additional insect pest that should be considered for its noxious activity on dried herbs (Limonta et al., 2010). This small geometrid moth feeds mainly on hay, chamomile (Candura, 1931a, 1931b), withered parts of plants, and dried herbs (Hausmann, 1997; Kratochvìl, 1948; Martinez and Coutin, 1985; Naves, 1995; Tempel, 1941), particularly *Foeniculum vulgare*, *Silybum marianum*, *Crataegus*

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https://doi.org/10.1016/j.jspr.2024.102466
Received 29 August 2024; Received in revised form 18 October 2024; Accepted 2 November 2024
Available online 7 November 2024

monogyna, *Angelica archangelica, Matricaria chamomilla* (Locatelli et al., 2005). Laboratory tests showed that *I. inquinata* can also develop on bran, maize flour, and wheat grains, which are rich in fibres, proteins, lipids, mineral salts, and vitamins (Locatelli et al., 2005) while *Moringa oleifera* dried leaves are less suitable (Limonta and Locatelli, 2021).

Historically, *I. inquinata* has never been a serious phytosanitary issue, but the recent climate change and the intensification of the production in some areas of the Mediterranean basin are causing a general increase of pest populations, leading to concerning infestations. The limited knowledge on the biology and ecology of *I. inquinata* represents the main constraint for the formulation of environmentally friendly control strategies that avoid the use of agrochemicals.

On the one hand, warehouses are extremely vulnerable if they are not properly isolated from the external environment and if the products to store are not accurately checked before being introduced (Manu et al., 2018). On the other hand, the environmental parameters such as temperature and relative humidity can be easily controlled through proper equipment (Atungulu et al., 2019; Beta and Ndolo, 2019; Johnson, 2020; Qin et al., 2019). The main problem associated with *I. inquinata* is that larvae feed hidden in the substrate, while adults are cryptic (Limonta et al., 2010). Accordingly, the specimens are difficult to detect when dried herbs are introduced into warehouses, leading to an underestimation of the infestations. If the environmental conditions of the warehouse are favourable, the species can close many generations in a short time, with a subsequent destruction of the whole stock of stored products (Limonta and Locatelli, 2015).

As temperature and relative humidity play a fundamental role during the ontogenetic life cycle of insects, the environmental conditions of the warehouses can be a powerful control method for constraining pest infestations (Adler, 2010; Yang et al., 2015). Unfortunately, to date there is a limited knowledge on the thermal response of *I. inquinata*, as well as the development under different conditions of relative humidity. Over the last 20 years, *I. inquinata* has been continuously reared under controlled conditions and under the same conditions of diet in the facilities of the Department of Food, Environmental and Nutritional Sciences of Università degli Studi di Milano. The datasets were the object of different studies over the years (Limonta et al., 2010; Limonta and Locatelli, 2015, 2018), but they can be combined altogether to provide more quantitative information on *I. inquinata*. Accordingly, this work aims to analyse the development times under these different conditions using a life table analysis approach, providing also the parameters of a set of development rate functions that lay the basis for further modelling the biology of this species.

After the aggregation of all the datasets available, the quantitative information we are going to introduce within this study will be presented in two steps. The first step of the research concerns the analysis of the differences in terms of development time of the egg, larva, and pupa stage reared under the same constant temperature and different relative humidity conditions (35 and 70 % RH, respectively). The second step, instead, will focus on the analysis of the thermal response of the species in terms of development, by estimating (per stage and per relative humidity) the parameters of the most common rate functions available in the current literature.

2. Materials and methods

2.1. Continuous rearing

Idaea inquinata was collected on *Hypericum perforatum* L. (Malpighiales: Hypericaceae) in a warehouse located in the southern part of Milano (Italy), and reared on an artificial diet in a thermostatic chamber (CFT 600, Piardi Tecnologie per il freddo, Castenedolo, IT) at 26 ± 1 °C, 70 ± 5% RH, and a photoperiod of 16:8 (light:dark) for 20 years. The food substrate was composed of an artificial diet that included 62 g of bran, 8 g of corn flour, 7 g of wheat flour, 4 g of wheat germ, 3 g of dried yeast, 9 g of glycerol, and 7 g of honey (Limonta and Locatelli, 2013).

Table 1
Experimental temperatures and relative humidities explored per stage of *Idaea inquinata*.

Life stage	35 %RH	70 %RH
Egg	15, 17, 21, 26, 29, 34, 36 °C	15, 17, 18, 21, 24, 26, 29, 32, 34, 36 °C
Larval stages	21, 26, 29, 34 °C	18, 21, 24, 26, 29, 32, 34 °C
Pupa	21, 26, 29 °C	21, 24, 26, 29, 32, 34 °C

Eggs were obtained by placing new emerged adults in a 2 L glass jar closed with tulle, turned upside down on a Petri dish with filter paper. Eggs were collected daily and transferred for the tests with a fine paint brush.

2.2. Development of Idaea inquinata under different conditions of temperature and relative humidity

Over the years, the life history of 24 h old eggs was monitored daily at different temperatures, namely, 15, 18, 21, 24, 26, 29, 32, and 34 ± 1 °C, photoperiod of 16:8 (light:dark), and relative humidities of 35 and 70% RH, respectively. Those independent experiments were carried out in climatic chambers (CFT 600, Piardi Tecnologie per il freddo, Castenedolo, IT) to analyse different aspects of the biology of this species, such as: *i)* thermal development at 26 and 29 °C and relative humidities of 50 and 70% (Limonta et al., 2010), *ii)* susceptibility of eggs to high and low temperatures and different RH (Limonta and Locatelli, 2015), and *iii)* postembryonic development at different constant temperatures and RH (Limonta and Locatelli, 2013). Besides the listed references, other datasets came from experiments carried out during master theses and/or internship periods. Since the rearing conditions were the same, we could combine the datasets. Unfortunately, not all the datasets were reporting the mortality of the individuals, this is the reason why in this study we will focus only on the development at the different temperatures and relative humidities. Notably, we focus on the development times of eggs, larvae (with no distinction between the instars), and pupae. The temperature and the relative humidities available for each stage are summarised in Table 1 and will be the starting point for the analysis described in the following sections.

The protocol applied in each constant condition of temperature and humidity was the following: after being collected from the continuous rearing described in Section 2.1, eggs were individually placed in glass jars (diameter 3.8 cm; height 2.5 cm) containing 0.1 g of artificial diet, which was replenished as needed. Glass jars were closed with wire nets to allow gaseous exchange. Fifty glass jars, each containing one egg, were considered for each rearing cycle and put in climatic chambers (CFT 600, Piardi Tecnologie per il freddo, Castenedolo, IT). The specimens were checked daily: during each inspection, the stage of the individuals was noted down up to the adult emergence phase. Life stages were distinguished in egg, larva (without considering the different instars), pupa, and adult.

2.3. Data analysis: comparison of the different relative humidities

As first step of the data analysis we focused on the differences, in terms of development time, between the relative humidities in each constant temperature explored. The comparison was carried out for the egg, larva, and pupa stages, where possible, using the R Studio software (CRAN, 2019). Data were analysed through a linear model (LM), considering relative humidity and development times as independent and dependent variables, respectively. Calculations were carried out through the *lm()* function within the native R environment. The normality of the residuals, instead, has been assessed using the *shapiro.test()* function included in the basic R software and double checked through a quantile-quantile (Q-Q) plot. Differences between the groups

were further assessed through a Bonferroni *post hoc* test ($\alpha = 0.05$) using the *emmeans()* function within the R package *emmeans* (Lenth, 2024), the *pairs()* function within the package *multcompView* (Graves et al., 2015), and the *cld()* function within the R package *multcomp* (Hothorn et al., 2008, 2016).The dataset and the script to fully reproduce the results of this part of the study are publicly available at https://github.com/lucaros1190/Idaea-inquinata-2024.

2.4. Life tables and development rate over the different temperatures

2.4.1. Life tables

The development times of the individuals under the different environmental conditions tested in Table 1 were processed to obtain the synthetic values composing the life tables according to Rossini et al. (2024), namely: mean, standard deviation, median, mode, skewness, and kurtosis. This analysis was carried out grouping the datasets per relative humidity (35 and 70% RH) and focusing on the different constant temperatures and life stages, as is common in studies of this type (Chi, 1988; Chi et al., 2020, 2023; Chi and Liu, 1985).

2.4.2. Development rate over temperature

Additional information from the dataset, organised as described in Section 2.4.1, can also be obtained using the development rate functions. Those expressions link the development rate of the i-th individual, $G_i(T)$, defined as the inverse of the development time $D_i(t)$, with the temperature T, providing a relevant information that supports pest control strategies and more elaborated mathematical models.

The current literature reports different development rate functions, and because of their empirical nature it is hard to choose *a priori* one of them (Rossini et al., 2020a). Accordingly, in this study we estimated the parameters of the most commonly used expressions, further analysing the goodness of fit. The first step concerned the conversion of the times in rates, according to the following expression (Damos and Savopoulou-Soultani, 2012; Rossini et al., 2019a):

$$G_i(T) = \frac{1}{D_i(T)} \tag{1}$$

After this conversion, the dataset was ready to be fitted by the following equations.

- The Logan development rate function (Logan et al., 1976):

$$G(T) = \psi\left[\exp(\rho T) - \exp\left(\rho T_M - \frac{T_M - T}{\Delta T}\right)\right] \tag{2}$$

where ψ and ρ are empirical parameters, T_M is the maximum temperature above which the development is theoretically not possible, and ΔT is the temperature range between the maximum of the function $G(T)$ and T_M.

- The Briére development rate function (Briere et al., 1999):

$$G(T) = aT(T - T_L)(T_M - T)^{1/m} \tag{3}$$

where a and m are empirical parameters, and T_L and T_M are the lower and maximum temperature thresholds below and above which the development is theoretically not possible, respectively.

- The Sharpe and De Michele rate function (Schoolfield et al., 1981; Sharpe and DeMichele, 1977):

$$G(T) = \frac{T \exp\left(A - \frac{B}{T}\right)}{1 + \exp\left(C - \frac{D}{T}\right) + \exp\left(E - \frac{F}{T}\right)} \tag{4}$$

where A, B, C, D, E, and F are parameters related to the enzyme kinetics

Table 2
Life tables parameters of *Idaea inquinata* at different constant temperatures and fixed relative humidity (35% RH). For each life stage (egg, larva, pupa) the moments of the distributions of the development times were calculated. N is the number of specimens involved in each computation.

35% RH																			
Temperature (±1 °C)	Egg development (days)						Larva development (days)						Pupa development (days)						
	N	Mean ± SD	Mode	Median	Skewness	Kurtosis	N	Mean ± SD	Mode	Median	Skewness	Kurtosis	N	Mean ± SD	Mode	Median	Skewness	Kurtosis
15	28	27 ± 3	29	29	−1.34	3.41	0	–	–	–	–	–	0	–	–	–	–	–
17	262	19 ± 2	19	19	−1.22	6.24	0	–	–	–	–	–	0	–	–	–	–	–
21	374	13 ± 2	13	13	0.21	2.28	5	180 ± 20	161	184	0.44	1.96	4	23 ± 2	21	22	0	1
26	315	8.6 ± 0.9	8	8	1.50	4.98	50	53 ± 5	54	52	−0.25	3.00	50	10 ± 3	8	10	1.12	3.87
29	310	6.3 ± 0.5	6	6	1.77	5.28	18	45 ± 7	38	44	0.54	2.59	18	10 ± 2	10	10	0.22	1.71
34	319	6.3 ± 0.7	6	6	2.11	6.94	7	36 ± 0	36	36	0	–	0	–	–	–	–	–
36	35	8.1 ± 0.3	8	8	2.66	8.11	0	–	–	–	–	–	0	–	–	–	–	–

Table 3
Life tables parameters of *Idaea inquinata* at different constant temperatures and fixed relative humidity (70% RH). For each life stage (egg, larva, pupa) the moments of the distributions of the development times were calculated. N is the number of specimens involved in each computation.

70 % RH																			
Temperature (± 1 °C)	Egg development (days)						Larva development (days)							Pupa development (days)					
	N	Mean ± SD	Mode	Median	Skewness	Kurtosis	N	Mean ± SD	Mode	Median	Skewness	Kurtosis		N	Mean ± SD	Mode	Median	Skewness	Kurtosis
15	101	26 ± 2	25	26	0.98	3.40	0	–	–	–	–	–		0	–	–	–	–	–
17	247	16 ± 3	17	17	−2.32	7.78	0	–	–	–	–	–		0	–	–	–	–	–
18	37	23 ± 3	22	22	0.46	1.78	15	79 ± 3	81	79	−0.08	1.83		0	–	–	–	–	–
21	342	12 ± 1	11	12	0.53	2.77	12	130 ± 60	214	104	0.51	1.79		9	21 ± 4	18	20	−0.48	2.27
24	54	9.8 ± 0.7	10	10	−3.35	13.00	32	50 ± 10	52	52	0.90	4.40		31	12 ± 2	14	12	0.19	4.50
26	364	7.3 ± 0.5	7	7	1.40	4.01	123	28 ± 3	26	28	0.80	2.92		123	9 ± 1	9	9	−0.18	3.68
29	366	6.4 ± 0.5	6	6	0.61	2.08	50	30 ± 3	27	29	0.43	1.77		50	9 ± 4	8	8	1.00	2.72
32	83	7 ± 2	6	6	2.03	5.28	52	43 ± 8	41	41	0.09	1.87		41	8 ± 4	7	7	0.36	2.00
34	330	6.3 ± 0.7	6	6	1.96	6.25	4	60 ± 10	50	61	0	1.54		4	10 ± 8	3	8	0.28	1.39
36	62	8.9 ± 0.8	9	9	0.08	1.68	0	–	–	–	–	–		0	–	–	–	–	–

(Rossini et al., 2019b).

- The Lactin-1 rate function (Lactin et al., 1995):

$$G(T) = \exp(a\,T) - \exp\left[a\,T_M - \left(\frac{T_M - T}{\Delta T}\right)\right] \tag{5}$$

where T_M is the maximum temperature above which the development is theoretically not possible, ΔT is the temperature range between the maximum of the function $G(T)$ and T_M, and a is an empirical parameter.

- The Lactin-2 rate function (Lactin et al., 1995):

$$G(T) = \exp(a\,T) - \exp\left[a\,T_M - \left(\frac{T_M - T}{\Delta T}\right)\right] + \lambda \tag{6}$$

where T_M is the maximum temperature above which the development is theoretically not possible, and ΔT is the temperature range between the maximum of the function $G(T)$ and T_M, and a and λ are empirical parameters.

The best fit parameters were estimated by a non-linear least-square regression carried out using the Matlab (v. 2023b) software. An evaluation of the fitting performances of the functions (2)–(6) was carried out by considering the coefficient of determination R^2, the root mean square error (RMSE), and through a χ^2-test as detailed in (Rossini et al., 2020b, 2021a). The script and the dataset to fully reproduce the results of this part of the study is available at https://github.com/lucaros1190/Idaea-inquinata-2024.

3. Results and discussion

3.1. Life tables at different constant temperatures and humidities

The first results of this study were the life tables at different constant temperatures and humidity, as described in Section 2.3.1. Notably, the mean development times and the parameters of the distributions of the raw data are listed in Table 2 for the case 35% RH and in Table 3 for the case 70% RH. The data suggests that the optimal temperature range for the development is 29–34 °C for both the relative humidities, even if the growth seems to be slower at 35% RH than 70% RH.

The moments of the distributions (i.e., mean, median, mode, skewness, and kurtosis) calculated on the datasets indicate that in most of the cases the data are far from Gaussian. This is a relevant aspect that supports what was already observed by Rossini et al. (2024) in other case studies and can be assessed by looking at the values in Tables 2 and 3 Right-skewed distributions usually have mean values higher than median and mode, and present positive skewness values, while left-skewed distribution usually have mode values higher than median and mean, and present low or negative skewness values.

This precondition suggests that eggs at 35% RH showed a Gaussian-like distribution only at 17 and 21 °C, while in the other cases the tendency is towards a left (15 °C) and right (26, 29, 34, 36 °C) skewness for low and high temperatures, respectively. A different scenario concerned the larvae at 35% RH, where the datasets at the four temperatures available did not show particular distribution trends over temperature: a right skewness has been observed at 21 °C, while the dataset at 26 and 29 °C was left skewed. The three temperature datasets for pupae at 35% RH showed a right skewness at 21 and 26 °C and a Gaussian-like trend at 29 °C.

The dataset at 70% RH, confirmed the variability of the distributions of the development times observed in the previous case (Table 3). Eggs were mostly right skewed, except at 17, 24 (left-skewed), and 36 °C (Gaussian-like), in contrast with the general trend observed at 35% RH, where temperature seemed to influence the distribution. A similar tendency to right-skewed distributions of the development times has been observed for larvae, that reported only one case of left skewness (18 °C) and Gaussian-like (32 °C). Pupae showed a more regular trend over

temperature, since the distributions were left-skewed at 21 and 24 °C, Gaussian-like at 26 °C and right-skewed at 29, 32, and 34 °C.

The identification of particular trends in the distribution of the development times over temperature is a relevant information from a pest management point of view. Right-skewed distributions of the times, in fact, suggest that the greatest portion of the individuals will develop faster, requiring an anticipated control action to reduce the population level. Conversely, left-skewed distributions suggest that the greatest portion of the population develops after the mean values. Completing the life tables with these additional parameters is accordingly of crucial importance, as mean and standard deviation implicitly assume the dataset distributed according to a Gaussian distribution (Najim et al., 2004). This representation of the life tables is still not common in entomology, and this is one of the few studies that extends the presentation of the results in that way.

The sizes of the datasets available were different from stage to stage and among the temperatures. As a consequence, the more accurate information concerns the egg stage, followed by larvae and pupae. This difference was mainly due to the purposes of the experiments, that over the years have been concentrated mostly on the egg stage. Besides this unbalance, all the dataset included in this study had a statistically meaningful size, allowing the further analysis we are going to present in the next section.

3.2. Differences in terms of relative humidities

Differences in terms of relative humidity of the development times between the stages at each constant temperature were assessed according to the methodology described in Section 2.3. The analysis showed overall statistical differences, underlying that relative humidity plays a crucial role, besides temperature, in the duration of the development time. Generally speaking, a lower relative humidity results in a longer mean development time, above all at low temperatures; this fact can be noted by comparing, stage by stage, the values listed in Tables 2 and 3 This difference is then reduced as temperature increase, even if still significant as we detail below.

Starting from the egg stage, significant differences between 35 and 70 % RH were assessed at 15 °C (LM, F = 11.0, NDF = 127, $p = 0.001$), 17 °C (LM, F = 274.8, NDF = 507, $p < 0.0001$), 21 °C (LM, F = 99.3, NDF = 717, $p < 0.0001$), 26 °C (LM, F = 563.6, NDF = 677, $p < 0.0001$), and 29 °C (LM, F = 17.4, NDF = 674, $p < 0.0001$), but not at 34 °C (LM, F = 0.02, NDF = 647, $p = 0.90$) and 36 °C (LM, F = 0.003, NDF = 95, $p = 0.95$). The development time of larvae, instead, was significantly different at 26 °C (LM, F = 896.1, NDF = 170, $p < 0.0001$), 29 °C (LM, F = 160.5, NDF = 66, $p < 0.0001$), and 34 °C (LM, F = 48.8, NDF = 9, $p = 0.0001$), but not at 21 °C (LM, F = 3.6, NDF = 15, $p = 0.08$). Only three temperatures were available to compare the development times of pupae at the two humidity levels: the only significant difference was observed at 26 °C (LM, F = 14.02, NDF = 170, $p < 0.0001$), while no effect was ascertained at 21 °C (LM, F = 0.52, NDF = 11, $p = 0.48$) and 29 °C (LM, F = 0.3, NDF = 66, $p = 0.59$).

The results of this part of the study provide other suggestions on the formulation of strategies to control this pest. Dried herbs are usually preserved in warehouses where the condition of relative humidity should be as low as possible (Calín-Sánchez et al., 2020; Orphanides et al., 2016). Those conditions are primarily set to preserve the organoleptic and quality properties of the products, but to reduce the risk of infection by pathogenic agents as well (e.g., fungi), avoiding contaminations by mycotoxins harmful for the consumers (Calín-Sánchez et al., 2020). In this section, we showed how conditions of low relative humidity can also reduce the risk of infestations by *I. inquinata*, significantly slowing down the development time of the different life stages. The positive control effect of relative humidity is amplified if combined with temperatures that are low or far from the optimum for the development of the species (29–34 °C).

Strategies based on the regulation of the environmental conditions in warehouses are not new in the case of stored product pests (Atungulu et al., 2019), and they are mostly based on the insights provided by life tables studies (Rossini et al., 2021b; Segers et al., 2024). The limitation of the pesticide treatments that many countries worldwide have recently applied is pushing the research on alternative and environmentally friendly pest management practices (Di Sora et al., 2024; Turco et al., 2024a, 2024b). Preventive actions, for instance, can be thermal treatments carried out just after the introduction of the stocks into warehouses through cooling or heating systems (Nasr et al., 2015; Yang et al., 2015). While cooling systems are mostly based on the use of air conditioning machines (Li et al., 2017; Porras-Amores et al., 2014; Wang et al., 2022), heating can be carried out in different ways. Microwaves (Abdelfattah and Sayed, 2022) or inflows of dry and hot air (Pappalardo et al., 2017) are two common techniques, but the choice of the temperature is influenced by three dominant factors: the cost of the operation, the maximum temperature that can be tolerated by the stocks, and

Table 4
Best fit parameters (±*SE*) of the functions (2)–(6) for the case at 35% RH. T_L, T_M, ΔT are expressed in °C, while the other parameters are empirical with no biological meaning. The goodness of fit, instead, is expressed by the coefficient of determination R^2, the number of degrees of freedom *NDF*, the χ^2-value, and the root mean square error *RMSE*.

Development rate function	Life stage	Best fit parameters (±*SE*)	Goodness of fit parameters
Logan (2)	Egg	$\psi = (7.5 \pm 0.4) \cdot 10^{-4}$ $\rho = 0.114 \pm 0.003$ $T_M = 37.65 \pm 0.08$ $\Delta T = 3.6 \pm 0.2$	$R^2 = 0.93$ $NDF = 1639$ $\chi^2 = 0.0091$ $RMSE = 0.0119$
	Larva	$\psi = (7 \pm 1) \cdot 10^{-4}$ $\rho = 0.1 \pm 0.2$ $T_M = 38 \pm 3$ $\Delta T = 4 \pm 8$	$R^2 = 0.70$ $NDF = 76$ $\chi^2 = 5.29 \cdot 10^{-6}$ $RMSE = 0.0028$
Briere (3)	Egg	$a = (1.49 \pm 0.02) \cdot 10^{-4}$ $T_L = 8.3 \pm 0.3$ $T_M = 36.32 \pm 0.04$ $m = 3.8 \pm 0.1$	$R^2 = 0.91$ $NDF = 1639$ $\chi^2 = 0.0494$ $RMSE = 0.0130$
	Larva	$a = (4 \pm 2) \cdot 10^{-5}$ $T_L = 16 \pm 2$ $T_M = 36 \pm 4$ $m = 3 \pm 4$	$R^2 = 0.7419$ $NDF = 76$ $\chi^2 = 5.4 \cdot 10^{-5}$ $RMSE = 0.0026$
Sharpe and De Michele (4)	Egg	$A = 97$ $B = 1482$ $C = 117$ $D = 2060$ $E = 101$ $F = 1454$	$R^2 = 0.92$ $NDF = 1637$ $\chi^2 = 0.0194$ $RMSE = 0.0124$
	Larva	$A = 98$ $B = 1487$ $C = 115$ $D = 1889$ $E = 104$ $F = 1446$	$R^2 = 0.72$ $NDF = 74$ $\chi^2 = 9.5 \cdot 10^{-5}$ $RMSE = 0.0027$
Lactin - 1 (5)	Egg	$\rho = (1.43 \pm 0.01) \cdot 10^{-1}$ $T_M = 39.1 \pm 0.1$ $\Delta T = 6.98 \pm 0.06$	$R^2 = 0.90$ $NDF = 1640$ $\chi^2 = 0.7041$ $RMSE = 0.0139$
	Larva	$\rho = 0.29 \pm 0.02$ $T_M = 35.4 \pm 0.3$ $\Delta T = 3.4 \pm 0.2$	$R^2 = 0.40$ $NDF = 77$ $\chi^2 = 0.0212$ $RMSE = 0.0039$
Lactin - 2 (6)	Egg	$\rho = (7.45 \pm 0.07) \cdot 10^{-3}$ $T_M = 40.8 \pm 0.2$ $\Delta T = 1.92 \pm 0.07$ $\lambda = -1.088 \pm 0.002$	$R^2 = 0.91$ $NDF = 1639$ $\chi^2 = 0.0626$ $RMSE = 0.0129$
	Larva	$\rho = (1.5 \pm 0.6) \cdot 10^{-1}$ $T_M = 39 \pm 3$ $\Delta T = 7 \pm 3$ $\lambda = (-1 \pm 1) \cdot 10^{-2}$	$R^2 = 0.73$ $NDF = 76$ $\chi^2 = 8.7 \cdot 10^{-5}$ $RMSE = 0.0026$

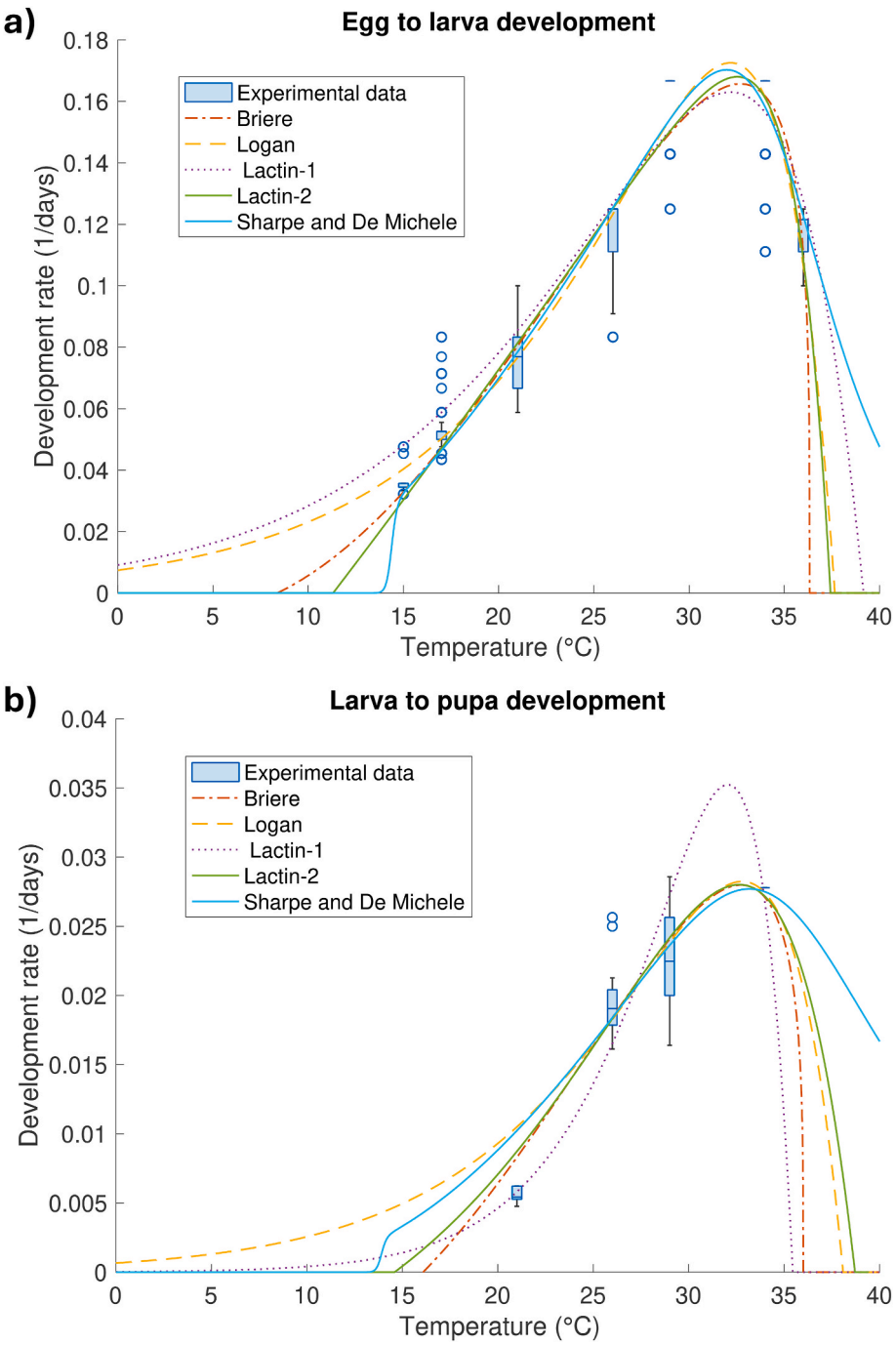

Fig. 1. Development rate over temperature at 35% RH for the egg and larval stages. Experimental data are indicated by the boxplot, while the different curves represent the best fit functions (2)–(6), whose parameters are listed in Table 4.

the minimum-high temperature that warrants the death of the greatest portion of the pests. It should be also considered that the exposition of the stocks to high temperatures for long times can decrease their quality and organoleptic properties (Mohapatra et al., 2015).

Thermal treatments can also be combined with controlled atmospheres, a technique that target mainly the preimaginal and adult stages and that consists of substituting the oxygen inside the warehouse with CO_2 or nitrogen (Mohapatra et al., 2015). This method can be both preventive or carried out regularly if producers foresee a longer period of storage in warehouses before the stocks reach or the market, or the next step of the food industry chain. Those examples justify the importance of life tables studies, as warehouses are peculiar environments closer to climatic chambers than to open fields.

3.3. Development rate functions parameters

The best fit parameters of the development rate functions (2)–(6) estimated for the case of 35% RH are listed in Table 4 and graphically represented in Fig. 1. The experimental dataset, in this case, allowed the parameter estimation only for the egg and larva stages (Fig. 1a and b, respectively), because three temperatures values were not sufficient to obtain reliable information in the case of pupae.

Proceeding by order, the dataset of the egg stage was well fitted by almost all the functions tested, even if the highest R^2 value was observed for the Logan equation (2). The lower thermal threshold is described only by the Brière equation (3), and its estimated value is of 8.3 ± 0.3 °C. The upper thermal threshold, instead, was described by the Logan (2),

Table 5
Best fit parameters (±*SE*) of the functions (2)–(6) for the case at 70% RH. T_L, T_M, ΔT are expressed in °C, while the other parameters are empirical with no biological meaning. The goodness of fit, instead, is expressed by the coefficient of determination R^2, the number of degrees of freedom *NDF*, the χ^2-value, and the root mean square error *RMSE*.

Development rate function	Life stage	Best fit parameters (±*SE*)	Goodness of fit parameters
Logan (2)	Egg	$\psi = (9.5 \pm 0.3)\cdot 10^{-3}$ $\rho = (1.18 \pm 0.09)\cdot 10^{-1}$ $T_M = 38.2 \pm 0.1$ $\Delta T = 5.0 \pm 0.5$	$R^2 = 0.88$ $NDF = 1982$ $\chi^2 = 0.0382$ $RMSE = 0.0146$
	Larva	$\psi = (2 \pm 1)\cdot 10^{-3}$ $\rho = (2 \pm 4)\cdot 10^{-1}$ $T_M = 34.2 \pm 0.2$ $\Delta T = 5 \pm 11$	$R^2 = 0.57$ $NDF = 284$ $\chi^2 = 2.55\cdot 10^{-4}$ $RMSE = 0.0060$
	Pupa	$\psi = (4 \pm 3)\cdot 10^{-3}$ $\rho = 0.12 \pm 0.04$ $T_M = 35 \pm 0$ $\Delta T = 2.0 \pm 0.7$	$R^2 = 0.17$ $NDF = 255$ $\chi^2 = 0.0452$ $RMSE = 0.0254$
Briere (3)	Egg	$a = (1.26 \pm 0.02)\cdot 10^{-4}$ $T_L = 6.6 \pm 0.4$ $T_M = 36.58 \pm 0.07$ $m = 3.2 \pm 0.1$	$R^2 = 0.88$ $NDF = 1982$ $\chi^2 = 0.0141$ $RMSE = 0.0145$
	Larva	$a = 2.5 \pm 0.3)\cdot 10^{-5}$ $T_L = 12 \pm 1$ $T_M = 34.4 \pm 0.3$ $m = 1.7 \pm 0.2$	$R^2 = 0.55$ $NDF = 284$ $\chi^2 = 0.0061$ $RMSE = 0.0044$
	Pupa	$a = (1.5 \pm 0.4)\cdot 10^{-4}$ $T_L = 10 \pm 0$ $T_M = 35 \pm 2$ $m = 4 \pm 2$	$R^2 = 0.20$ $NDF = 255$ $\chi^2 = 0.0283$ $RMSE = 0.0444$
Sharpe and De Michele (4)	Egg	$A = -1$ $B = 7$ $C = -6$ $D = 72$ $E = 4$ $F = 0.7$	$R^2 = 0.73$ $NDF = 1980$ $\chi^2 = 0.0720$ $RMSE = 0.0220$
	Larva	$A = 13$ $B = -26$ $C = 24$ $D = 116$ $E = 5$ $F = -386$	$R^2 = 0.71$ $NDF = 282$ $\chi^2 = 0.0142$ $RMSE = 0.0049$
	Pupa	$A = 4$ $B = 13$ $C = 8$ $D = -13$ $E = -0.2$ $F = -0.7$	$R^2 = 0.24$ $NDF = 252$ $\chi^2 = 0.0067$ $RMSE = 0.0436$
Lactin-1 (5)	Egg	$\rho = (1.40 \pm 0.01)\cdot 10^{-1}$ $T_M = 38.89 \pm 0.08$ $\Delta T = 7.10 \pm 0.05$	$R^2 = 0.88$ $NDF = 1983$ $\chi^2 = 0.0699$ $RMSE = 0.0149$
	Larva	$\rho = (10.0 \pm 0.1)\cdot 10^{-1}$ $T_M = 38 \pm 1$ $\Delta T = 10 \pm 1$	$R^2 = 0.30$ $NDF = 285$ $\chi^2 = 0.0263$ $RMSE = 0.0076$
	Pupa	$\rho = (1.67 \pm 0.09)\cdot 10^{-1}$ $T_M = 37 \pm 0$ $\Delta T = 6.0 \pm 0.3$	$R^2 = 0.18$ $NDF = 256$ $\chi^2 = 0.0575$ $RMSE = 0.0449$
Lactin-2 (6)	Egg	$\rho = (7.36 \pm 0.09)\cdot 10^{-3}$ $T_M = 42.1 \pm 0.2$ $\Delta T = 2.5 \pm 0.1$ $\lambda = -1.076 \pm 0.002$	$R^2 = 0.88$ $NDF = 1982$ $\chi^2 = 0.0150$ $RMSE = 0.0146$
	Larva	$\rho = 0.11 \pm 0.02$ $T_M = 37 \pm 1$ $\Delta T = 9 \pm 1$	$R^2 = 0.62$ $NDF = 284$ $\chi^2 = 2.42\cdot 10^{-6}$
		$\lambda = (-5 \pm 2)\cdot 10^{-2}$	$RMSE = 0.0056$
	Pupa	$\rho = (7.9 \pm 0.7)\cdot 10^{-3}$ $T_M = 37 \pm 0$ $\Delta T = 1 \pm 0$ $\lambda = -1.12 \pm 0.02$	$R^2 = 0.21$ $NDF = 256$ $\chi^2 = 0.0131$ $RMSE = 0.0441$

Brière (3), Lactin-1 (5), and Lactin-2 (6) equations, that indicated values in the range 36–40 °C, circa. Besides the differences in the upper values provided by the development rate functions (2)–(6), the optimal temperatures, namely the abscissa corresponding to the maximum of equations (2)–(6), were almost coinciding and centred around 33 °C.

The situation was slightly different in the case of larvae, where the general performance of equations (2)–(6) in describing the experimental data was lower. Besides this overall lower performance, the Brière equation showed the best goodness of fit values and a low thermal limit of 16 ± 2 °C, a higher value with respect to eggs. The upper thermal limits, instead, were in the range 35–39 °C, circa, values that are comparable with the egg stage. Fig. 1b shows that all the equations had a similar trend, with no exceptional variations with respect to each other, and an optimal value centred around 32 °C. The only exception was the Sharpe and De Michele equation (4), that indicated a lower optimal temperature value with a corresponding higher development rate - that corresponds to a faster growth of larvae.

A different scenario was assessed for the development at different constant temperatures and 70% RH. The results of this part of the study are listed in Table 5, and graphically represented in Fig. 2. In this case the dataset allowed the estimation of the parameters of equations (2)–(6) for the egg, larva, and pupa stages, conversely to the case of 35% RH. Proceeding by order, the dataset of the egg stage was overall well-represented by all the development rate functions, even if the best fit performance was carried out by the Brière (3) and the Lactin-2 (6) equations. The lower thermal threshold indicated by the Brière equation (2) was 6.6 ± 0.4 °C, lower with respect to the case of 35% RH. The maximum thermal threshold for the development, instead, was in the range of 36–42 °C, with Logan (2) and Lactin-2 (6) reporting the lowest and highest values, respectively. The optimal temperatures were all centred around 32 °C, unless the Sharpe and De Michele equation (4) that indicated a value around 30 °C.

The fitting performances of equations (2)–(6) for the dataset of larvae was overall lower, if compared to eggs, and can probably be due to a higher variance of the dataset. The larval stage covers a great percentage of the overall life cycle, and the higher variability (and variance, accordingly) in the development times can be a biological mechanism that the species has, to survive in case of adversities. Fig. 2b shows a general variability of the best fit functions with respect to the other cases explored in this study, while the best fit performance was carried out by the Sharpe and De Michele (4), strictly followed by the Lactin-2 (6). The lower thermal threshold indicated by the Brière (3) is of 12 ± 1 °C, a lower value with respect to the case at 35% RH, while the upper threshold falls in the range 34–38 °C. The different equations indicate contrasting results concerning the optimal thermal value for the development, as Sharpe and De Michele (4) and Lactin-1 (5) indicate a value around 28 °C and the other ones around 30 °C.

A similar scenario in terms of fit performance was assessed for the dataset of pupae, however, the higher variance of the data caused a general decrease of the goodness of fit indicators. Unlike larvae, equations (2)–(6) had a similar trend (Fig. 2c), even if the Lactin-2 (6) was the best in terms of fitting performance. The lower thermal threshold was 10 °C, intermediate value between eggs and larvae under the same conditions of humidity, while the upper thermal threshold fell in the range 35–37 °C. The optimal temperature value was instead centred around 32–33 °C unless in the case of the Sharpe and De Michele (4),

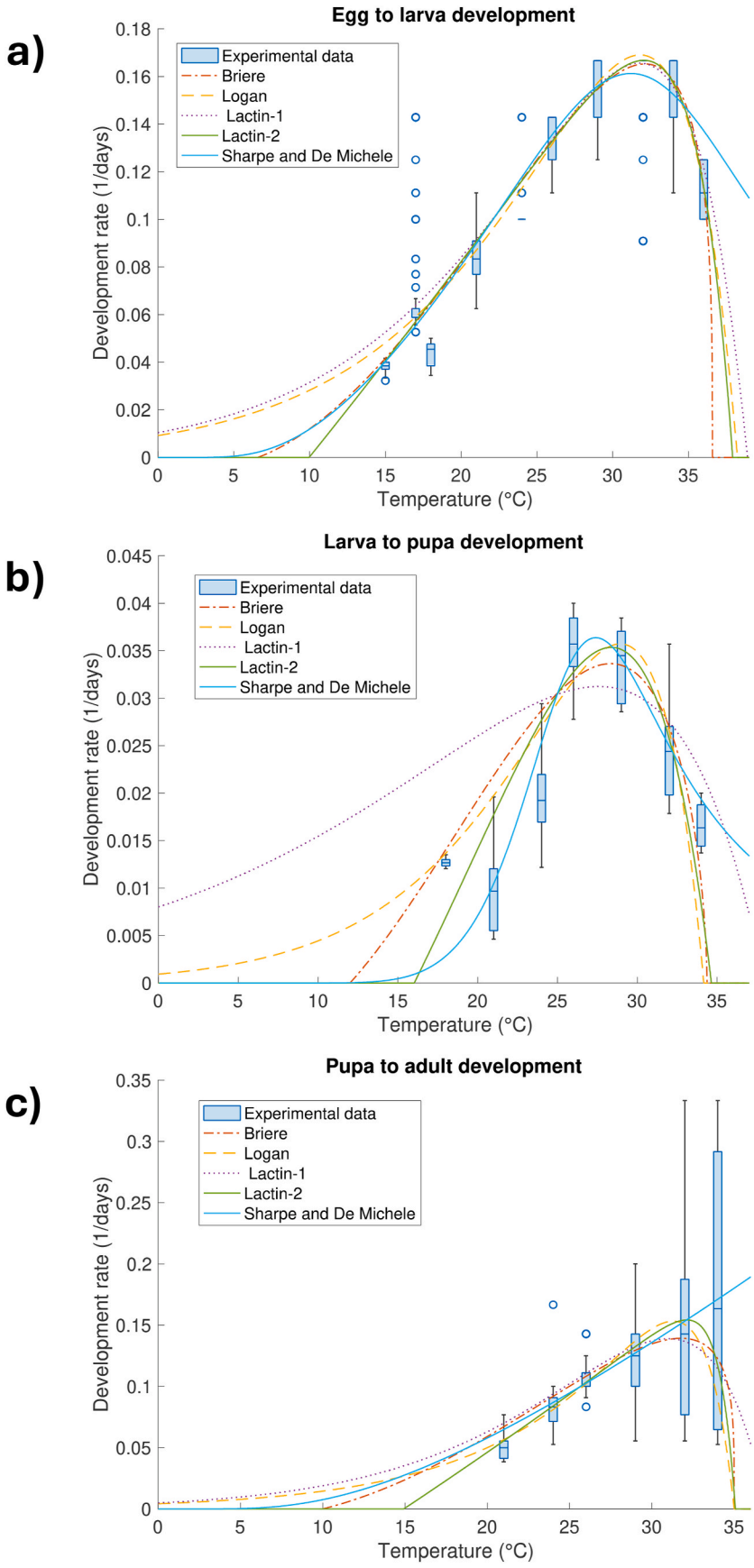

Fig. 2. Development rate over temperature at 70% RH for the egg, larval, and pupa stages. Experimental data are indicated by the boxplot, while the different curves represent the best fit functions (2)–(6), whose parameters are listed in Table 4.

that indicates values not biologically reliable for this stage. The low reliability of equation (4) can be justified by the high correlation between its parameters, that makes their estimation extremely difficult for some datasets (Schoolfield et al., 1981).

This part of the study provided a more accurate overview of the thermal development of *I. inquinata*, underlying that the relative humidity affects the development time. The best fit functions, in fact, confirmed, even if in an empirical way, what has been statistically proven in Section 3.2. The mathematical interpretation extends the scenario discussed in Section 3.1 and opens the door to further applications of physiologically based models.

The literature offers several theoretical frameworks that can be applied to this case of study, as for instance the models presented in (Bono Rosselló et al., 2022, 2023; Buffoni and Pasquali, 2007; Rossini et al., 2021a, Rossini et al., 2022; Rossini et al., 2024), leading to the development of *ad hoc* decision support systems. The possibility of exploring the future scenarios *in silico* is an additional step forward towards the formulation of sustainable control strategies (Dalal and Singh, 2017), as the producers may explore the effect of different environmental condition profiles. Accordingly, decisions can be made in a more rigorous way, optimising the use of the resources with a subsequent decrease of the production costs (Rossi et al., 2019).

4. Conclusions

This study explored the thermal development of *Idaea inquinata* at different constant temperatures and humidities, by combining datasets provided by 20 years of experiments in climatic chamber. This pool of quantitative information has been introduced for the first time, and deserves future improvements about mortality, adult lifespan, and egg production under similar circumstances. Despite this limitation, we showed the utility that our results may have to protect dried herbs in warehouses by *I. inquinata* infestations. We think that this study can be either of inspiration for cases of similar pests, or a starting point to develop digital tools that help farmers in reaching the goal of a sustainable production.

CRediT authorship contribution statement

Luca Rossini: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Formal analysis, Data curation, Conceptualization, Methodology. **Daria Patrizia Locatelli:** Validation, Resources, Methodology, Investigation, Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Lidia Limonta:** Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization, Project administration, Resources, Validation, Writing – review & editing.

Declaration of competing interest

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

Acknowledgements

The authors are grateful to the anonymous reviewers for their comments and suggestions, which have been greatly helpful for the improvement of this manuscript. L.R. is funded by the European Commission under the Marie Sklodowska Curie Actions Postdoctoral Fellowship (MSCA-PF-2022) project “PestFinder” Grant n. 101102281.

Data availability

The dataset and the scripts to fully reproduce the results of this work are publicly available at https://github.com/lucaros1190/Idaea-inquinata-2024

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