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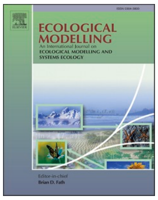

# Ground-truthing predictions of a demographic model driven by land surface temperatures with a weed biocontrol cage experiment

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ABSTRACT

Herbivorous insects play important roles in agriculture as pests or as weed biological control agents. Predicting the timing of herbivore insect population development can thus be of paramount importance for agricultural planning and sustainable land management. Numerical simulation models driven by temperature are often used to predict insect pest population build-up in agriculture. Such simulation models intend to use station-derived temperatures to drive the development of the target insect, although this temperature may differ substantially from that experienced by the insect on the plant. To improve the estimations, it has been suggested to replace air temperature in the model by land surface temperature (LST) data. Here, we use a numerical simulation model of insect population dynamics driven by either air temperature (combined with atmospheric temperature soundings) or land surface temperature derived from satellites to predict the population trends of the leaf beetle *Ophraella communa,* a potential biological control agent of *Ambrosia artemisiifolia* in Europe. For this, we conducted an extensive field experiment that included caged *O. communa* populations at five sites along an altitudinal gradient (125–1250 m a.s.l.) in Northern Italy during 2015 and 2016. We compared our model predictions using air or land surface temperature with observed beetle population build-up. Model predictions with both air and land surface temperatures predicted a similar phenology to observed populations but overestimated the abundance of the observed populations. When taking into consideration the error of the two measurement methods, the predictions of the model were in overlapping timeframes. Therefore, the current model driven by LST can be used as a proxy for herbivore impact, which is a novel tool for weed biocontrol.

## 1. Introduction

Insect herbivores are considered to be fundamental for ecosystem structure and functioning due to their impact on vegetation composition and productivity (Crawley 1983). The impact is particularly significant in the case of agricultural pests or when applied as biological control agents of weeds. Insect herbivores can cause vast crop losses in agriculture, and insects like the Colorado potato beetle (*Leptinotarsa decemlineata* Say), cotton bollworm (*Helicoverpa armigera* Hübner) or fall armyworm (*Spodoptera frugiperda* J.E. Smith) attract global awareness as serious crop pests (Liu et al., 2012; Kriticos et al., 2015; Kumar et al., 2018).

Classical biological control of invasive plant species refers to the deliberate release of specialist herbivore insects collected in the invasive plant's native range in order to reduce its abundance and/or further spread into new geographic areas (Müller-Schärer and Schaffner 2008).

These classical biological control agents are selected on being either monophagous, or attacking few closely related plant species. This reduces non-target impacts on local crops and vegetation (Müller-Schärer and Schaffner 2008). Currently, less than 1% of all intentional releases

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of classical weed biological control agents are estimated to have a potential to lead to negative effects at the population level of nontarget species (Hinz et al., 2019). Insects such as the saltcedar leaf beetle (*Diorhabda elongata* Brullé*)*, the mottled water hyacinth weevil (*Neochetina eichhorniae* Warner) or the cochineal *Dactylopius opuntiae* (Cockerell) are examples of successful biological control agents used to manage weeds (Schwarzländer et al., 2018; Hoffmann et al., 2020).

The insect's impact on plant performance usually increases with the density of insect herbivores (Myers and Sarfraz 2017). Therefore, being able to predict insect herbivore population dynamics can be critical for making sound management decisions (Harms et al., 2020). In agricultural systems, pest predictive models are used to adjust timing for management decisions such as the timing of application of insecticides (Magarey et al., 2015; Johnson et al., 2016). Similarly, modeling the demography of biological control agents could be used to predict biocontrol impact and inform whether additional management is needed to control a target weed (Mvandaba et al., 2019; Augustinus et al., 2020a,b). Furthermore, predicting climate-dependent phenology of potential biological control agents could prevent release of organisms in a novel range if there is a phenological mismatch (Harms et al., 2020).

Demographic models of insects are in general driven by temperature measurements for local predictions of population dynamics, or interpolated datasets of air temperature to make predictions for larger areas (Damos and Savopoulou-Soultani 2012). A challenge with air temperatures, however, is to obtain reliable high-quality spatially continuous data. Air temperatures are generally provided by local weather stations, which can be located at long distance from another, making interpolated estimations inaccurate. An alternative to the utilization of interpolated air temperature estimates for modeling ecological phenomena is the use of satellite information and products (Lensky and Dayan 2011; Blum et al., 2013; Lensky et al., 2018). Land surface temperatures (LST) derived from satellite measurements may be used to drive insect population models, providing spatially continuous assessments of population dynamics ( Blum et al., 2015, 2018). These data are easily available globally and free of charge with high spatial resolution (Shiff et al., 2021). In general, differences between surface (LST) and air (i.e., measured at 2 m above the surface) temperatures are related to vegetation cover and atmospheric circulation (Lensky et al., 2018). The difference between the two measures is usually larger at day time; LST daily mean temperature is expected to record higher temperatures than the observed air temperature. When local temperature differences can be estimated, they can be used to adapt the satellite-derived LST as inputs in the model, resulting in more accurate model predictions for insect herbivore dynamics ( Blum et al., 2015; Suggitt et al., 2011).

Recent agricultural and ecological studies used thermal infrared or microwave measures to determine LST to predict insect densities (Muharam et al., 2017), especially in areas where only a few or no weather stations exist (Da Silva et al. 2015). A numerical simulation of olive fly (*Bactrocera oleae* Gmelin) population dynamics driven by derived-LST tree canopy temperature (calculated from the retrieved Moderate Resolution Imaging Spectroradiometer [MODIS] LST data) showed a high degree of correlation with trapping data in several geographic locations of the Near East (Blum et al., 2015). The same model was also successfully applied to predict the population dynamics of the polyphagous cotton bollworm (*Helicoverpa armigera*) breeding in commercial corn and tomato plantations (Blum et al., 2018). This method has not been used in the context of weed biocontrol yet, where it can be a useful tool to make this management method more predictable.

Here we applied the approach described above to model and forecast the population trends of a phytophagous biological control candidate of the invasive common ragweed *Ambrosia artemisiifolia* L. (Asteraceae) in Europe, the beetle *Ophraella communa* LeSage (Chrysomelidae). We contrasted air temperature and MODIS-derived LST as an input source to drive the beetle's model. We did not correct the LST data for local variation (, Blum et al., 2015; Suggitt et al., 2011), because these corrections are based on knowledge of local temperature variation between LST and air temperature, which can be prohibitively challenging to obtain for large-scale geographical predictions. Resulting forecasts were validated using data from a field experiment conducted in Italy during the summers of 2015 and 2016. The sites differed in terms of elevation and temperature conditions, providing an experimental diverse natural ground to evaluate the abilities of uncorrected LST-derived temperature vs. on-site collected temperature as drivers of the beetle's population dynamics models.

## 2. Material and methods

### 2.1. Study species

*Ambrosia artemisiifolia* is a North-American annual weed that has invaded ranges on all continents except Antarctica. In Europe, it is considered a noxious weed since the 1920s (Csontos et al., 2010). Besides being a costly weed in spring-sown crops, *A. artemisiifolia* has attracted particular attention because of its highly allergenic pollen, resulting in high medical costs and decrease in human well-being in the sensitized population (Mouttet et al., 2018; Müller-Schärer et al., 2018, Schaffner et al. 2020). The leaf beetle *O. communa*, which is native to North America, was accidentally introduced in China in 2001 (Meng and Li 2005), where it is now used as a biological control agent of *A. artemisiifolia* (Zhou et al., 2017). In Europe, the leaf beetle was found for the first time in 2013 in Northern Italy and Southern Switzerland (Müller-Schärer et al., 2014) and it has expanded its range to the Balkan region (Augustinus et al., 2015; Lommen et al., 2017; Zadravec et al., 2019; Horváth and Lukátsi 2020). While the use of *O. communa* as a biological control agent was initially ruled out because it can conclude its life cycle on sunflower, no non-target attacks have been reported in its native and imported range on sunflowers (Zhou et al., 2011) or native European plants (Augustinus et al., 2020c). *Ophraella communa* overwinters at the adult stage, and can complete up to seven generations per season, depending on temperature (Zhou et al., 2010). In Europe, eggs are laid in batches as soon as the adults encounter seedlings of the annual host plant in spring. Egg deposition continues until mid-August (Augustinus et al., 2020a), with cessation of oviposition probably cued by a shorter photoperiod and decreasing temperature, as has been shown for *O. communa* populations in China (Zhu et al., 2012). All larval stages and adults feed on the green parts of the host plant. In Europe, the majority of leaf damage is observed in late August when *O. communa* abundance peaks (Augustinus et al., 2020a).

Since the first observations of high population densities of *O. communa* in Northern Italy, aerial ragweed pollen concentrations have decreased by 80%, which cannot be explained by changes in climate or land use (Bonini et al., 2015a,b). While ecological suitability analyses combined with temperature and humidity-driven vital rates suggest that *O. communa* can reach population densities as observed in Northern Italy also in other parts of Europe (Augustinus et al., 2020b), no demographic model that may help predicting population densities of this beetle in a given year or region has been published so far.

### 2.2. Field experiment

In the summer of 2015 and 2016, we conducted field-cage experiments to assess the temperature and relative humidity (RH)-dependent developmental rate of *O. communa* on *A. artemisiifolia*. The experiments were conducted at five sun-exposed sites in Northern Italy with similar inclines, 20–50 km from Milan, Lombardy (Fig. 1, Appendix A). In order to create a climatic gradient, we selected the sites along an altitudinal gradient from 125 to 1250 m a.s.l. (Magenta, "Mag", at 125 m; Communita Montana, "CM" at 250 m; Fogliaro, "Fog" at 550 m; Eremo, "Ere" at 770 m and Piani d'Erna "PdE2 at 1250 m). The experiments were conducted within 1 × 2 × 1 m (l x w x h) cages consisting of aluminum frames and a zipper-equipped gauze (Diatex SA, France).

*Ambrosia artemisiifolia* plants were grown in 2014 and 2015 from

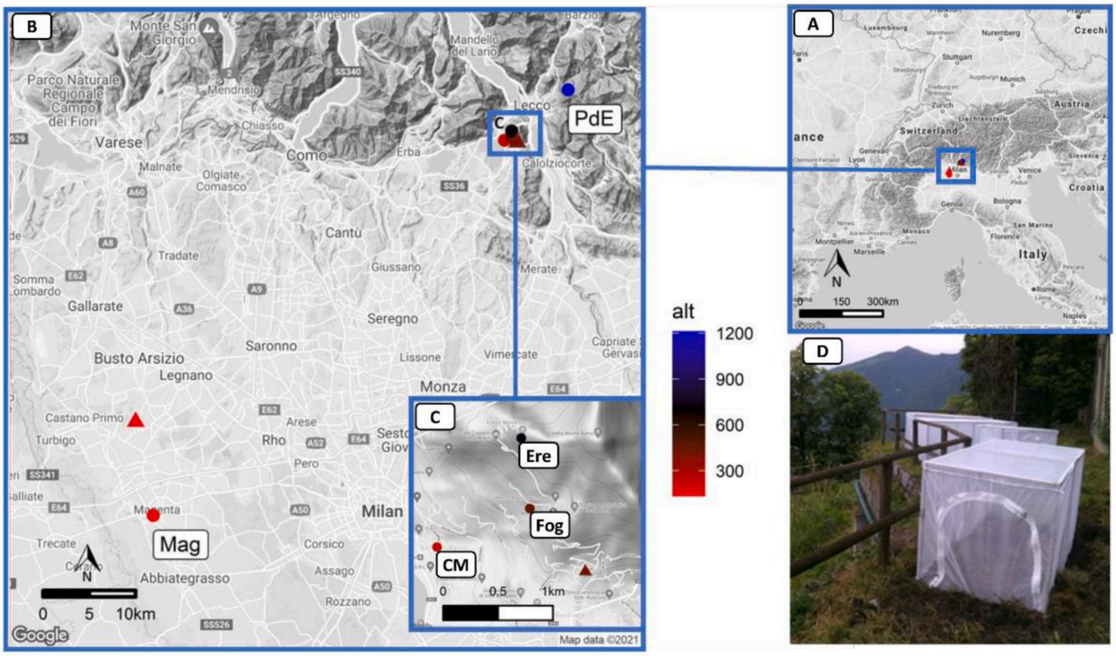

**Fig. 1.** A-C: Locations of weather stations (triangles) and experimental sites (circles). D: picture of an experimental site with experimental cages.

seeds collected in Busto Arsizio (Lombardy) in the previous season. All plants were grown in the greenhouse of Parco Monte Barro, Centro Flora Autoctona in Galbiate (359 m a.s.l.). Seedlings were transferred from seed trays to 9 cm square pots filled with standard garden soil and transferred to the soil within the field experimental cages when they had 12–15 leaves. We planted 12 plants per cage.

In early July 2015 and 2016, we released 20 freshly hatched *O. communa* adults (10♂, 10♀) per cage, two cages per site. The beetles were individually marked with nail polish dots on the elytra, (color coded for sex, and patterns for individuals). In each site, we set up two experimental cages (=replicates) that were monitored for two years. Once a week, we visited all the experimental cages and counted fertile eggs (excluding black, desiccated or hatched eggs), pupae and marked (initially released) and unmarked (offspring) adults.

### 2.3. Temperature data

We downloaded the 1 km land surface temperature (LST) product (MYD11A1) from NASA's (MODIS) via Google earth engine (Gorelick et al., 2017). The LST product was downloaded for day and night (1:30AM/PM). When temperature data were missing due to cloud cover, we estimated the missing values by taking the average temperature of the past 18 years for the given Julian date (Lensky and Dayan 2011). LST was downloaded for all pixels where experimental cages were located, except for three sites. In the experimental site of Communita Montana ('CM') at 245 m a.s.l., which included a nearby water body, we used an adjacent pixel instead to prevent overestimations of LST at night and underestimation at day since water-bodies are known to alter LST measurements (Gunawardena et al., 2017). The sites 'Fog' (550 m a.s.l.) and 'Ere' (770 m a.s.l.) were on the lower and upper edge of the same pixel (Fig. 1C). Since these sites are likely to experience different temperatures from each other, we downloaded the temperature measurements of adjacent pixels with the same altitudes and inclines as the sites, and averaged the temperature values of the pixel with the experimental site with the temperatures of the adjacent pixels. Temperature measurement error per day and site was taken from the product "LST error flag". Daily average air temperature for all the different experimental sites was obtained from two weather stations which were <10 km away from the experimental sites (Arconate SMR and Galbiate DW6022). We used a temperature measurement error of ±0.4 °C. We then downloaded the atmospheric temperature sounding for the corresponding dates of 1608 LIML weather station in Linate to adjust for temperature differences along the altitudinal gradient per day. In-cage local temperature measurements were also obtained with data-loggers (ELV TFD128) but were disregarded since they showed a high variability due to improper shielding from solar radiation.

### 2.4. Numerical simulation model of insect pest population dynamics

We used the stage-structured, continuous time-age population model driven by temperature described in Blum et al. (2018) to simulate the population dynamics of the leaf beetle *O. communa*.

This insect population model is based on a population density function described by a series of differential equations:

$$\frac{dN_i(t)}{dt} = \frac{k}{del}[N_{i-1}(t) - N_i(t)] - \mu_i(t)N_i(t) \tag{1}$$

where each life stage (i.e., egg, larva, pupa, pre-oviposition, and adults) is composed by $k$-age cohorts ($i = 1,2,3,\ldots,k$) and calculated by a differential equation in a sequential order. $\mu_i(t)$ in Eq. (1) is the cohort $i$ attrition at time $t$, $del$ is the average developmental time per life stage, and $N_i(t)$ is the cohort $i$ population density. Time and age are measured in degree days ($DD = 0.5^*(T_{max} + T_{min}) - T_{critical}$), which is calculated using the rectangular method (Arnold 1959). The equation is solved in the model numerically, using the Euler method. The population flux ($r_i(t)$) from one age cohort to another is described as:

$$r_i(t) = \frac{k * N_i(t)}{del} \tag{2}$$

Thus, eqn. (1) becomes:

$$\frac{dr_i(t)}{dt} = \frac{k}{del}\left\{ r_{i-1}(t) - \left[1 + \mu_i(t)\cdot\frac{del}{k}\right]\cdot r_i(t)\right\} \tag{3}$$

In order to calculate the critical temperature ($T_{critical}$) and the developmental time of each life stage ($del$), the model assumes a linear relationship between developmental rate and temperature,

$$r(T) = bT + a \quad (4)$$

where $b$ is the slope and $a$ is the intercept of such relationship. Then, the critical temperature ($T_{critical}$) and the stage developmental time (*del*) are calculated from eqs. (5) & 6 (Damos and Savopoulou-Sultani, 2012):

$$T_{critical} = -\frac{\boldsymbol{b}}{\boldsymbol{a}} \quad (5)$$

$$del = \frac{1}{b} \quad (6)$$

The observed variance (*var*) of the physiological time in day degrees (*DD*) derived from experimental settings is used to calculate the number of age cohorts ($k$) within each life stage (Vansickle, 1977):

$$\boldsymbol{k} = \frac{\boldsymbol{del}^2}{\boldsymbol{var}}. \quad (7)$$

Mortality and egg production rates were calculated as a function of temperature following data from Zhou et al. (2010). Pre- and post-oviposition adult mortality rates were assumed to be independent of temperature. $T_{critical}$, *del*, $k$, and $\mu$ used in the model are provided in Appendix 1.

### 2.5. Analysis

To compare and validate model output driven by the two different sources of temperatures (LST and MET) with the experimental data, we calculated the mean square of the prediction error (MSPE) per life stage, site and year:

$MSPE = \Sigma(\mathrm{p} - \mathrm{o})^2$ (eqn. 8)where p is the number predicted by the model, and o is the number observed in the experiment at the same date. We then divided this value by the average of the MSPE for the LST and the MET model to obtain the relative mean square prediction error (RMSPE).

Weather data were adapted for analysis in R, using the packages readxl (Wickham and Bryan 2016), reshape 2 (Wickham 2007) and plyr (Wickham and Wickham 2016) for data transformation and inference.

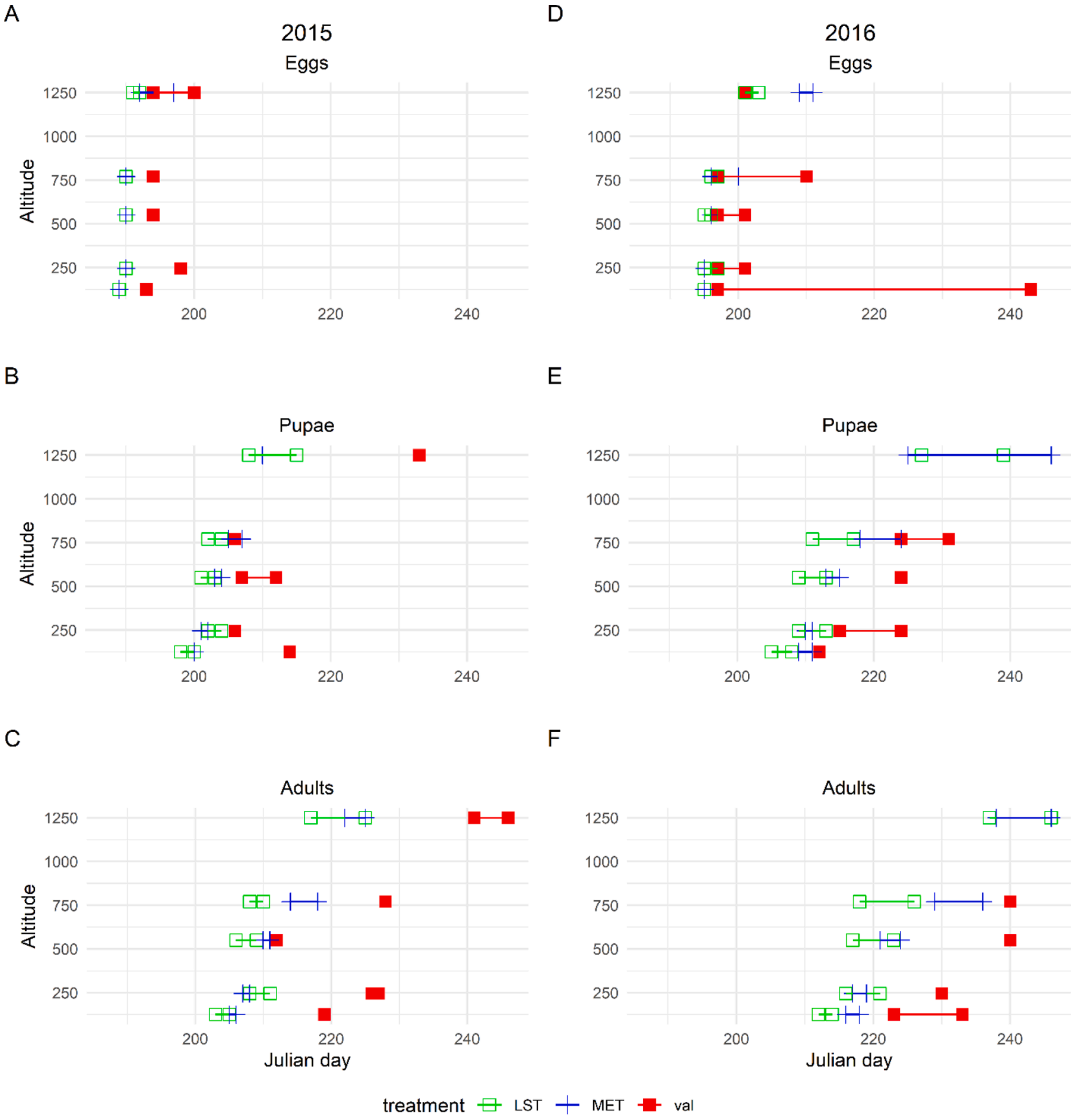

**Fig. 2.** Predicted and observed phenology of *O. communa* F1 eggs, pupae and adults in the experimental sites along the altitudinal gradient during 2015 and 2016. Green, empty squares show earliest and latest first occurrence based on model predictions driven with land-surface temperatures (± measurement error), blue plusses show earliest and latest first occurrence based on meteorological station data (± measurement error), and red, filled squares show earliest and latest first occurrences observed in the field experiment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Graphical representation of data was conducted in ggplot2 (Wickham 2009), ggmap (Kahle and Wickham 2013), and gridExtra (Auguie et al., 2017). The insect population model was run in IDL (Interactive Data Language Harris Geospatial Solutions).

## 3. Results

The model simulations estimated shorter developmental time both using LST data and air temperatures derived from meteorological stations. When considering the errors of both temperature measurement methods, the developmental time ranges overlapped in all but one case, indicating that the developmental time estimates were similar (Fig. 2).

Models driven with either air temperatures or LST produced a bimodal pattern of egg numbers (Fig. 3). The second peak of forecasted egg population coincides with the emergence of the F1 adults produced by adults at the start of the experimental populations. Though noted in the observed data, the bi-modal pattern was much more pronounced in model predictions, with the second simulated egg-crest being higher than the first simulated crest (see e.g. model predictions for the four lowest sites in Fig. 2a).

The model simulations estimated higher population abundances than observed in the experiments. The estimates using LST data predicted higher populations than the simulation using air temperatures derived from meteorological stations (Fig. 3). Predicted population increase was much higher than observations across life stages, sites, and years, except for the predicted number of eggs at Piani d'Erna ('PdE') at 1250 m a.s.l. in 2016 when using air temperature as a driver of the model (Fig. 3).

Abundance increased earlier in the LST-driven model, particularly for the pupal stage, but also for other life stages (Fig. 3). As a result, the MSPE was almost always lower for the model driven by the air temperature (Table 1).

## 4. Discussion

The model simulation was able to closely approximate the phenology of *O. communa,* both when driven with LST and air temperatures. However, the models generally overpredicted the number of beetles. Below we discuss these results from a technical, biological and practical perspective.

### 4.1. Technical perspective

Predictions of the model driven by LST resulted in a shorter developmental time and in higher population densities compared to the model driven by air temperature (i.e., from meteorological stations and interpolations). This is not surprising, since LST estimates are in general higher than the air temperature measurements, especially during the daytime (Trigo et al., 2008), and LST were not corrected for these deviations (see for example Blum et al., 2015). The higher LST therefore might have resulted in a faster accumulation of DD and a shorter developmental time of the beetles. The earlier the adults emerge and start laying eggs, the longer they can keep producing offspring before the photoperiod-induced cessation of egg deposition. For example, in The Eremo site (770 m), a second increase in the number of eggs is forecasted earlier in the model driven by LST, which results in a second increase in the pupae and adult populations ('second offspring generation') in mid-August of 2015, which was not observed in the model driven by air temperatures. In this case, phenology is out of phase and more generations than actually observed can be predicted. A correction of the LST would probably improve the model fit to the validation data, but requires local knowledge for further upscaling on a larger geographic area. In earlier work on predicting biocontrol agent impact in its potential range, the focus of predicting density-dependent impact on the target plant was by using phenology as an indicator for herbivore population densities. For instance, Mouttet et al. (2018) and Schaffner et al. (2020) predicted that a decrease of ~80% of aerial pollen of *A. artemisiifolia* was depending of *O. communa* reaching at least 3 generations before the onset of flowering. Hence, similar impact in Europe was estimated to be as large only in locations where *O. communa* could conclude at least 3 generations per year. Both air temperature and LST-driven models overpredicted population densities, while phenology was described rather well. Therefore, LST-driven models could be used in the same way as models driven by data derived from meteorological stations and interpolations, as in Mouttet et al. (2018) and Schaffner et al. (2020).

### 4.2. Biological perspective

The model predictions at the coldest site, which is most likely at the edge of the climatic niche of *O. communa*, better approximated the observed trends of the beetle populations. The data used to parametrize the model (Appendix A) were obtained from studies conducted in constant temperature laboratory experiments (Zhou et al., 2010, see Appendix 2). Our observations, on the other hand, were collected under ambient temperature conditions in an open field experiment. This might have affected the ability of the model to properly simulate beetle development and growth because of beetle behavior and general patterns in developmental times of insect populations at lower temperature thresholds.

Eigenbrode et al. (2015) showed that insects in field environments can use basking behavior to increase body temperature (and therefore metabolisms) compared to the air temperature. Since the data used to parametrize our model were collected in incubators, our model does not consider this mechanism. This implies that model predictions in a colder environment should be closer to observations from a varying-temperature environment, which is the case in the predictions of our model.

The overpredictions of the model could also be explained by the general trends of insect population developments at the edge of their physiological range. When comparing developmental rates of 29 species of terrestrial insects, Paaijmans et al. (2013) found that temperature fluctuation around low mean temperatures increased fitness, while fluctuation around high mean temperatures decreased fitness compared to the use of parameters derived under constant high temperature conditions. Temperature fluctuations around high temperatures result in the need of energy expenditure on production and breakdown of heat shock proteins, thus decreasing insect fitness (Chen et al., 2018, 2019 ). An additional factor affecting forecasting may have been related to the fact that we have not considered humidity-related parameters in the model. We did not consider mortality related to relative humidity in this model, which could have affected model predictions, over-predicting abundance. Since temperature and relative humidity are intercorrelated by nature, relative humidity at high temperatures will be lower if absolute humidity stays the same. Low relative humidity has been shown to have a negative effect on population growth of several insect species (Simelane, 2007; Lu and Wu 2011, Augustinus & Sun et al. 2020), and it is expected that insects will encounter lower relative humidity levels at the upper edge of their thermal range.

### 4.3. Practical perspective

The inclusion of density-dependent factors or humidity-driven mortality could help improve the model forecasting abilities. However, estimating insect abundance for single species over a larger area in absolute numbers is a very challenging endeavor. For example, in pest monitoring, most integrated pest management procedures use pest traps to estimate optimal timing, but normally they use an experience-based threshold, and not a trap-based estimation of absolute abundance of pest insects (Adams et al., 2017). These kinds of datasets are not available for *O. communa* populations, partially because studies of overwinter survival, and therefore estimates for population densities, have focused

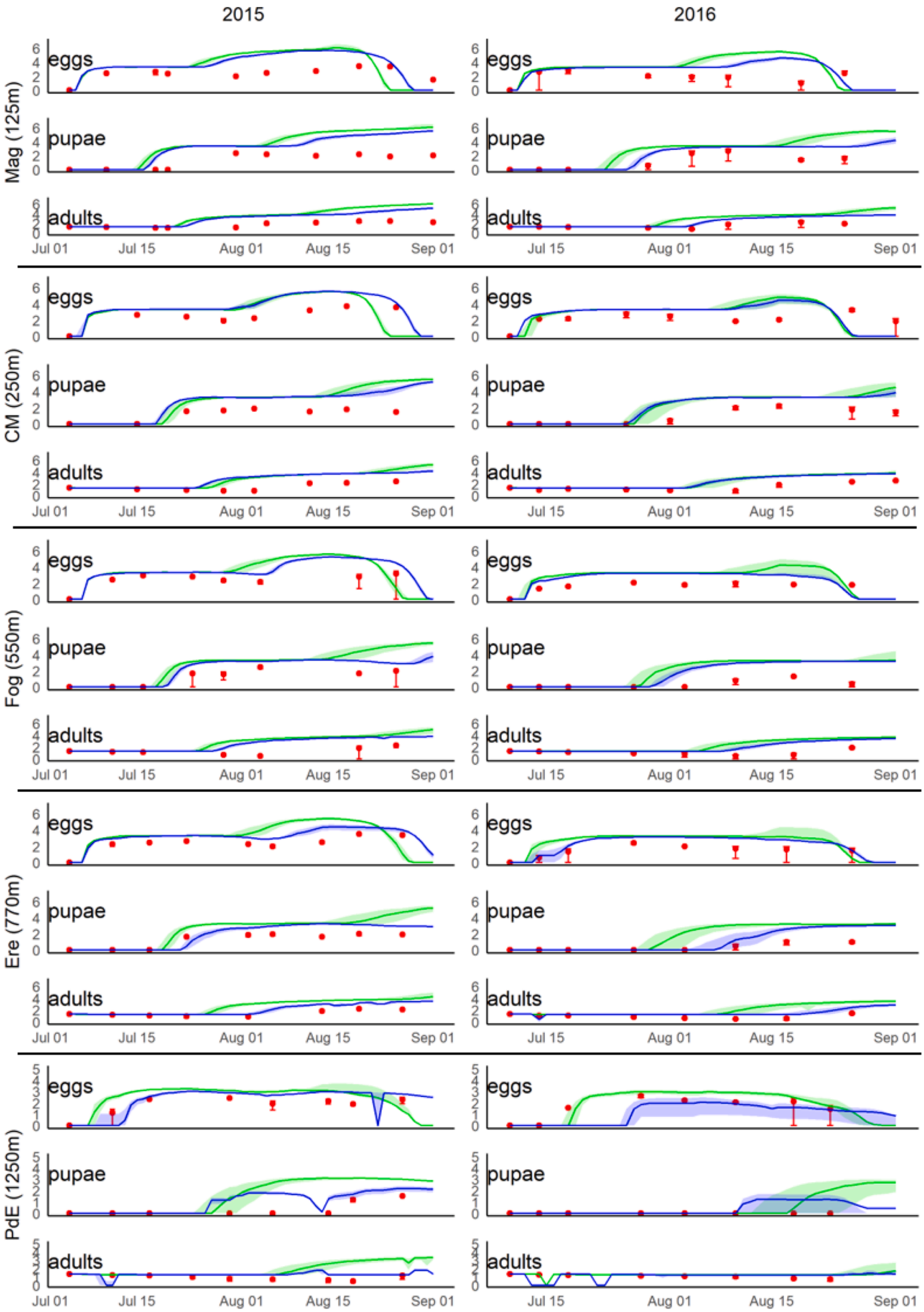

**Fig. 3.** Predicted vs. observed abundance numbers of *O. communa* in 2015 (left column) and 2016 (right column). Predictions of the model driven by LST (green) and air temperatures (in blue) with respective temperature error (ribbon). The red points show the validation data, the vertical lines show the variation within the validation data. All data are displayed on a logarithmic scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
The relative root mean squared error (r-RMSE), scaled to 0–1 of model calculations vs. observed populations for each site and year. A smaller r-RMSE means a better prediction of the model.

| | 2015 | | | | | 2016 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mag | CM | Fog | Ere | PdE | Mag | CM | Fog | Ere | PdE | |
| eggs | 0.975 | 0.91 | 0.855 | 1 | 1 | 0.93 | 0.955 | 0.655 | 0.785 | 0.89 | LST |
| | 0.025 | 0.09 | 0.145 | 0 | 0 | 0.07 | 0.045 | 0.345 | 0.215 | 0.11 | MET |
| pupae | 0.99 | 1 | 1 | 1 | 1 | 0.99 | 0.99 | 0.57 | 0.86 | 0.925 | LST |
| | 0.01 | 0 | 0 | 0 | 0 | 0.01 | 0.01 | 0.43 | 0.14 | 0.075 | MET |
| adults | 0.990.01 | 1 | 0.99 | 1 | 1 | 0.705 | 0.78 | 0.715 | 0.99 | 0.575 | LST |
| | 0.01 | 0 | 0.01 | 0 | 0 | 0.295 | 0.22 | 0.33 | 0.01 | 0.425 | MET |

on physiological or evolutionary changes (Zhou et al., 2013; Tanaka and Murata 2016) or host plant utilization (Watanabe and Hirai 2004), but have not given any estimates for overwinter survival. Furthermore, studies on impact of *O. communa* on individual *A. artemisiifolia* plants and populations which included measurements of *O. communa* abundance did not show clear correlation between beetle abundance and level of damage to the plant in field experiments (Augustinus et al., 2020a; Lommen et al., 2018; ). Without dependable methods to estimate *O. communa* density in the field, and without a clear measurement of per capita impact on *A. artemisiifolia* in a heterogeneous environment, we do not think including density-dependence or humidity-driven mortality would make the model any more accurate, while phenology has been identified as a predictor for impact (Mouttet et al., 2018; Augustinus et al., 2020b, Schaffner et al., 2020)

Therefore, the presented model can still be used to compare potential *O. communa* population build-up in suitable ranges in Europe to its current range. In Northern Italy, where the beetle is present, the aerial pollen concentrations have decreased by ~80% (Bonini et al., 2015a,b). This strong decrease is explained by the timing of the 3rd generation of *O. communa*. The exponential increase of *O. communa* results in high impact on male flower maturation and pollen release (Augustinus et al., 2020b; Mouttet et al., 2018; Schaffner et al., 2020). While *O. communa* phenology is highly influenced by temperature, *A. artemisiifolia* flowering onset is influenced by photoperiod (Leiblein-Wild and Tackenberg 2014). A model for the plant based on photoperiod, combined with this model to refine predictions on where in Europe *O. communa* will be able to conclude its 3rd generation before the plant starts flowering would be useful to predict impact, both in the long-term and in real-time. Therefore, this numerical simulation model can be used as a novel method to predict the impact of *O. communa* on *A. artemisiifolia* in Europe, both driven with LST and air temperature–driven models, and could also be used for different weed biocontrol agents.

## Credit author statement

**Benno A. Augustinus**: Conceptualization, Investigation, Writing-Original Draft, Visualization, Funding acquisition. **Moshe Blum**: Methodology, Software, Formal Analysis. **Sandra Citterio**: Investigation, Resources. **Rodolfo Gentili**: Investigation, Resources. **David Helman**: Methodology, Formal analysis, Supervision. **David Nestel**: Writing – Review & Editing, Supervision, Funding acquisition. **Urs Schaffner**: Writing – Review & Editing, Supervision, Funding acquisition. **Heinz Müller-Schärer**: Writing – Review & Editing, Supervision, Funding acquisition. **Itamar M. Lensky**: Conceptualization, Methodology, Validation, Resources, Writing – Review & Editing, Supervision, Funding acquisition

## 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.

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## Appendix

We took the laboratory results of Zhou et al. (2010), and Eqs. (5)-7 to calculate the critical temperature ($T_c$), developmental time (*del*) in degree days, and the number of substages (*k*) for each stage of *O. communa.*

| Stage | eggs | larva | Pupae | pre-oviposition | adults |
|---|---|---|---|---|---|
| $T_c$ [ °C] | 11.10 | 14.79 | 6.35 | 13.04 | 0.53 |
| *del* [*DD*] | 91.01 | 117.70 | 145.22 | 360.30 | 1264.39 |
| *k* | 42.00 | 90 | 119 | 110 | 18 |

Temperature ( °C) dependent oviposition (# of eggs):
$\text{Lay}(T) = -0.1703T^2 + 12.59T - 173.91$
Temperature ( °C) dependent mortality rate (μ) for each life stage:
Egg: $\mu(T) = 0.0001273T^2 - 0.0066658T + 0.088886$

Larva: $\mu(T) = 0.00007821T^2 - 0.00424T + 0.05966$

Pupae: $\mu(T) = 0.00001908T^2 - 0.001047T + 0.014481$

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