

Predicting impact of a biocontrol agent: integrating distribution modeling with climate-dependent vital rates

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Abstract. Species distribution models can predict the suitable climatic range of a potential biological control agent (BCA), but they provide little information on the BCA's potential impact. To predict high population buildup, a prerequisite of biocontrol impact, studies are needed that assess the effect of environmental factors on vital rates of a BCA across the environmental gradient of the BCA's suitable habitats, especially for the region where the BCA is considered for field release. We extended a published species distribution model with climate-dependent vital rates of *Ophraella communa*, a recently and accidentally introduced potential BCA of common ragweed, *Ambrosia artemisiifolia* in Europe. In field and laboratory experiments, we collected data on climate-dependent parameters assumed to be the most relevant for the population buildup of *O. communa*, i.e., temperature driving the number of generations per year and relative humidity (RH) determining egg hatching success. We found that *O. communa* concluded one generation in 334 cumulative degree days, and that egg hatching success strongly decreased from > 80% to < 20% when RH drops from 55% to 45% during the day. We used these values to spatially explicitly project population densities across the European range suitable for both *A. artemisiifolia* and the beetle and found that the present distribution of the beetle in Europe is within the range with the highest projected population growth. The highest population density of *O. communa* was predicted for northern Italy and parts of western Russia and western Georgia. Field observations of high impact on *A. artemisiifolia* with records of 80% aerial pollen reduction in the Milano area since the establishment of *O. communa* are in line with these predictions. The relative importance of temperature and RH on the population density of *O. communa* varies considerably across its suitable range in Europe. We propose that the combined statistical and mechanistic approach outlined in this paper helps to more accurately predict the potential impact of a weed BCA than a species distribution model alone. Identifying the factors limiting the population buildup of a BCA across the suitable range allows implementation of more targeted release and management strategies to optimize biocontrol efficacy.

Key words: *Ambrosia artemisiifolia*; bioclimatic range; biocontrol insect; biological invasions; demography; *Ophraella communa*; range prediction; relative humidity; temperature; weed biocontrol.

INTRODUCTION

Biological invasions by alien plant species can result in devastating impacts on the invaded ecosystems (Vilà et al. 2011). Accordingly, sustainable management of invasive alien plant species is considered one of the biggest challenges conservation biologists will face in the next decades (Kettenring and Adams 2011). Classical biological control of weeds, i.e., the use of specialist natural enemies from the native range to reduce densities of invasive alien plant species below an economic and ecological threshold, is considered as one of the most

suitable management options against invasive alien plant species, owing to its effectiveness and relatively high environmental safety (Müller-Schärer and Schaffner 2008, Winston et al. 2014). Predicting the impact of BCAs on the target plant populations remains, however, a challenge in weed biological control (Heimpel and Cock 2018, Paynter et al. 2018, Schwarzländer et al. 2018). Insect population growth is highly dependent on weather, which makes climate suitability an important part of the selection process of weed BCAs (Zalucki and Van Klinken 2006, Robertson et al. 2008). So far, most attention has been given to habitat suitability of a potential biological control candidate (Hoelmer and Kirk 2005, Mukherjee et al. 2011, Sun et al. 2017, 2018). Gassmann (1996), however, argued that the crucial attribute for successful biological control is high population

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buildup of the BCA, as only high densities of the herbivore insect population are expected to result in significant impact on the populations of the target weed (Myers and Sarfraz 2017, Rand et al. 2017, McEvoy 2018). This is supported by the fact that successful biological control of invasive alien plant species is usually linked to population outbreaks of the natural enemies, during which they may reach densities several orders higher than known from their native range (Gassmann 1996, Müller-Schärer and Schaffner 2008). A better understanding of the factors affecting the population dynamics of weed BCAs will thus be key for improving the prediction of their potential impact across the area invaded by the target plant.

Temperature and relative humidity (RH) are generally considered to be the most important climatic factors affecting the population buildup of insects (Odum 1983). Temperature is an essential climatic factor driving insect population densities and is thus used for pest predictive modeling in the agricultural context (Venette 2015, Johnson et al. 2016, Magarey and Isard 2017, Blum et al. 2018). Besides temperature, RH is also known to strongly influence insect demography, with low RH often resulting in reduced survival or female fitness (Zhou et al. 2010a, Holmes et al. 2012, Wigglesworth 2012). Insect eggs may be particularly sensitive to low RH (Sabelis 1985, Schausberger 1998) as they are immobile and have a large relative surface area, which makes them prone to desiccation (Krysan 1976, Wigglesworth 2012). Numerous studies have shown that low RH negatively affects egg hatching rate of insects from a wide range of taxa (e.g., Sabelis 1985, Chaudry and Alikhan 1990, Bethke and Redak 1996, Byrne et al. 2002, Simelane 2007, Lu and Wu 2011). Within the physiological limits, temperature affects insect population density primarily via developmental time, which may prevent a species to complete its life-cycle or reduce the number of generations in multivoltine species (Milbrath et al. 2014, El Iraqi and Hmimina 2016). In contrast, RH is likely to influence population density by affecting the numbers that develop per generation. For example, Byrne et al. (2002) concluded that the reason for the poor establishment and variable impact of a chrysomelid BCA, *Gratiana spadicea* Klug, in the introduced range was more likely drought stress than temperature, since RH dropped below the calculated lethal humidity for eggs each month of the year.

The accuracy of population density estimation depends on detailed and long-term systematic monitoring, which requires considerable efforts (Zeng et al. 2015). As an easier and quicker method, species distribution models (SDMs) have been proposed to predict also population densities (Oliver et al. 2012), since SDMs reflect the extent to which local environments meet the niche requirements of the species and thus a species' overall performance (Thuiller et al. 2014). However, the relationship between suitability predictions and population densities often showed uncertainty and

contradicting results (Thuiller et al. 2014). Oliver et al. (2012) found a significant positive relationship between habitat suitability and population density for both butterflies and birds, while Csergő et al. (2017) showed that the population growth rate of 34 plant species was not correlated with climate suitability.

Keith et al. (2008) and Gallien et al. (2010) suggested combining statistical and mechanistic models as a two-step approach to make reliable and robust predictions. Following this, we start with published SDMs and explicitly incorporate the environmentally (temperature and RH) dependent vital rates (developmental time and hatching success) of a BCA that we experimentally assessed to improve the prediction of the BCA's population density, and ultimately impact within the eco-climatically suitable area. We deliberately kept the mechanistic part simple to provide a quick method to increase the meaningfulness of an SDM. This work is based on the premise that consideration of the effects of temperature and RH on the population buildup of a BCA in areas suitable for both the target weed and the herbivore allows us to make testable and hopefully more accurate predictions regarding the impact of the BCA in the introduced range than estimates based on SDMs only.

We explored the above mentioned effects with the invasive alien plant *Ambrosia artemisiifolia* L. (Asteraceae), or common ragweed, and one of its potential BCAs, the North American leaf beetle *Ophraella communa* LeSage (Coleoptera: Chrysomelidae), which was accidentally introduced and first reported in Europe in 2013 (Müller-Schärer et al. 2014). *Ambrosia artemisiifolia* has particularly raised awareness for invasive alien plant species in Europe (Kettunen et al. 2009). The main issue with *A. artemisiifolia* is its production of a large number of highly allergenic pollen, resulting in huge health costs through decreased quality of life and productivity of the sensitized population (Burbach et al. 2009, Smith et al. 2013, Mouttet et al. 2018, Müller-Schärer et al. 2018). Furthermore, it is a major agricultural weed, especially in spring-sown crops (Burbach et al. 2009, Smith et al. 2013, Müller-Schärer et al. 2018).

Classical biological control has been successfully applied against *A. artemisiifolia* in China, using the accidentally introduced *O. communa* and the deliberately released stem-galling moth *Epiblema strenuana* Walker (Zhou et al. 2014). *Ophraella communa* can reach up to six or seven generations per year in southern China (Zhou et al. 2014) and four or five generations per year in Japan (Yamanaka et al. 2007). The difference is likely due to temperature differences along the latitudinal gradient. In Europe, *O. communa* starts laying eggs on *A. artemisiifolia* as soon as the first seedlings emerge in early April, indicating that temperature might be a main driver for voltinism in this invaded range. Under laboratory conditions, female *O. communa* enter reproductive diapause under short-day conditions (12 h daylight) and

at a temperature of 20°C (Zhu et al. 2012). Zhou et al. (2010a) showed that a decrease in constant RH from 90% to 60% reduced the survival rate of *O. communa* eggs by approximately 30%, while other life stages were less affected (9% lower larval survival and 2% lower pupal survival at 60% RH compared to 90% RH). In Europe, some areas invaded by *A. artemisiifolia* have RH values that are considerably lower than those studied by Zhou et al. (2010a), e.g., <30% during the daytime in central Hungary. Hence, Europe urgently needs better prediction on the relative importance of temperature and RH on the population buildup of *O. communa*.

Here, we asked (1) how does temperature affect the development rate of *O. communa* and thus the number of generations per year before the observed initiation of the reproductive diapause in the suitable area in Europe, (2) how does RH affect the egg hatching success of *O. communa* and thus the population buildup within and across generations, (3) what spatially explicit variation in abundances do we expect for *O. communa*, and (4) what is the spatially explicit relative contribution of temperature and RH to population densities of *O. communa* in the environmentally suitable area in Europe? The overall objective of our two-step approach was to improve with limited additional resources the predictiveness of the pre-release impact assessment for weed BCAs and to identify the specific factors limiting their population buildup, which would allow a more targeted release and management strategy.

MATERIAL AND METHODS

Study species

Ambrosia artemisiifolia is a North American Asteracean that has invaded areas outside its native range in all continents except Antarctica. In Europe, the annual plant has been considered a weed since the early 1920s (Csontos et al. 2010). It is invasive in more than 30 countries (Essl et al. 2015) and has reached the status of a flagship invader because of its impact on human health (Sheppard et al. 2006). Up to date, *O. communa* has been found in Europe predominantly in and close to the Po plain (Augustinus et al. 2015, Lommen et al. 2017), which is a relatively warm and moist area compared to other parts of Europe invaded by *A. artemisiifolia* (Chapman et al. 2017, Sun et al. 2017). In 2017, *O. communa* has also been recorded from Slovenia and Croatia (M. Cristofaro, *personal observations*). *Ophraella communa* overwinters as adults. In northern Italy, the leaf beetle reaches three to four generations and females were observed to lay eggs from April to August (B. Augustinus and S. T. Lommen, *unpublished data*). The cessation of oviposition in northern Italy in early September, when day length is approximately 13 h and average temperature starts dropping below 20°C, is in line with the experimental studies on the initiation of reproductive diapause in *O. communa* (Zhu et al. 2012).

Both adults and larvae feed on the green parts of *A. artemisiifolia* plants, which can result in defoliation rates of up to 100% before the monoecious plants form flowers, preventing pollen and seed production (Müller-Schärer et al. 2014). In Northern Italy, *O. communa* has been shown to reduce populations on a local scale (Lommen et al. 2018) and, since the arrival of the beetle, airborne *A. artemisiifolia* pollen counts have dropped by 80%, which cannot be explained by meteorological factors or land use changes (Bonini et al. 2015a,b).

Effect of temperature and relative humidity on vital rates of Ophraella communa

Effect of temperature on developmental time in the field.—The temperature-dependent developmental time of *O. communa* from egg to adult was experimentally assessed at five sites along an altitudinal gradient of 1,100 m in the Southern Alps, approximately 50 km north of the Milan area, in the summer of 2016. We followed two cohorts of egg batches (one starting end of June, one starting early August). Potted *Ambrosia artemisiifolia* plants with freshly laid eggs were individually caged and brought out to the field sites, which we visited weekly to count the number of eggs (hatched or unhatched), pupae, and adults (see Mouttet et al. [2018] for further details). Temperature-dependent pre-oviposition time of *O. communa* was assessed in an experiment in July 2016 at the same sites as described before. Ten newly emerged females were released together with 10 males in a 1 × 2 × 1 m cage with 12 *A. artemisiifolia* plants, in two cages per site. We recorded the first date of egg deposition.

To assess the temperature conditions required for a complete generation, we measured temperature and relative humidity data locally in 5-min intervals inside and outside of the cages with climate data loggers, (Elektronik AG, Leer, Germany). In addition, we collected weather data from a local weather station (Arconate, of the Servizio Meteorologico Regionale Lombardia), which is ~7.5 km away from the lowest experimental site. The locally collected weather data were considerably different from the weather station data, with more extreme values (higher temperature, lower RH) during the warmest times of sunny days. For the analysis and projection of our climate-dependent data, we chose to use the weather station data, since the available gridded climate data are based on weather station data, rather than on land surface or leaf surface temperatures and RH. We estimated the temperatures for the different sites by reducing the temperatures of the weather station by 0.65°C per 100 m altitudinal gain (ICAO 1993), which is well in line with the temperature attenuation per 100 m calculated from the measures taken with the climate data loggers (0.69°C).

We estimated the mean generation time by calculating the mean cumulative degree days (CDD) for every replicate by counting the average number of days until adult emergence and added the CDD for the mean

pre-oviposition period to it. CDD were calculated using the single sine wave method (Roltsch et al. 1999), with 13.34°C as the minimum development threshold temperature for all immature stages (Zhou et al. 2010b). To calculate the standard error (SE) of the CDD, we first estimated SEs for the developmental period from egg to adult and for the pre-oviposition period using 1,000 bootstrap replicates, respectively. As we found no reports of a relationship between the duration of the two periods of *O. communa* development, we considered them as independent and thus used the sum of the two SEs to represent the SE of the CDD over one generation.

Effect of relative humidity on the egg hatching rate.—The effect of RH on egg hatching rate, defined here as the percentage of fertilized eggs that successfully hatch, was determined in a growth-chamber experiment at the University of Fribourg. *Ambrosia artemisiifolia* plants were grown from seeds collected in Busto Arsizio, Italy, in 2015 and 2016. Seeds were germinated in closed Petri dishes on moist filter paper in a climate chamber at 18–26°C, with a photoperiod of 16:8 (light:dark). After germination, seedlings were transplanted in standard potting soil and kept in the biosecurity greenhouse at University of Fribourg, with a light regime of 16:8 (light:dark) and temperatures of 13–29°C. *Ophraella communa* were collected in Grugliasco, northern Italy, in September 2016 and reared in the quarantine facility of the Biology Department, University of Fribourg, at 26°C during the day and 17°C during the night, at 60% RH and a daylight regime of 16:8 (light:dark).

Three days before treatments were set up, 12 *A. artemisiifolia* plants in the vegetative state (8–12 leaves) were exposed to *O. communa* adults (20 females and 20 males) of various ages in a cage and daily inspected for newly laid egg batches. To prevent insects from crawling into the soil, we covered the top of the pot with a filter paper disc before exposure to *O. communa* adults. Small leaves were removed to ensure that the egg-infested leaves were suitable for the experiment. Leaves with at least one egg batch consisting of more than 10 eggs were cut off the plant at the leaf petiole with a sharp scalpel blade and randomly assigned to a treatment. Leaves with egg batches with <10 eggs were discarded.

Of 50-mL Falcon tubes (Fisher Scientific, Hampton, New Hampshire, USA) were filled with water and sealed with Parafilm (Bernis Company, Neenah, Wisconsin, USA). The Parafilm was punctured with a needle and the petiole of a leaf with eggs was inserted into the tube, sealing the hole. The tubes with leaves were put in a holder for 50-mL tubes. The holders stood on a plastic plate, of which the borders were lined with double-sided sticky tape to prevent larvae from crawling away. The tubes were placed in two KB 8400 FL incubators (Termaks, Bergen, Norway) with programmable humidity, light and temperature functions.

Each RH treatment was conducted with at least 15 replicates. The driest RH treatment was based on the

climate data recorded between mid and end of August from a site in the Pannonian plain (data from the weather station at Hodmezovasarhely, Hungary), one of the warmest and driest regions of the *A. artemisiifolia* distribution in Europe. The incubators were programmed in order to match the hourly variation in RH and temperature under natural conditions as closely as possible (Appendix S1: Figs. S1 and S2). The additional RH treatments were set at the RH of the driest treatment plus 7%, 14%, 17%, 20%, and 24%, respectively (Appendix S1: Fig. S3), while temperature and light regimes were kept identical among treatments. The light regime was set to mimic the daytime in Hungary in late July (14:10 light:dark). We measured egg hatching rate across the six RH treatments, with the treatments randomly assigned to one of the two incubators. Each RH treatment lasted 12 d. Data from one run had to be omitted from the analysis because of technical problems with the incubator.

After assigning the egg batches to a treatment, they were inspected daily and their status (alive, dead, hatched, and unfertilized) recorded. We scored eggs as “dead” if they turned black, as “hatched” when a hole was found in the egg and the egg was empty, and as “unfertilized” when the eggs became flat without turning black. Hatching success was calculated as the percentage of hatched eggs relative to fertilized eggs (sum of hatched and dead eggs). The experiments ran from March through July 2017.

For validation of our treatments, temperature and RH were measured with loggers (ELV TDF 128) in each incubator every 5 minutes. Due to technical limitations of the incubators, we did not get an exactly evenly spaced RH range. To account for this variation, we averaged all measured RH values measured from 14:30 to 15:30 by the data loggers in the middle of the incubator. We fitted generalized linear mixed models (GLMM) using the lmer function of the lme4 package (Bates et al. 2015) using the RH treatments as a fixed factor and incubator and date of start of the replicate as random factors. As response variables we tested hatching time (number of days from egg deposition until first hatching egg of batch), hatching interval (number of days from first to last egg hatching within a given batch) and egg batch size using a Poisson distribution, and hatching success using a binomial distribution. Gompertz models have been used to describe the effect of environmental factors on egg hatching success (Omkar and Mishra 2010, Quiroz et al. 2015). We fitted a three-parameter modified Gompertz model to the experimental RH data to determine the hatching success with the formula

$$HS_i = f_i(RH_i) = (1 - \alpha) \times e^{(-\beta \times e^{(-\gamma \times RH_i)})} + \alpha \quad (1)$$

where i refers to the selected month ($i = 4-8$; April–August), α is the baseline of hatching success that is assumed to have a maximum value of 1, β denotes the displacement across the x -axis (RH of the month i) and

γ is the rate of increase (Gompertz 1825). The method of least squares was used to fit the Gompertz model and optimal-fit parameter estimates were obtained using the Nelder Mead algorithm in *optim*, a general purpose optimization function of *stats* package (R Core Team 2018). To estimate the confidence intervals of the three parameters of the Gompertz model, 1,000 bootstrap estimates were performed using the boot function of the *boot* package (Canty and Ripley 2017). The Akaike Information Criterion (AIC) was used to select the most appropriate model. We found that the Gompertz model results in a lower AIC than a logistic function, with 170.74 and 884.71 for Gompertz and logistic model, respectively. We thus chose the Gompertz model for computing hatching success, as lower AIC values indicate more information preserved in the model and thus greater model performance.

Modeling population density

Number of generations of Ophraella communa.—To estimate the number of generations of *O. communa* across its suitable area in Europe, we used the above obtained average CDD, based on a base temperature T_{base} of 13.34°C (Zhou et al. 2010b) for the period from the egg stage to adult emergence of *O. communa*, and added the accordingly calculated CDD for the pre-oviposition period to achieve the CDD for one generation, since earlier results show a highly significant linear relationship between developmental time and temperature (Zhou et al. 2010b). The number of generations (G) was calculated for every month or the whole growing season, using the formula

$$G_i = \frac{\bar{T}_i \times \text{days}}{\text{CDD}_{\text{bootstrap}}} \quad (2)$$

where i refers to the selected month ($i = 4-8$; April–August), \bar{T}_i is the average temperature of the month i , $\text{CDD}_{\text{bootstrap}}$ refers to the 1,000 bootstrap estimates. SE of the generation was therefore calculated based on the above 1,000 bootstrap estimates (Appendix S2: Fig. S1).

Relative humidity estimation and hatching rate of Ophraella communa across the European range.—We used monthly average RH and monthly minimum and maximum temperature derived from CRU CL2.0 data sets (New et al. 2002) at 10-min spatial resolution (~20 km closer to the equator) to estimate the RH in the afternoon of each day, i.e., at 15:00, based on the method proposed by Kriticos et al. (2012). We used the RH at 15:00, which was the driest hour in the field measurements in the Pannonian plain and in the measurements of the weather station in Hodmezovasarhely, and because it is indicative for the driest 6 hours of the day (B. Augustinus, *personal observation*). The climatic data are considered from April to August, i.e., the egg-laying period of *O. communa* in Europe. The egg hatching rate

was therefore calculated based on the above obtained Gompertz formula and estimated RH (Appendix S2: Figs. S2 and S3).

Abundances of Ophraella communa.—We calculated the potential maximum population density of *O. communa* in Europe using the average climate of the total egg laying period (April–August) and the average climate per month. For this, we assumed no shortage of the host plants and no effects of natural enemies. To consider monthly variation, population density was calculated for every month separately, using the number of overwintering females or females of the previous month, the number of eggs per female, hatching rate and the number of generations per month. The values for August were then used as the final population density (PD) and thus abundance (model I), using the formula

$$\text{PD}_i = G_i \times \frac{\text{PD}_{i-1}}{2} \times 25 \times \text{HS}_i, \quad (3)$$

$$\text{PD}_{\text{mod1}} = \text{PD}_8 \quad (4)$$

where i is the selected month ($i = 4-8$; April to August), for the first month of the growth season, April, we considered the number of overwintering females is 1 as a start simulation point. Thus, we assumed that the number of overwintering females was the same across the suitable area in Europe. The average number of eggs laid per female was assumed to be 25, based on previous studies (Yamazaki et al. 2000, Fukano et al. 2016). The relationship between suitability from SDM (using the data from Sun et al. 2017) and population density of *O. communa* calculated from model I was also evaluated.

To explore the relative importance of the average temperature and RH on the population density of *O. communa*, we modeled the population density based on the average temperature and RH from April to August (model II), using the formula

$$\text{PD}_{\text{mod2}} = f_{\text{pd}}(\bar{T}_a, \overline{\text{RH}}_{1500}) = \frac{25 \times f_h(\overline{\text{RH}}_{1500})^{G_{\bar{T}_a}}}{2} \quad (5)$$

where $f_{\text{pd}}(\bar{T}_a, \overline{\text{RH}}_{1500})$ refers to the population density function of average temperature and average RH at 15:00, $f_h(\overline{\text{RH}}_{1500})$ is the Gompertz function of average RH for hatching success, and $G_{\bar{T}_a}$ is the number of generations calculated based on the average temperature from April to August with $\text{CDD}_{\text{bootstrap}}$. SE of the population density (PD_{mod2}) is calculated based on the 1,000 bootstrap replicates (Appendix S2: Fig. S4). To test for the agreement between the model I and II, we computed the correlation between the predictions obtained from the two models (see Appendix S2: Figs. S4–S6).

Relative importance of temperature and RH on population density.—The relative importance can be derived from

the slope of temperature (slope_T) vs. the slope of RH (slope_{RH}), using the following formula (Eqs. 6–8):

$$\text{slope}_T = \frac{f_{pd}(\overline{T}_{av} + 1, \overline{RH}_{1500}) - f_{pd}(\overline{T}_{av} - 1, \overline{RH}_{1500})}{2(T_{\max} - T_{\min})} \quad (6)$$

$$\text{slope}_{RH} = \frac{f_{pd}(\overline{T}_{av}, \overline{RH}_{1500} + 1) - f_{pd}(\overline{T}_{av}, \overline{RH}_{1500} - 1)}{2(RH_{\max} - RH_{\min})} \quad (7)$$

$$\begin{aligned} &\text{Relative importance of average temperature } (T\%) \\ &= \frac{\text{slope}_T}{\text{slope}_T + \text{slope}_{RH}} \times 100 \end{aligned} \quad (8)$$

The relative importance of average temperature and RH are first presented in a heat map and then transferred into a spatial map.

All analyses were done within the predicted suitable range of both *A. artemisiifolia* and *O. communa* in Europe, using the raster layer obtained from Sun et al. (2017). All analyses were performed using R statistical software, version 3.5.0 (R Core Team 2018).

RESULTS

Effect of temperature on the developmental time of *Ophraella communa*

Based on a T_{base} of 13.34°C (Zhou et al. 2010b), *O. communa* developed from egg to adult in 280.93 ± 6.64 CDD (mean \pm SE) and females started laying eggs after 53.11 ± 4.45 CDD, resulting in a complete generation of 334.04 ± 11.09 CDD.

Effect of relative humidity on egg hatching rate of *Ophraella communa*

RH significantly affected the egg hatching success of *O. communa* (generalized mixed model, $P < 0.001$, $z = 8.75$; further details provided in Appendix S3). The curve of egg hatching success starts at a plateau of approximately 20% egg hatching rate below 45% RH, followed by a steep incline from 20–80% egg hatching rate between 45% and 55% RH, and then reaches a plateau of ~90% egg hatching rate from higher than 55% RH (Fig. 1; Table 1). The Gompertz model explains 30% of the variation in hatching rate with RH (Fig. 1).

In contrast to egg hatching rate, egg hatching time (linear mixed model, $t = -1.495$, $P = 0.536$) or hatching interval (linear mixed model, $t = -1.376$, $P > 0.231$) were not significantly affected by RH. Also, egg batch size did not differ among RH treatments (linear mixed model, $t = -0.019$, $P > 0.979$; see Appendix S3).

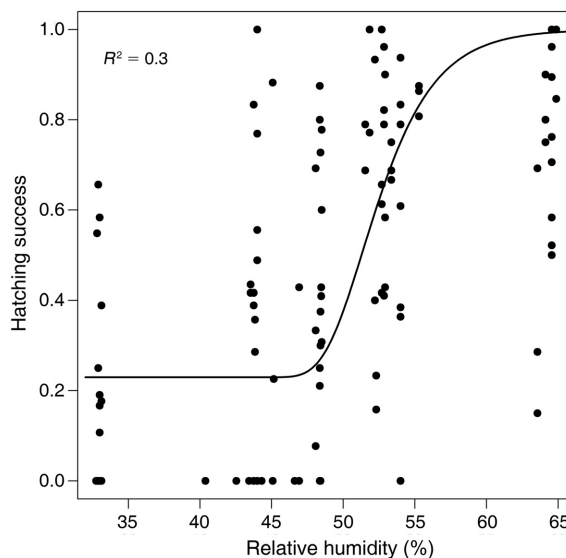


FIG. 1. Gompertz curve (solid line) fitted to the hatching rates determined in the experimental relative humidity study. Each dot represents an egg batch.

Estimated population density of *O. communa* across Europe

The highest average hatching rate of *O. communa* across its suitable area in Europe was found north of the Alps, in northern Italy, Slovenia and along the east coast of the Black Sea in Russia and Georgia, and the highest number of generations was predicted for central and northern Italy, northern Serbia, northern Bulgaria, southern Romania and Georgia (Fig. 2). In general, hatching success was negatively correlated with number of generations ($df = 3165$, $P < 0.001$, $\text{cor} = -0.25$).

The highest population density of *O. communa* was predicted for northern Italy and parts of western Russia and western Georgia (Fig. 3). The predicted population density of *O. communa* based on monthly temperature and monthly RH (model I, Eq. 4) is highly positively correlated with average temperature and average RH (model II, Eq. 5) for the period of April to August ($P < 0.001$, $\text{cor} = 0.87$; Appendix S2: Fig. S6). Our results also showed that the suitability level derived from SDM explained a significant, but still very low part of the variation of the population density of *O. communa* ($P < 0.001$, $R^2 = 0.03$; Appendix S2: Fig. S7).

TABLE 1. The optimal parameters of the Gompertz model that fit relative humidity (RH) data to determine the hatching rate with their standard errors (SE) and 95% bias-corrected accelerated (BCa) confidence intervals (CI).

Parameter	Original	SE	5% BCa CI	95% BCa CI
α	0.23	0.1	0.15	0.46
β	1.1×10^8	0.33	1.1×10^8	1.1×10^8
γ	0.36	0.16	-0.06	0.37

Average temperature contributed more than RH to population density of *O. communa*, when RH was above 52% at 15:00, while average RH was a key climatic factor when it was below 48% at 15:00 (Fig. 4). We found that the best climatic conditions to achieve a high population density of *O. communa* are 23°–25°C (average temperature, April–August) and 53%–65% (average RH, April–August) at 15:00 (Appendix S2: Fig. S8). This information was then used to map the relative importance of the two climatic factors on the population density of *O. communa* within its suitable area in Europe (Fig. 5). Population density of *O. communa* in the Apennines, north of the Alps, north of the Dinaric Alps, in Romania and along the Black Sea coast of Russia and Georgia is shown to be primarily affected by temperature, while population density south of the Massif Central, south of the Dinaric Alps, in Serbia, western Georgia and a small part of western Russia is predicted to be largely affected by RH (Fig. 5).

DISCUSSION

Our study reveals that both temperature and RH affect vital rates of *O. communa* and that adding physiologically-based demographic data to a SDM results in predictions of significant variation in the population

density of *O. communa* across the climatically suitable regions in Europe. The currently invaded range by *O. communa* in Northern Italy is predicted to support one of the highest population growth rates in Europe, which is in line with our observation of 80% pollen reduction in this area (Bonini et al. 2015a,b). Other regions that appear particularly suitable for high population densities are the warm and moist areas in western Georgia and the Krasnodar region. Our findings suggest that both temperature and RH affect population dynamics, but that the relative importance of these two environmental variables varies across the suitable range.

Impact of temperature and RH on vital rates of *O. communa*

In our field experiments, *O. communa* completed a generation from egg to reproductive adult in 334.04 ± 11.09 CDD, which is similar to the earlier experiments by Zhou et al. (2010b), which suggested it would take 307.20 CDD. The discrepancy in these values could be explained with the nature of the different studies. First, Zhou et al. (2010b) did not include the CDD of the pre-oviposition period. Secondly, we describe the results of field experiments, while the experiments of

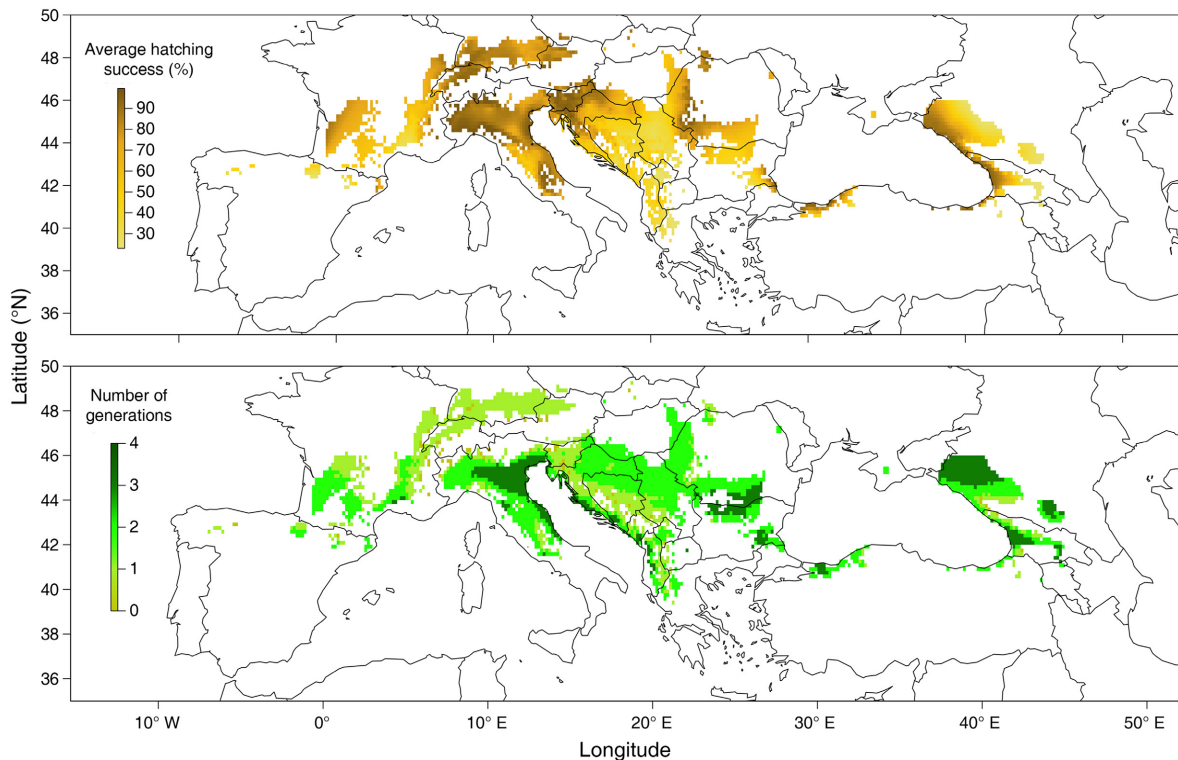


FIG. 2. Average hatching rate of *Ophraella communa* during the growth period from April to August (top), and number of generations of *O. communa* in August (below) across the European range climatically suitable for both *Ambrosia artemisiifolia* and *O. communa*.

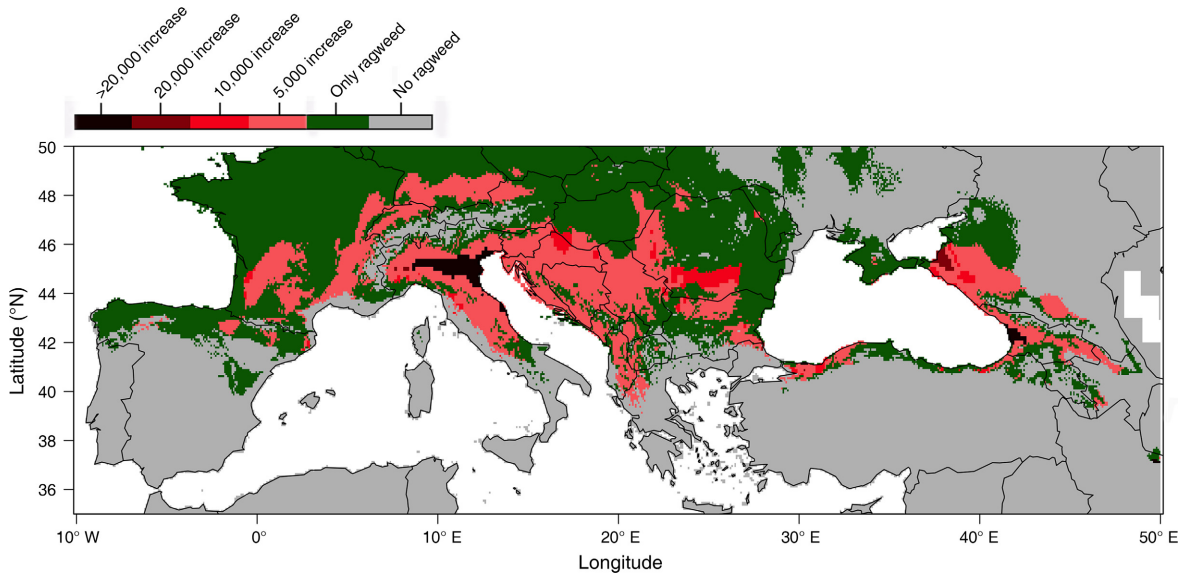


FIG. 3. Population density of *Ophraella communa* based on average relative humidity and relative temperature from Model II (Eq. 5). Gray color indicates the area not suitable for both *A. artemisiifolia* and *O. communa*; green color indicates the area suitable for *Ambrosia artemisiifolia* but not for *O. communa*; reddish colors indicate the area suitable for both *A. artemisiifolia* and *O. communa*: the darker the reddish color, the higher the density.

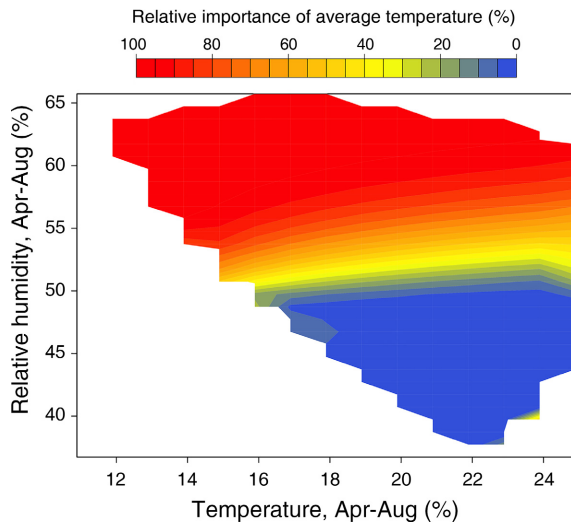


FIG. 4. Heat map of relative importance of temperature vs. relative humidity (given as percentage importance of temperature) across the suitable European area of both *Ambrosia artemisiifolia* and *Ophraella communa*. Values are means. Red color represents a higher importance of temperature (April–August) and blue color represents a higher importance of relative humidity (April–August) on the population density of *O. communa*.

Zhou et al. (2010b) were conducted under constant temperatures in a laboratory environment. In a field experiment with fluctuating temperatures and solar exposure, insects can adjust their body temperatures by their behavior like hiding from the sun or basking (Eigenbrode et al. 2015). The sigmoid form of the fitted curve

for the relationship between RH and egg hatching rate showed a strong decrease when RH dropped below 55% during the driest time of the day (see Fig. 1). In laboratory experiments using constant RH levels, Zhou et al. (2010a) found that egg hatching success of *O. communa* was significantly higher at 75% and 90% RH, compared to 60% RH. In the area in Europe that is climatically suitable for *O. communa*, average RH does not reach such high average values, largely because of a significant drop in RH during daytime. In order to approximate field conditions, we included daily variation in our treatments. We found a hatching rate of >85% at RH of 65%, which is considerably higher than that found by Zhou et al. (2010a), who report a hatching rate of $55.6\% \pm 1.6\%$ at 60% RH and $84.5\% \pm 1.3\%$ at 75% RH.

We used weather station data for our estimations since the readily available gridded climate datasets are based on weather station data. The climate data we measured in the field, however, showed more extreme values than the values of nearby weather stations. The shaded data loggers used to obtain these data were placed in between the plants to display the temperature and RH experienced by the insects. Weather stations follow a protocol that provides standardized measurements of temperatures on a global scale, but they measure air temperature, not foliage or land surface temperatures (Mendelsohn et al. 2007). Using land surface or foliage surface temperatures might improve predictions of the insect’s demography, as it did for population models of the olive fruit fly (*Bactrocera oleae* Rossi) (Blum et al. 2015) and cotton bollworm, *Helicoverpa armigera* Hübner (Blum et al. 2018). When making predictions

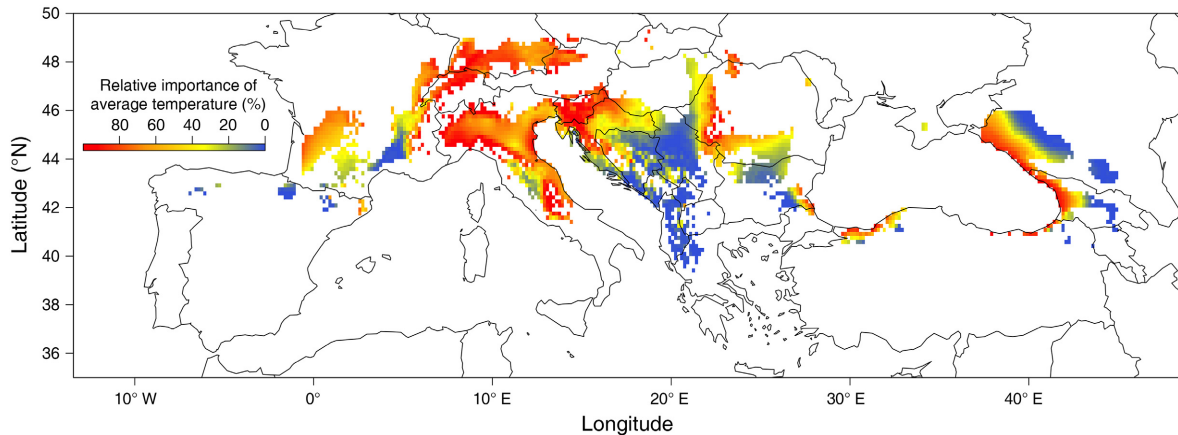


FIG. 5. The relative importance of average temperature vs. average relative humidity (given as percentage importance of temperature) across the suitable European area of both *Ambrosia artemisiifolia* and *Ophraella communa*. Red color represents a higher importance of average temperature (April–August) and blue color a higher importance of average relative humidity (April–August) on the population density of *O. communa*.

for specific areas and population densities, this discrepancy in temperature and RH should be considered.

The effect of RH on egg hatching rate has been estimated for various insect species (Schaber et al. 1975, Bethke and Redak 1996, Simelane 2007, Norhisham et al. 2013), but the demographic consequences have only been assessed in a few cases (Chaudry and Alikhan 1990, Byrne et al. 2002). For example, Lu and Wu (2011) showed that low humidity had a detrimental effect on *Apolygus lucorum* (Meyer-Dür) (Heteroptera: Miridae) egg hatching rate, resulting in a lower intrinsic capacity of increase (r_m) and finite rate of increase (λ). They used this knowledge to explain outbreak events of this pest of cotton, especially after heavy rain. Bearing in mind the considerable effect of RH on predicted *O. communa* population growth, we propose to more often include RH-dependent mortality when studying the demography of insect BCAs. The correlation between estimates for average RH over April–August (model II, Eq. 5) and average RH per separate month (model I, Eq. 4) is relatively high (0.87, see Fig. S4), indicating that trends in relative importance of temperature and RH are stable over the whole period. As *O. communa* was detected in 2018 in the northern parts of the Balkan Peninsula in Slovenia and Croatia (M. Cristofaro, *personal communication*), our predictions regarding its population density can probably be tested soon.

To illustrate the approach of combining SDMs with experimental assessments of the climate dependency of vital rates, we focused on the effect of two climatic variables on selected vital rates of *O. communa*. While the laboratory data by Zhou et al. (2010a,b) suggest that temperature particularly affects the development time and RH primarily the egg hatching rate of *O. communa*, other abiotic or biotic factors may also affect its population dynamics. For example, density-dependent mortality at later developmental stages through competition

and predation may compensate for a high egg hatching rate. It should be noted, though, that *O. communa* does not yet have specialized enemies in its introduced range (Müller-Schärer and Schaffner 2008). Nevertheless, as all introduced species interact with resident species across different trophic levels, predictions on population densities of BCAs should also consider consequences of potentially climate- or habitat-dependent biotic factors (Van der Putten et al. 2010).

Predicting climate suitability for biological control agents and their abundances

A common approach to assess habitat suitability of BCAs is to estimate its potential range using SDMs (Trethowan et al. 2011, Sun et al. 2017). SDMs are purely numerical tools, combining species observations with environmental estimates and projecting these over a novel range (Elith and Leathwick 2009). In the case of *O. communa*, habitat suitability level explained a significant but a very low part of the variation in density in our study, suggesting the notion that habitat suitability based on SDMs may be an unreliable proxy for population dynamics (Thuiller et al. 2014). However, as the impact of an invasive species, such as a classical BCA, is often described as the product of its distribution, abundance, and the per capita effect on the target plant (Parker et al. 1999), abundance is an important factor that needs to be taken into account if one wants to improve predictions on the impact of potential BCAs (Gassmann 1996). Mechanistic models are often used to analyze the mechanisms underlying the spatial pattern of population dynamics (Vinatier et al. 2011). However, only a few studies attempted to link statistical and mechanistic methods (Ehrlén and Morris 2015). For example, Kearney and Porter (2009) reviewed how physiologically based SDMs can be developed for different organisms in

different environmental contexts; and Buckley (2007) showed how geographic variation in traits and life histories influences lizard population densities.

In summary, we propose that our approach allows a simple projection of the population growth at a given site in the suitable area relative to other sites that the BCA is able to colonize, of the region that is considered for field release, or relative to a site where we already know the population growth and/or the impact of the BCA. Furthermore, our approach allows us to analyze the relative importance of changes in temperature and RH affecting demography of the BCA, especially in view of inferring management decisions.

Management implications

Our study revealed that the projected population growth of *O. communa* in its currently colonized area in northern Italy is among the highest in Europe, together with areas in western Georgia and the Krasnodar region, where *A. artemisiifolia* is also highly invasive (Reznik 2009). The high *O. communa* densities observed in Northern Italy since its detection in 2013 and the concomitant 80% reduction in airborne pollen concentrations cannot be explained by meteorological factors (Bonini et al. 2015a,b). Hence, our findings suggest that *O. communa* will be able to drastically reduce pollen production and related health costs also in western Georgia and the Krasnodar region, provided that the beetle is able to actively colonize these regions. Considering the benefit of *O. communa* in other parts of Europe (Bonini et al. 2015a,b, Mouttet et al. 2018), a risk-assessment of human-assisted dispersal of the beetle in these regions should be considered.

A way to further increase the impact of *O. communa* on *A. artemisiifolia* in Europe is then to adopt a mass rearing program, as it is currently practiced in China (Zhou et al. 2009). Targeted mass releases of beetles could be envisaged in areas where low RH during a certain period in spring may slow down the population growth of *O. communa*. For example, parts of southeastern France, which harbor high *A. artemisiifolia* densities and are characterized by relatively dry conditions in April, may be potential target areas for mass releases in May.

In other regions, where RH is limiting population establishment and/or population density throughout the season, successful biological control of *A. artemisiifolia* may require introducing a different, more drought-resistant strain of *O. communa*, or of a different BCA, which is less susceptible to low RH. An example for such a region is the Pannonian plain in Hungary, where *A. artemisiifolia* is a particularly problematic weed (Kórmíves et al. 2006). For areas predicted to have lower *O. communa* densities and that are more sensitive to temperature, e.g., North of the Alps, one can test for the possibility to develop a cold-tolerant/resistant strain. Zhou et al. (2013) recently studied the potential of *O. communa* to adapt to cold temperatures to assess the

possibility of an expansion toward northern China. Their results indicate that cold hardiness of *O. communa* can be promoted by cold acclimation in the previous generation, and that it might counterbalance reduced survival in the next generation, when insects are tracking their host plants into colder climates.

CONCLUSIONS

We propose combining statistically based SDM with the experimental assessment of climate-dependent vital rates for improving the prediction of the potential population growth of BCAs. Our results on *O. communa* show that the relative importance of climatic factors affecting population growth greatly differs spatially across the range that is climatically suitable for both the plant invader and its BCA. From a management perspective, we advocate the proposed combined approach as a step forward to improve predicting the impact in weed biological control programs as well as to increase impact by conducting informed management.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2003/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hs0r9e4>