OENO One
VINE AND WINE OPEN ACCESS JOURNAL
By IVES International Viticulture & Enology Society

DOI: https://doi.org/10.20870/oeno-one.2023.57.1.7250
OPEN ACCESS

ORIGINAL RESEARCH ARTICLE

Exploring future changes in synchrony between grapevine (*Vitis vinifera*) and its major insect pest, *Lobesia botrana*

Victorine Castex[1], Iñaki García de Cortázar-Atauri[2], Martin Beniston[1], Jérôme Moreau[3], Mikhail Semenov[4], Markus Stoffel[1,5,6] and Pierluigi Calanca[7]

[1] Institute for Environmental Sciences, Climate Change Impacts and Risks in the Anthropocene (C-CIA), University of Geneva, Switzerland
[2] INRAE, US1116 AgroClim, Avignon, 84914, France
[3] Université de Bourgogne Franche-Comté, UMR 6282 Biogéosciences, Equipe Ecologie-Evolutive France, and Centre d'Études Biologiques de Chizé, UMR 7372, CNRS & La Rochelle Université France
[4] Rothamsted Research, Harpenden, AL5 2JQ, United Kingdom
[5] Department F.A. Forel for Environmental and Aquatic Sciences, University of Geneva, Switzerland
[6] Department of Earth Sciences, University of Geneva, Switzerland
[7] Agroscope, Agroecology and Environment, Switzerland

*correspondence: victorine.castex@gmail.com

Associate editor:
Annette Reineke

Received:
9 November 2022
Accepted:
23 January 2022
Published:
13 February 2023

ABSTRACT

The European grapevine moth (*Lobesia botrana*) is one of the major pests of the grapevine (*Vitis vinifera*) in Europe. The phenology of both the insect pest and the plant has already changed over the last decades in response to rising temperatures, with a tendency towards an earlier development. The impact of a warming climate, among other factors, could alter matches in phenology between two trophic levels, being either beneficial or detrimental to V. vinifera. As a consequence, when considering a European latitudinal transect, the changes toward synchrony or a mismatch are not fully understood. In this study, we applied the results of sequential models to simulate the phenological development of *V. vinifera* from dormancy to physiological maturity of Chardonnay or a similar grape variety. Likewise, we simulated the phenology of *L. botrana* with a process-based voltinism model. Both models were calibrated and validated in previous studies. The present study aims at simulating the future evolution of both trophic levels under changing climatic conditions at four representative European locations by using quasi-transient climate scenarios up to the year 2100 that consider the RCP4.5 and RCP8.5 greenhouse-gas forcing pathways. Although some physiological adaptations could alter these results, simulations of synchrony under climate change are crucial for the adaptation of grape cultivation and varieties. This modelling work seeks to improve our understanding of the probable shifts in the timing and spatial distribution of the plant-insect interactions in a warmer climate and how this may impact their synchrony. A risk index of damage has been implemented for the different sites and greenhouse gas forcing trajectories. Results suggest an increasing damage risk for *V. vinifera* close to the timing of harvests in northern Europe. They also point to increasing mortality rates of the fourth generation of *L. botrana* in southern Europe, where temperatures will increasingly reach the upper thermal limit for insect development.

KEYWORDS: Phenological models, climate change scenarios, trophic interactions, synchrony, risk, voltinism

INTRODUCTION

The phenology of plants and insects is primarily dictated by temperature (Caffarra *et al*., 2012; Prevéy *et al*., 2017), but also by other climatic factors such as photoperiod and precipitation. Ample observational evidence exists that reveals such links between temperature and the phenology of various European plants that generally lead to earlier or later physiological development according to varieties or locations (Caffarra and Eccel, 2010; Martínez-Lüscher *et al*., 2016; Menzel *et al*., 2020; Ramos and Martínez de Toda, 2022). Temperature is also identified as the dominant abiotic factor affecting herbivorous insects (Bale and Hayward, 2010; Nelson *et al*., 2013; Roditakis and Karandinos, 2001; Tzanakakis *et al*., 2017) and their life-history traits (Corcket *et al*., 2017). Related to this, previous work has shown that increasing temperatures are affecting the physiology, abundance, distribution and phenology of insect herbivores (Kistner, 2017; Singer and Parmesan, 2010).

The life cycle of pests is closely related to host plant phenology, usually showing a high degree of synchrony across the season due to their long coevolution (Welch and Harwood, 2014). Climate change could disrupt this synchrony in phenology between plants and insects if the response to warming does not occur in parallel (Ayres and Lombardero, 2000; Caffarra *et al*., 2012; Reineke and Thiery, 2016; Van Asch *et al*., 2007). This could lead in the first instance to an incapacity for insect pests to feed or lay eggs on the host plants. An increasing mismatch between plant and host phenology would have consequences on agricultural production and implications for plant protection, potentially reducing the pressure of pests on the vines in some areas or seasons but increasing the risks of pest damage in others (Castex *et al*., 2020; Martín-Vertedor *et al*., 2010; Thiéry and Moreau, 2005).

A sector in which such changes would be of high relevance is viticulture. Grapevine (*Vitis vinifera*) is a perennial crop of high cultural and economic value worldwide. The possibility to anticipate the likely impacts of climate change on the phenology of grapevine and its pests is of crucial importance for any adaptation process. Numerous studies address the impacts of climate change on grapevine phenology at various scales and for different regions (Caffarra and Eccel, 2011; García de Cortázar-Atauri *et al*., 2017; Ramos and Martínez de Toda, 2022). Among these, studies at larger scales often have focused on the climatic suitability of grapevine, considering both early and late ripening varieties (Fraga *et al*., 2016; Malheiro *et al*., 2010; Morales-Castilla *et al*., 2020; Nesbitt *et al*., 2022; Parker *et al*., 2013). Phenological models for *V. vinifera* have been developed and validated using historical observations (García de Cortázar-Atauri *et al*., 2017; Morales-Castilla *et al*., 2020; Parker *et al*., 2011; Parker *et al*., 2013; Parker *et al*., 2020).

Many pests can cause damage to grapevines, but the European grapevine moth (*Lobesia botrana*, Denis and Schiffermüller) (Lepidoptera: Tortricidae) is the most widespread (Amo-Salas *et al*., 2011; Delbac and Thiéry, 2016; Reineke and Thiéry, 2016). *L. botrana* is a multivoltine species, undergoing two to four generations per year depending on climate and latitude (Martín-Vertedor *et al*., 2010). The first generation (G1) of *L. botrana* generally impacts *V. vinifera* less than subsequent generations, as buds and flowers do not enable the development of eggs and larvae quite as well as for later generations. The second (G2) and third (G3) generations are the more damaging as eggs and larvae can develop properly on berries (Moreau *et al*., 2009; Thiery, 2008). When climatic conditions allow its development, a fourth (G4) generation can be observed that can totally compromise the harvest (Milonas *et al*., 2001; Thiery, 2008; Thiéry *et al*., 2014). Changing climatic conditions have been shown to affect the developmental rates and population dynamics of *L. botrana* (Caffarra *et al*., 2012; Gilioli *et al*., 2016; Gutierrez *et al*., 2012, 2018; Martín-Vertedor *et al*., 2010; Thiéry and Moreau, 2005). These effects could be further enhanced under higher CO_2 concentrations, for example through an increase in food intake and damage to leaves (Becker *et al*., 2022; Reineke and Selim, 2019). If some generations are more damaged than others, protection measures can be necessary for all generations when the economic thresholds are reached (Vassilou *et al*., 2009).

However, mismatches and overlaps between the trophic levels (i.e., plants and insects) are key issues when it comes to better understanding the impacts of warming temperatures on the food-web system and its possible adaptation mechanisms (Ayres and Lombardero, 2000). Models are powerful tools to evaluate the effects of climate change on trophic interactions between the host (*V. vinifera*) and the pest (*L. botrana*). A rich variety of approaches can be found in the scientific literature, including, for example, process-based demographic models (PBDMs) that describe population dynamics (Gutierrez and Ponti, 2013; Ponti *et al*., 2018; Wermelinger *et al*., 1991). Generic and/or large-scale phenological models (Baumgärtner *et al*., 2012) have been used to simulate the impacts of warming temperatures on *L. botrana*. Other models like the CLIMEX model (Beddow *et al*., 2010) have been employed to simulate the occurrence of the key pest stages around the time of harvest. In a previous work (Castex *et al*., 2020) we described a new multi-voltinism model adapted to *L. botrana* (Lobesia Generic Model or LGM), using a large compilation of phenological observations throughout Europe. We calibrated and validated the model showing that it is possible to represent *L. botrana* multi-voltinism at different European locations with a single set of parameters.

This work aims at exploring the impacts of possible future climates on the interaction between pest (*L. botrana*) and host (*V. vinifera*) development by using validated phenological models and applying a range of climatic scenarios. We use the LGM approach (Castex *et al*., 2020) for *L. botrana* and a combination of the BRIN model (Garcia de Cortazar-Atauri, 2009) and Wang and Engel's (1998) curvilinear beta function (García de Cortázar-Atauri *et al*., 2010) to simulate *V. vinifera* development. In addition, we implement a risk index of damage that quantifies the synchrony between *L. botrana* and its host, *V. vinifera*, specifically for the mature stage of *V. vinifera* that can be parasitized by the second (G2) and third (G3) generations of *L. botrana* according to latitude. We target in particular the maturity of *V. vinifera* and the peak of *L. botrana*'s adult flights of the third generation representing 50 % of its distribution (or G3_50). We assume that there is a high risk of damage whenever G3_50 appears in a ±15 day time window around the period of maturity.

To illustrate the impacts of climate change in different European vineyards, we used climatic scenarios from four sites spanning a latitudinal range of more than 10 degrees (from 36.7°N to 47.2°N), namely Stäfa (Switzerland), Avignon (France), Yecla and Sanlucar (both Spain). We used both the RCP4.5 and RCP8.5 concentration pathways (IPCC, 2013) to assess the response of plant and pest phenologies. A broad range of grapevine varieties are currently cultivated in Europe, each characterized by its own thermal requirements (Jones, 2007). For comparison purposes, we nevertheless limit our analysis to Chardonnay, one of the best-studied grape varieties (Wolkovich *et al*., 2018) and a proxy for early ripening varieties. Finally, we discuss how this work can contribute to a reduction of the impacts of current agricultural practices on the environment by limiting the use of phytosanitary treatments by adapting plant protection measures and varieties to new climate conditions.

MATERIAL AND METHODS

1. Sites

We used published observational datasets (Castex *et al*., 2020) from four sites located along a climatic transect running from Southern Europe to the Alpine region (Figure 1 and Table 1). The extreme latitudes are Sanlucar (Spain, 36.7°N; location 1 in Figure 1) and Stäfa (Switzerland, lat. 47.2°N; location 4 in Figure 1), giving a geographic extent of 10.5 degrees of latitude. The two other sites, Yecla (Spain, 38.6°N; location 2 in Figure 1) and Avignon (southern France, 43.9°N; location 3 in Figure 1) are located between the northern and southern sites.

At Stäfa, the northernmost site, the climate can be classified as temperate oceanic with a mean annual temperature of around 11 °C (referred to as cool climate in our study) according to the Köppen classification (Peel *et al*., 2007). At Avignon (15 °C), Yecla (14.5 °C) and Sanlucar (16.5 °C), the climate can be classified as a hot summer Mediterranean climate (referred to as "warm climate" in our study). All complementary information related to observed data, data providers and meteorological data for each observation site are available in ESM1.

2. Climate change projections

We considered local climate change scenarios consistent with the representative concentration pathways (RCP) 4.5 and 8.5 (IPCC, 2013). To account for uncertainties related to the choice of Global Climate Models (GCMs), we considered 5 representative GCMs available from the CMIP5 data repository (Taylor *et al*., 2012): EC-Earth, GFDL-CM3, HadGEM2-ES, MIROC5, and MPI-ESM-MR. A preliminary analysis suggests that these GCMs reflect most of the climate uncertainty characterizing the CMIP5 ensemble. Furthermore, these 5 GCMs provide a good overlap of the range of climate projections provided by a selection of GCMs used in the CORDEX experiment (Jacob *et al*., 2014).

Following Semenov and Stratonovitch (2015), we developed local-scale projections for each RCP and GCM spanning the years 2011–2100 with the help of the LARS-WG weather generator. For local-scale projections, we used

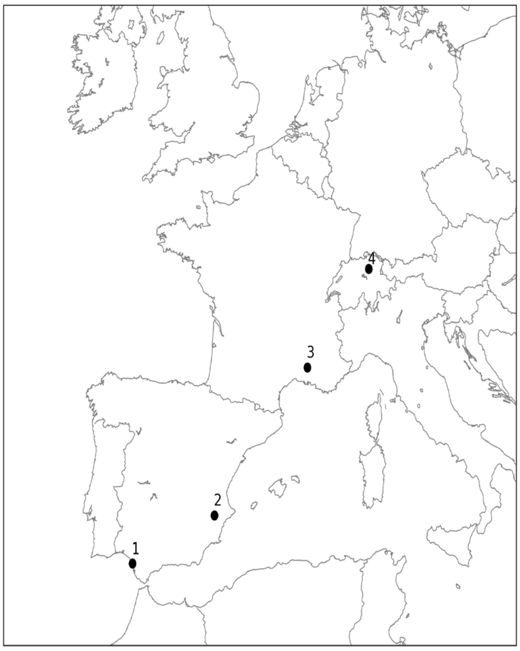

FIGURE 1. Map of the study sites in Europe with the selected sites 1—Sanlucar; 2—Yecla; 3—Avignon and 4—Stäfa (produced with MakeMap from an open source code).

daily mean, minimum and maximum temperature but we only used daily mean temperature for the analysis (ESM1). For each site, we trained LARS-WG using ancillary weather data covering the period 1981-2017 (Stäfa), 1990–2017 (Avignon), 1996-2017 (Yecla) and 2004–2017 (Sanlucar). Statistical tests incorporated in LARS-WG, in particular, the Kolmogorov–Smirnov test and the t-test (Semenov *et al*., 1998; Semenov and Stratonovitch, 2015), indicated a good performance of the weather generator (no significant differences at $p < 0.05$, in most cases even $p < 0.01$, between statistics obtained from observed data and statistics inferred from the simulated data). We specified the climate change signal required to generate data for 2011-2100 based on changes in monthly statistics derived from the output of each GCM. In practice, we generated quasi-transient time series for 2011–2100 using the climate change signal of successive, non-overlapping 10-year time windows (2011-2020, 2021-2030, …, 2091-2100).

3. Phenological Models

3.1. Phenological model for Lobesia botrana

According to climate and latitude, a multivoltine species such as *L. botrana* can complete from two (in northern parts of Europe) to four (in southern parts of Europe) generations per year (Martín-Vertedor *et al*., 2010). The first generation (G1) is usually seen as causing less damage than the second (G2) and third (G3) generations, as eggs and larvae of the last generations develop better on mature grapes. A fourth (G4) generation can be observed only in southern regions of Europe, where and when climatic conditions enable such a development (Vassiliou, 2009). This last generation is not always recorded as it occurs during or after harvest time and generally does not require monitoring or protection measures.

The model used in this study is the Lobesia Generic Model (LGM), developed by Castex *et al*. (2020). LGM assembles and adapts existing model components allowing the simulation of representative stages of development (10 % and 50 % of the male flights—see ESM2 for details) of an adult population from the end of the diapause in early spring to the last flight in autumn. In the calibrated version of Castex *et al*. (2020), LGM only requires a single set of parameters and a single response function to temperature, represented by the curvilinear Wang and Engel function (Castex *et al*., 2020; ESM 3). The equations and parameters used to simulate overwintering and adult development are available in ESM4a and ESM 4b.

Note that LGM assumes that the emergence of the first adult generation from diapause (G1) in spring (northern hemisphere) cannot occur for days whose duration is less than 12 hours, corresponding to the day of year (DOY) 78 (March 18) on average over our latitudinal transect (Baumgärtner *et al*., 2012; Castex *et al*., 2020). The model further assumes the end of the development of the last generation in synchrony with the maturity stage (harvest) of *V. vinifera* (Figure 2), based on the premise that a generation developing after maturity will not be able to feed on *V. vinifera* and will enter in diapause. All results and validation of the model were summarized in a previous study and available in ESM 5.

3.2. Phenological model for Vitis vinifera

Vitis vinifera is characterized by various phenological stages describing its development. In this study, we focused on budbreak (BBCH 09), flowering (BBCH 65), veraison (BBCH 85), and physiological maturity (BBCH 89) assuming that this last stage also defines the harvest date (Bloesch and Viret, 2008; Hess *et al*., 1997).

Various phenological models exist in the literature to describe grapevine development (Garcia de Cortazar-Atauri *et al*., 2017) but we selected a sequential model that allows the calculation of the entire cycle from dormancy until maturity. This model combines the BRIN model (Garcia de Cortazar-Atauri, 2009), which simulates the occurrence of budbreak by taking into account dormancy, and Wang and Engel's (1998) curvilinear beta function to simulate flowering, veraison, and maturity (García de Cortázar-Atauri *et al*., 2010) (ESM 4b). All simulations of the phenological development of *V. vinifera* were carried out on the PMP5 – Phenological Modeling Platform 5.7 (Chuine *et al*., 2013). To simplify the analysis, we limited our attention to the Chardonnay grape variety, which is commonly found throughout much of Europe. Concerning the parameterization of the model, we refer to ESM 5.

3.3. Assumptions made by combining the trophic levels

We present the conceptual modelling framework for examining the interactions between pests and hosts in Figure 2, emphasizing the structure of the phenological models, but also showing the relevant phenological phases, the key variables and the functions used. In this context, it is important to note that the two phenological models adopt the same temperature response function (Wang and Engel, 1998) to represent plant and insect development (see ESM4b).

In practical terms, we made several assumptions to simplify the analysis of the interactions between *L. botrana* and *V. vinifera*:

1- We defined synchrony between the pest and the host with respect to the time when adults of *L. botrana* can be hosted on *V. vinifera.* Similarly, we assumed a mismatch (or asynchrony) if *L. botrana* development was limited by the absence of a corresponding stage in *V. vinifera*.

2- We assumed a single variety of *V. vinifera*, namely Chardonnay, as a proxy for early ripening varieties that can support even the earliest generation of *L. botrana*.

3- Voltinism of *L. botrana* was measured with the 10 % (Gn_10) and 50 % (Gn_50) of each generation of adults. In this study, we focused on the 10 % and 50 % of the generation when referring to the beginning of the generation and the highest concentration of the population respectively.

4- The risk of damage on V. vinifera is important with the 2nd and 3rd generations of L. botrana. In this study, we focused

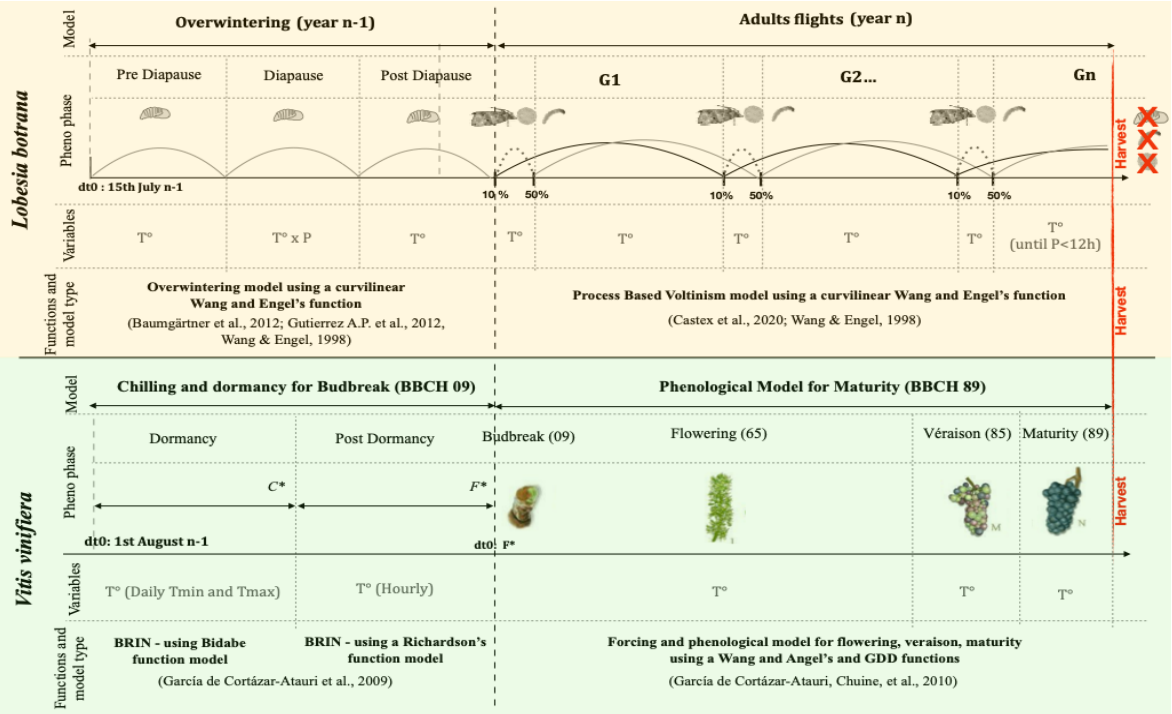

FIGURE 2. Conceptual modelling framework adopted to combine the life cycles of the grapevine moth (*Lobesia botrana*) and the grapevine (*V. vinifera*). The model assumes that the cohorts of *L. botrana* that have not invaded the berries at the time of harvest will not be able to feed anymore and will eventually enter into diapause. The scheme shows the 10 % and 50 % thresholds of each adult generation targeted by LGM, the subsequent stages (eggs, larvae, chrysalids, etc.) and important dates in the seasonal development of V. vinifera. G1, G2 … Gn = 1st, 2nd …generation of *L. botrana*; T° = temperature; P = photoperiod and dt0 = overwintering (for *L. botrana*). For *V. vinifera*, C* and F* are the critical thresholds for chilling (dormancy) and forcing (post-dormancy) accumulation respectively.

on the damage (by eggs and larvae) of the last generation (G3) that overlaps with the maturity of *V. vinifera.*

5- We assumed that excessively high temperatures (above 32 °C) could imply a lower rate of development for the last generation of L. botrana (Castex et al., 2020; ESM 3).

6- The study only looked at changes in behaviour but did not consider the physiological adaptation of the pest and its host to climate change.

3.4. Risk index of damage

An added value for this study has been the elaboration of a risk index of damage of *L. botrana* on *V. vinifera* combined with a projection under future climate change. We look at the risk of damage to *V. vinifera* by considering whether there is an overlap or not of the first, second and third generations of *L. botrana* with the flowering, veraison and maturity stage of *V. vinifera*, respectively. We focus on the 3rd generation of *L. botrana,* as it is known to be the most damaging (Moreau *et al.*, 2015). We calculate the risk of damage of *L. botrana* G3-50 on *V. vinifera* maturity (harvest) in relation to the temporal gap between G3-50 and maturity, assuming that the risk is high whenever the gap is less than 15 days but moderate to low whenever the gap greater than 16 days. Our assumption of a critical threshold of 15 days is based on observations that this is the time that enables *L. botrana* larvae to develop on *V. vinifera* at the maturity stage (harvest) (Moreau *et al.*, 2015) for each site. The risk is represented by the median value and defines whether the risk is high (<15 days separating G3-50 from maturity) or rather moderate to low (>16 days separating G3-50 from maturity).

RESULTS

1. Projections

Simulations of the development of *L. botrana* and *V. vinifera* under future climatic conditions were undertaken using the local-scale climate scenarios described in the previous section (EC.EARTH, GFDL.CM3, HadGEM2.ES, MIROC5 and MPI.ESM.MR). Statistics of the values for each phenological stage and for each species are described in ESM6a and ESM6b. Results are illustrated in Figure 3 and represent the mean and standard deviation obtained with the entire dataset previously described. For reasons of simplicity, we present only results for the 50 % threshold of each generation of *L. botrana*. In all cases, we summarize the output for 5 climatic models through their median values. The spread represents the data falling between the 5th and 95th percentile.

1.1. Lobesia botrana

Figure 3 illustrates that little seasonal shift exists on the date of appearance of *L. botrana* generations G1 and G2, irrespective of latitude and climate scenario. Nevertheless,

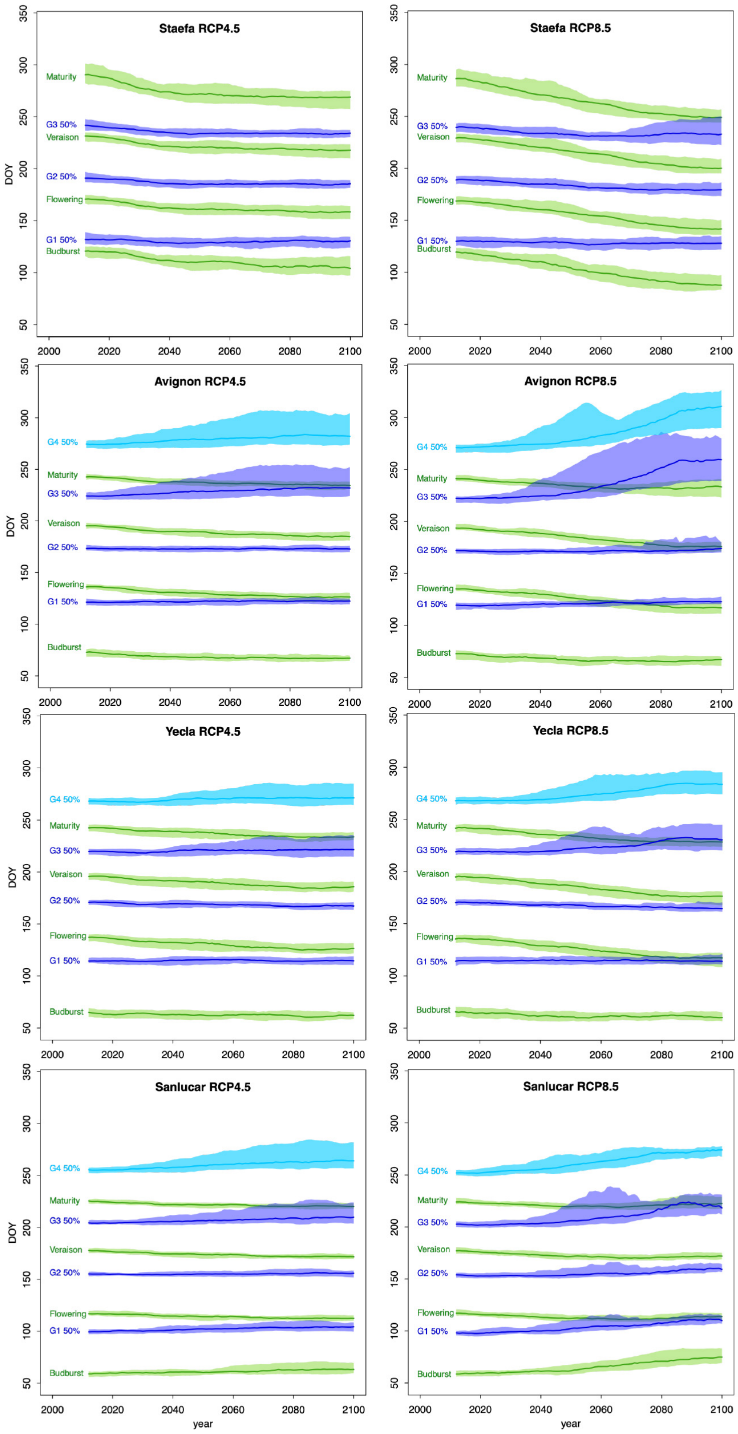

FIGURE 3. Simulation of *V. vinifera* and L. botrana phenology. From top to bottom, or north to south: Stäfa, Avignon, Yecla and Sanlucar, for RCP4.5 (left) and RCP8.5 (right). The phenological stages of *V. vinifera* from budbreak (BBCH 09) to flowering (BBCH 65), veraison (BBCH 85), and maturity (BBCH 89) are represented in green. The development of L. botrana in terms of the presence of 50 % of adults for generations 1, 2 and 3 (or G1_50 to G3_50) is given in dark blue and the same percentage for the fourth generation (G4_50) is shown in light blue. The spread of simulations considers the data occurring between the 5th and 95th percentiles and the solid lines represent the median values.

shifts emerge with respect to the date of appearance of G3. The models simulate the appearance of a potential new generation (G4), in Avignon, Yecla and Sanlucar. This new generation is currently observed only at Sanlucar but always appears after harvest.

Under RCP4.5, the northernmost site, Stäfa, could see the emergence of a third generation (G3), with adults appearing before the date of maturity of *V. vinifera*. Under RCP8.5 the model suggests that this additional G3 could overlap with the maturity of *V. vinifera*. This new generation G3 does not develop under present climate conditions at this site.

For Avignon, Yecla and Sanlucar the model suggests little change in the date of G3_50 up to the middle of this century, but a shift toward a progressively later appearance during the second half of the century, as compared to 2010. This is more evident under RCP8.5 than under RCP4.5, as the stronger climate warming signal will eventually force temperatures to fall outside the optimum range of *L. botrana* development. More specifically, under the RCP8.5 scenario, the simulations suggest a delay of roughly 40, 15 and 20 days in G3_50 at Avignon, Yecla and Sanlucar, respectively, by the end of the century as compared to what is simulated under today's climate (Table 1).

1.2. ***Vitis vinifera***

The simulations indicate that *V. vinifera* maturity will be more sensitive to warming conditions at northern latitudes (Stäfa) compared to southern latitudes (Avignon, Yecla, Sanlucar), with an anticipation of the dates of key developmental stages of around 20 (RCP4.5) to 31 days (RCP8.5) by the end of the century (Table 1). In southern latitudes, where the climate is already warm, smaller shifts are observed. Figure 3 indicates for the end of the century either an earlier maturity by 4 days (RCP4.5) or no difference in the date of harvest (RCP8.5).

At Yecla, Avignon and Stäfa the results suggest earlier dates for all stages from budburst to maturity. These changes are more pronounced at Stäfa, showing anticipation of the harvest date of up to 30 days by the end of the century under RCP8.5 (Table 1) compared to today. On the other hand, in warmer climates such as the one characterizing Sanlucar, results point to a later budburst date (BBCH 09) in the future. This is mainly due to warmer temperatures during winter, which significantly delays dormancy breaks and also the post-dormancy period.

1.3. Interactions between ***Lobesia botrana*** and ***Vitis vinifera***

Results presented in Figure 3 suggest that the time gaps between the corresponding phenological stages of the two trophic levels could evolve at approximately the same pace across the different latitudes considered here. The simulations indicate that *L. botrana* G1 will always be in a position to feed on *V. vinifera*, as budburst will continue to occur before the appearance of G1, even under warmer conditions. The occurrence of G2 generally occurs closer to the veraison stage in the future, but with no consequences for *V. vinifera* as 50 % of G2 is predicted to appear before veraison, except for Avignon and Yecla under RCP8.5. For Avignon, Yecla and Sanlucar, the model results indicate that a fourth generation (G4) of *L. botrana* could emerge, suggesting also that this additional generation would occur after the maturity of *V. vinifera* and, therefore, would not be able to feed on early ripening varieties such as Chardonnay.

The most interesting findings concern the interactions between the G3 phase of *L. botrana* and the maturity of *V. vinifera* (BBCH 89). Under RCP4.5, the climate of Stäfa can still be considered relatively cool and both trophic levels will shift in harmony, yet with a progressive convergence of G3 toward maturity (Figure 3). On the contrary, the rapid advance of the maturity of *V. vinifera* projected for Avignon, Yecla and Sanlucar, and the delay of G3_50 simulated for both climate scenarios will challenge the development of G3 in southern Europe. Indeed, RCP8.5 simulations suggest the possibility that beyond 2060 to 2080 (depending on location), G3_50 could actually develop after maturity, with implications for the survival of such a population under the considered scenarios.

1.4. Risk of damage of ***L. botrana*** G3_50 on ***V. vinifera*** maturity

The combination of two trophic levels and the projections of future climatic scenarios allowed us to implement a risk index of overlap, highlighting the damage that *L. botrana* could exert on *V. vinifera.* Figure 4 illustrates the time gap between the appearance of key phenological stages of *L. botrana* and those of *V. vinifera* as a function of mean temperature. Negative values indicate that selected *L. botrana* stages occur ahead of the corresponding *V. vinifera* stage. A "critical" time window is set at ±15 days, representing the time window during which *L. botrana* can potentially lead to significant damage.

Figure 4 emphasises the fact that high risks are expected when the mean temperature between August to mid-October lies between 23 °C and 27 °C. With RCP4.5 such conditions emerge only at the three southern sites, but with RCP8.5, as

TABLE 1. Gap between *V. vinifera* maturity and *L. botrana* G3_10 and G3_50.

	Maturity/Harvest (BBCH 89)		*L. botrana G3_10*		*L. botrana G3_50*	
Stäfa	***-20***	***-31***	-6	0	-6	1
Avignon	*-7*	**-8**	**9**	***41***	**10**	***43***
Yecla	*-7*	**-12**	2	***20***	4	***23***
Sanlucar	-4	0	5	**16**	*7*	**19**
	RCP4.5	RCP8.5	RCP4.5	RCP8.5	RCP4.5	RCP8.5

High risk is defined when there are less than 15 days separating G3-50 from maturity. The difference in the number of days between the periods 2010–2030 and 2080–2100 for *V. vinifera* maturity and the G3_10 and G3_50 phases of *L. botrana* for two climate change scenarios (RCP4.5 and 8.5). Highlighted in italic are shifts less than 7 days, in bold shifts between 8 and 15 days, and in bold and italic shifts corresponding to more than 15 days separating the two-time horizons.

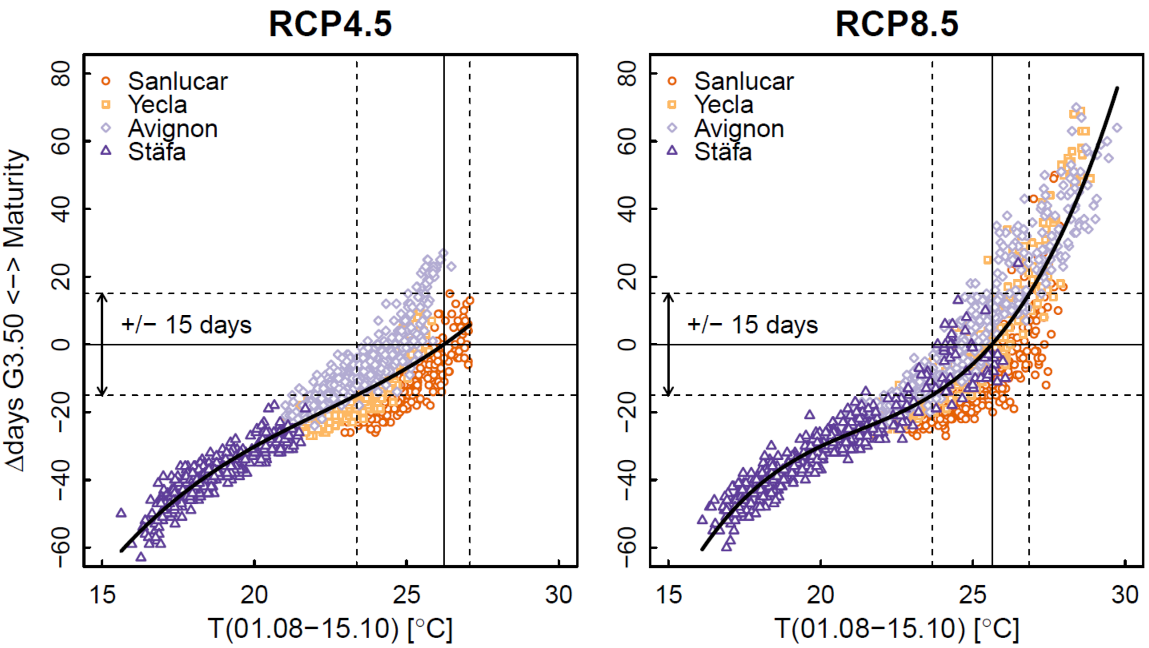

FIGURE 4. Dependence on mean temperature (period August 1st till October 14) of the risk of damage by *L. botrana* G3-50 on *V. vinifera* at maturity (harvest).

The simulations are based on RCP4.5 (left) and RCP8.5 scenarios. Different colours identify the four study sites (Sanlucar in orange, Yecla in yellow, Avignon in light blue and Stäfa in dark blue). The thick continuous line is a polynomial regression line fit to the data ensemble. The dashed horizontal lines indicate the critical time gap of +/- 15 days, which is assumed to represent the time window during which damage is potentially large. The dashed vertical lines indicate the temperatures corresponding to the beginning and end of the critical window.

warming progresses, conditions favour more frequently the synchrony between *L. botrana* G3_50 and the grapevine maturity stage at Stäfa as well. The figure also emphasized once again the fact that for the RCP8.5 scenario, very high temperatures (>32 °C, see ESM 4b) occurring at the southern sites during the second half of the century lead to a higher probability of mismatch between the two trophic levels, with a timing of *L. botrana* G3_50 well beyond the maturity period of *Vitis vinifera*. Figures for each phenological stage are described in ESM7.

In summary, projections reveal a striking change in the interactions between the trophic levels according to latitude. Table 2 provides a summary of the shifts expected by 2080-2100 as compared to the period 2010-2030 for maturity and G3_50. The numbers emphasize the opposite evolution of phenological development for *V. vinifera* and *L. botrana* at the southern sites and highlight the marked difference in the magnitude of these changes between RCP4.5 and RCP8.5.

Comparison of the changes in *L. botrana* voltinism and in maturity dates of *V. vinifera* under future projections clearly point to the risk of damage that some regions could experience in the future. Under RCP4.5 in Avignon, the risk of overlapping of *V. vinifera* maturity with 50 % of the third generations of *L. botrana* (G3) will very likely increase by 2080-2100.

At the northern latitude site (Stäfa), under RCP4.5, the gap between grapevine maturity and G3 of *L. botrana* will likely remain around 30 days and will, thus, present little risk at the time of harvest. Thus, under RCP8.5, Stäfa will only experience a moderate risk as less than 12 days are modelled between harvests and G3, compared to 45 days under RCP4.5.

DISCUSSION

1. Increasing risk of damage in Northern Europe

Despite the uncertainty of the potential biological adaptation or resilience, our results highlight increasing risks of overlaps between *L. botrana* G3_50 and the grapevine maturity at the three southernmost sites under RCP4.5 as well as at Stäfa under RCP8.5. In this regard, the combination of the results of the two phenological models with future climate projections confirm the expected northward shift of optimal conditions for both trophic levels (Rudolf and Singh, 2013; Svobodová *et al*., 2014; Thomson *et al*., 2010). A warmer climate might result in earlier or longer periods of overlap in the future, especially around 2060 at the northern sites (Figure 4).

From Avignon to the northernmost site, Stäfa, an earlier onset and shorter duration of *V. vinifera* development are projected to occur. The vulnerability of *V. vinifera* increases if the risk of overlap is higher (i.e., a smaller number of days between *V. vinifera* maturity/harvest and the occurrence of *L. botrana* G3_50) since in this case a larger presence of eggs, larvae and caterpillars of the third generation of *L. botrana*

TABLE 2. Risk of overlap between maturity (BBCH 89) of *V. vinifera* and the last generation of *L. botrana* (G3_50) under warming conditions in the future.

		RCP4.5	RCP8.5
	Mean periods	G3_50—Maturity	G3_50—Maturity
Stäfa	2010-2030	**-47**	**-45**
	2080-2100	**-33**	-12*
Avignon	2010-2030	-17	**-18**
	2080-2100	1*	**33**
Yecla	2010-2030	**-22**	**-22**
	2080-2100	11*	-14*
Sanlucar	2010-2030	**20**	**21**
	2080-2100	8*	1*

The table indicates the difference in the number of days between maturity and G3_50 for each site and each RCP for the periods 2010-2030 and 2080-2100. Positive values indicate that the maturity of V. vinifera will occur before *L. botrana* G3_50. Negative values indicate that the maturity of *V. vinifera* will occur after *L. botrana* G3_50. A median value is considered as well to determine whether the risk of damage is high (values with * <15 days) or, on the contrary, rather moderate to low (values in bold >16 days).

feeding in berries can be expected at maturity (harvest) (Thiery, 2008).

Our results generally confirm that *L. botrana* will, overall, benefit from more favourable climatic conditions for developing and feeding on its host *V. vinifera* in the future, which is expected to lead to more damage to *V. vinifera* (Reineke and Selim, 2019), especially around the harvest time. For example, at Stäfa, projections suggest no pressure of *L. botrana* G1_50 on *V. vinifera* flowering under RCP4.5, whereas pressure would be much stronger under the RCP8.5 scenario. In addition, future climatic conditions may allow the emergence of a third generation of *L. botrana* at Stäfa even under RCP4.5 (Figure 3). Under RCP8.5, the third generation of *L. botrana* would have the time to fully develop before harvest, increasing the chance of trophic overlap and ultimately negative pressures on its host.

At the southern sites (Sanlucar, Yecla and Avignon), LGM simulated a fourth generation of *L. botrana* which, at first sight, could suggest the potential for yet higher damage risks. However, this fourth generation always appears after grape maturity, a result that is governed by our choice of limiting the analysis to Chardonnay, an early-ripening grapevine variety. As illustrated in Figure 3, for varieties reaching maturity later even under future global warming conditions (e.g., Mourvèdre), the chance of matching between G4_50 and maturity would be higher. Moreover, one should bear in mind that *L. botrana* is a polyphagous insect, and could, therefore, lay eggs on other plants or other *V. vinifera* varieties even in regions where early ripening varieties such as Chardonnay are common, which would in any case allow the development of an additional generation (Thiery, 2008; Torres-Vila *et al*., 1999).

2. Towards a mismatch of trophic levels in Southern Europe

In southern Europe, both trophic levels are expected to slow down their development, as temperatures will occasionally exceed the upper thermal limit for optimal development. The extremely warm and dry conditions projected in Sanlucar for late spring, summer and early autumn can result in heat stress and further slow or inhibit the development of *V. vinifera* later in the season (Kizildeniz *et al*., 2018; Martínez-Lüscher *et al*., 2016; Morales-Castilla *et al*., 2020). This can also be explained by a longer period necessary to accumulate chilling units during warmer winters, which will eventually lead to a later emergence from dormancy (Chuine *et al*., 2016; Lavee and May, 1997, Tzanakakis *et al*., 2017).

Regarding *L. botrana,* in spite of the fact that more generations could emerge under warming conditions, its late-season development may possibly be restricted not only by photoperiod but also by temperatures that will remain outside its optimum range for development (Fraga *et al*., 2012; Gutierrez *et al*., 2018; Ramos and Jones, 2018; Reis *et al*., 2021a; Van Asch *et al*., 2007). Above optimal temperatures could induce even higher mortality rates, especially for the last generation, when mean daily temperatures exceed 32 °C. This is a temperature threshold used in the LGM (Castex *et al*., 2020) and other studies (Gutierrez and Ponti, 2013; Ponti *et al*., 2018) that inhibit the defensive capability of *L. botrana* against natural enemies (Reis *et al*., 2021a). The LGM does not consider variables such as precipitation and relative humidity which might indeed change the thresholds inducing *L. botrana* mortality.

If extremely warm conditions could potentially increase synchrony between *L. botrana* G3_50 and *V. vinifera* maturity around 2060 at Avignon for example, *L. botrana* G3_50 would no longer be able to overlap with the maturity of *V. vinifera* appearing earlier in Sanlucar. A mismatch between the two trophic levels could, thus, potentially result in higher mortality rates of *L. botrana* toward the end of the season and, thus, the parasite would be unable to feed or host on *V. vinifera* (Amo-Salas *et al*. 2011; Gutierrez *et al*., 2018). Other studies find similar results with asynchrony, especially between G3 and the veraison at the end of the century (Reis *et al*., 2021b).

In terms of risk (Figure 4 and Table 2) for *V. vinifera*, the presence of *L. botrana* G3_50 would be highly damaging at the crucial moment of harvesting by cumulating the presence of eggs, larvae and caterpillars (Thiery, 2008). If an overestimation by the mid-21st century could be inherent to the model setup, we cannot exclude the possibility of extremely warm conditions negatively impacting the reproductive performance and abundance of *L. botrana* (Iltis *et al*., 2020). Extreme heat or drought could also reduce the pressure of *L. botrana* on *V. vinifera* in the following year by reducing the diapausing population (Nelson *et al*., 2013).

3. Adaptation to climate change

Likewise, several studies reported that increased warming, CO_2 concentrations and dryness in southern Europe will likely result in a loss of viticultural suitability, whereas warming conditions could improve winegrowing conditions in northern Europe (Fraga *et al*., 2013, 2016; Moriondo *et al*., 2013; Reineke and Selim, 2019). For comparative purposes, we considered only the parameters pertaining to the Chardonnay variety in our simulations. The objective was not to analyse Chardonnay's phenology in a warmer climate, but rather to compare the voltinism of *L. botrana* at different sites with an early variety of references. In fact, the results obtained in this study suggest that early ripening varieties like Chardonnay could be cultivated in northern regions of Europe until late into this century under RCP4.5, but not necessarily under RCP8.5. Despite possibilities to improve varieties, it is likely that physiological adaptation of early-ripening varieties to warmer conditions may not be possible at all in southern Europe, implying that growers would anyway prefer to focus on growing varieties with higher thermal requirements (Morales-Castilla *et al*., 2020; Wolkovich *et al*., 2018).

However, if adaptive responses in thermal limits are expected, changes in climate variability and more frequent extreme events will make their modelling much more difficult and less predictable (Bennett *et al*., 2021). In general terms, the risk of damage will be lower in the future in southern Europe due to a higher number of days separating *L. botrana* and *V. vinifera*, especially under RCP8.5 where *L. botrana* might develop after the critical stages of development of *V. vinifera*. However, in northern Europe, the risk will increase as the number of days between *L. botrana* G2_50 and veraison or *L. botrana* G3_50 and maturity is expected to be smaller (≤10 days), leading to a strong overlap between the trophic levels and high risks of damage (Figure 4 and Table 2).

Our study only looked for the thermal aspects and their effects on phenology in relation to climate change and did not account for the evolutionary potential of *L. botrana* in terms of voltinism. Existing literature suggests that the plasticity of *L. botrana* could indeed improve its performance under warming conditions (Svobodová *et al*., 2014; Thiéry *et al*., 2014; Van Asch *et al*., 2007), resulting in an extension of its distribution range and higher abundance and survival rates (Bale and Hayward, 2010; Colinet *et al*., 2015; Sassi and Tylianakis, 2012; Thiery, 2008; Thiéry and Desneux, 2018). Since it is a polyphagous insect, *L. botrana* could lay eggs on other plants or other *V. vinifera* varieties and nonetheless develop all the following stages, thereby enabling the emergence of an additional generation (Iltis *et al*., 2020; Thiery, 2008; Torres-Vila *et al*., 1999). Considering a late-ripening variety (e.g., Mourvèdre), *V. vinifera* could be affected by a fourth generation (G4) of *L. botrana.* This points to a possible trade-off between the need to improve harvests and the need to minimize risks from pests occurring late in the season.

CONCLUSIONS

By simulating phenological changes in the life cycle of *V. vinifera* and *L. botrana* at the European scale and under warming conditions with the use of generic models, this study provides important insights for the evaluation of opportunities and risks related to synchrony and mismatches of the trophic levels of both plants and insects in a mid- to long-term (2050-2100) perspective.

In northern Europe (Stäfa), changes in climate will provide better opportunities for herbivores to feed and lay eggs on their host. The simulations highlight increasing synchrony between *L. botrana* and *V. vinifera* at sites such as Stäfa, because of an earlier exit from diapause in winter and higher rates of development. Warming conditions will allow the emergence of a new generation of *L. botrana* (increased voltinism) that could appear more frequently and an overlap with *V. vinifera* (earlier budbreak and maturity), thereby increasing the risk of possible damage, even considering the more moderate RCP4.5 greenhouse-gas scenario that projects a global temperature increase of 2 °C compared to preindustrial period.

In southern Europe (Avignon, Yecla and Sanlucar), host and pest development could become more asynchronous, especially when looking at G3 and maturity. Extremely high temperatures, like those predicted for Sanlucar, will not advance the phenology of both *L. botrana* and *V. vinifera*; they will likely develop at a slower pace and later in the season. Such changes could also induce a disruption of the food web of *L. botrana* with its host *V. vinifera* because the latter would reach maturity earlier in the season compared to today's conditions and could entail higher mortality for the third generation of *L. botrana* (G3). The last (fourth) generation that is currently observed in some parts of southern Europe could, therefore, disappear as the climate becomes too warm, thereby exceeding the upper thermal limits for optimal development. In this scenario, the obvious consequence would be the decreasing pest pressure toward the end of the growing season, at harvest time and, thus, a lower risk of damage.

Nevertheless, higher mortality of *L. botrana* also means that other varieties that are more adapted to warm climates could become more vulnerable to pest attacks in the future. The simulation of future synchrony between *L. botrana* and other varieties of *V. vinifera* at different sites and under warming conditions is, thus, expected to provide further insights into the topic and would be of high interest in the future for grapevine growers. As the rate of phenological advances seems to be more important at higher than at lower latitudes, the northern regions of France and Switzerland could, therefore, become more at risk and suffer from more rapid changes than the sites located at mid and southern latitudes (Spain) where climate has always been warm.

Even if some aspects of the life cycle of pests and hosts depend on the availability of other trophic levels and physiological adaptation, the combination of generic models adopted in this study allows us to go beyond what has been achieved in previous studies. Such biological adaptations are already observed in both species under study and could increase the uncertainty of the predictions but these issues are not the focus of the present study. The modelling of *L. botrana* at the European scale has allowed us to take a different look into the possible future expansion of voltinism and the risk of parasitism of *L. botrana* on *V. vinifera*. The findings supported the interest in combining modelling and phenological studies for future predictions. Species interactions and climate change are likely to have strong impacts on agriculture and future research should increase the combined studies at different spatial and temporal scales to improve adaptation and mitigation processes, including new agricultural practices and pest-control mechanisms.

ACKNOWLEDGEMENTS

This work was possible thanks to Denis Thierry and Amelia Caffarra for their insight during initial discussions and Vivian Zufferey for his insights during the drafting of this paper. A special thanks to J.V. Badia Ballester and Dr Josep Armengol for their support and collaboration.

Rothamsted Research receives grant-aided support from the Biotechnology and Biological Sciences Research Council through Designing Future Wheat [BB/P016855/1] and Achieving Sustainable Agricultural Systems [NE/N018125/1].

REFERENCES

Amo-Salas, M., Ortega-López, V., Harman, R., & Alonso-González, A. (2011). A new model for predicting the flight activity of Lobesia botrana (Lepidoptera: Tortricidae). *Crop Protection*, *30*(12), 1586–1593. https://doi.org/10.1016/j.cropro.2011.09.003

Ayres, M. P., & Lombardero, M. J. (2000). Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of The Total Environment*, *262*(3), 263–286. https://doi.org/10.1016/S0048-9697(00)00528-3

Bale, J. S., & Hayward, S. a. L. (2010). Insect overwintering in a changing climate. *Journal of Experimental Biology*, *213*(6), 980-994. https://doi.org/10.1242/jeb.037911

Baumgärtner, J., Gutierrez, A. P., Pesolillo, S., & Severini, M. (2012). A model for the overwintering process of European grapevine moth Lobesia botrana (Denis & Schiffermüller) (Lepidoptera, Tortricidae) populations. *Journal of Entomological and Acarological Research*, *44*(1), 2. https://doi.org/10.4081/jear.2012.e2

Becker, C., Herrmann, K., & Reineke, A. (2022). Biological control in a changing climate: Plant-mediated impact of elevated CO2 concentration on Lobesia botrana eggs and egg parasitism by Trichogramma cacoeciae. *Journal of Pest Science*. https://doi.org/10.1007/s10340-022-01545-w

Beddow, J. M., Kriticos, D., Pardey, P. G., & Sutherst, R. W. (2010). Potential global crop pest distributions using CLIMEX: HarvestChoice applications. *St. Paul, MN: University of Minnesota, HarvestChoice*.

Bennett, J. M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R., Araújo, M. B., Algar, A. C., Clusella-Trullas, S., Hawkins, B. A., Keith, S. A., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Morales-Castilla, I., & Olalla-Tárraga, M. Á. (2021). The evolution of critical thermal limits of life on Earth. *Nature Communications*, *12*(1), 1198. https://doi.org/10.1038/s41467-021-21263-8

Bloesch, B., & Viret, O. (2008). Stades phenologiques repères de la vigne. *Rev Suisse Vitic Arboric Hortic*, *40*(6), I–IV.

Caffarra, A., & Eccel, E. (2010). Increasing the robustness of phenological models for *Vitis vinifera* cv. Chardonnay. *International Journal of Biometeorology*, *54*(3), 255–267. https://doi.org/10.1007/s00484-009-0277-5

Caffarra, A., & Eccel, E. (2011). Projecting the impacts of climate change on the phenology of grapevine in a mountain area. *Grape and Wine Research*, *17*(1), 52–61. https://doi.org/10.1111/j.1755-0238.2010.00118.x

Caffarra, A., Rinaldi, M., Eccel, E., Rossi, V., & Pertot, I. (2012). Modelling the impact of climate change on the interaction between grapevine and its pests and pathogens: European grapevine moth and powdery mildew. *Agriculture, Ecosystems & Environment*, *148*, 89–101. https://doi.org/10.1016/j.agee.2011.11.017

Castex, V., Garcia De Cortazar Atauri, I., Calanca, P., Beniston, M., & Moreau, J. (2020a). Assembling and testing a generic phenological model to predict Lobesia botrana voltinism for impact studies. *Ecological Modelling-under Review*. https://doi.org/10.1016/j.ecolmodel.2020.108946

Castex, V., García de Cortázar-Atauri, I., Calanca, P., Beniston, M., & Moreau, J. (2020b). Assembling and testing a generic phenological model to predict Lobesia botrana voltinism for impact studies. *Ecological Modelling*, *420*, 108946. https://doi.org/10.1016/j.ecolmodel.2020.108946

Chuine, I., Bonhomme, M., Legave, J.-M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A., & Améglio, T. (2016). Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology*, *22*(10), 3444–3460. https://doi.org/10.1111/gcb.13383

Chuine, I., García de Cortázar-Atauri, I. G., Kramer, K., & Hänninen, H. (2013). Plant Development Models_2013. In M. D. Schwartz (Ed.), *Phenology: An Integrative Environmental Science* (pp. 275–293). Springer Netherlands. https://doi.org/10.1007/978-94-007-6925-0_15

Colinet, H., Sinclair, B. J., Vernon, P., & Renault, D. (2015). Insects in Fluctuating Thermal Environments. *Annual Review of Entomology*, *60*(1), 123–140. https://doi.org/10.1146/annurev-ento-010814-021017

Corcket, E., Giffard, B., & Sforza, R. F. H. (2017). Food Webs and Multiple Biotic Interactions in Plant–Herbivore Models. In *Advances in Botanical Research* (Vol. 81, pp. 111–137). *Elsevier*. https://doi.org/10.1016/bs.abr.2016.10.002

Delbac, L., & Thiéry, D. (2016). Damage to grape flowers and berries by Lobesia botrana larvae (Denis & Schiffernüller) (Lepidoptera: Tortricidae), and relation to larval age: Larval age and damages by Lobesia botrana. *Australian Journal of Grape and Wine Research*, *22*(2), 256–261. https://doi.org/10.1111/ajgw.12204

Fraga, H., García de Cortázar Atauri, I., Malheiro, A. C., & Santos, J. A. (2016). Modelling climate change impacts on viticultural yield, phenology and stress conditions in Europe. *Global Change Biology*, *22*(11), 3774–3788. https://doi.org/10.1111/gcb.13382

Fraga, H., Malheiro, A. C., Moutinho-Pereira, J., & Santos, J. A. (2012). An overview of climate change impacts on European viticulture. *Food and Energy Security*, *1*(2), 94–110. https://doi.org/10.1002/fes3.14

Fraga, H., Malheiro, A. C., Moutinho-Pereira, J., & Santos, J. A. (2013). Future scenarios for viticultural zoning in Europe: Ensemble projections and uncertainties. *International Journal of Biometeorology*, *57*(6), 909–925. https://doi.org/10.1007/s00484-012-0617-8

García de Cortázar-Atauri, Chuine, I., Donatelli, M., Parker, A. K., & Van Leeuwen, C. (2010). A curvilinear process-based phenological model to study impacts of climatic change on grapevine (*Vitis vinifera* L.). *Proceedings of Agro*, 907–908.

García de Cortázar-Atauri, I., Duchêne, E., Destrac-Irvine, A., Barbeau, G., De Rességuier, L., Lacombe, T., Parker, A. K., Saurin, N., & Van Leeuwen, C. (2017). Grapevine phenology in France: From past observations to future evolutions in the context of climate change. *OENO One*, *51*(2), 115. https://doi.org/10.20870/oeno-one.2016.0.0.1622

Gilioli, G., Pasquali, S., & Marchesini, E. (2016). A modelling framework for pest population dynamics and management: An application to the grape berry moth. *Ecological Modelling*, *320*, 348–357. https://doi.org/10.1016/j.ecolmodel.2015.10.018

Gutierrez, A. P., & Ponti, L. (2013). Eradication of Invasive Species: Why the Biology Matters. *Environmental Entomology*, *42*(3), 395–411. https://doi.org/10.1603/EN12018

Gutierrez, A. P., Ponti, L., Cooper, M. L., Gilioli, G., Baumgärtner, J., & Duso, C. (2012). Prospective analysis of the invasive potential of the European grapevine moth Lobesia botrana (Den. & Schiff.) in California. *Agricultural and Forest Entomology*, *14*(3), 225–238. https://doi.org/10.1111/j.1461-9563.2011.00566.x

Gutierrez, A. P., Ponti, L., Gilioli, G., & Baumgärtner, J. (2018). Climate warming effects on grape and grapevine moth (Lobesia botrana) in the Palearctic region: Climate warming effect on grape and grapevine moth. *Agricultural and Forest Entomology*, *20*(2), 255–271. https://doi.org/10.1111/afe.12256

Hess, M., Barralis, G., Bleiholder, H., Buhr, L., Eggers, TH., Hack, H., & Strauss, R. (1997). Use of the extended BBCH scale—General for the descriptions of the growth stages of mono- and dicotyledonous weed species. *Weed Research*, *37*, 433–441. https://doi.org/10.1046/j.1365-3180.1997.d01-70.x

Iltis, C., Moreau, J., Pecharová, K., Thiéry, D., & Louâpre, P. (2020). Reproductive performance of the European grapevine moth Lobesia botrana (Tortricidae) is adversely affected by warming scenario. *Journal of Pest Science*, *93*(2), 679–689. https://doi.org/10.1007/s10340-020-01201-1

IPCC (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley, Eds.; pp. 1–30). Cambridge University Press. https://doi.org/10.1017/CBO9781107415324.004

Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O. B., Bouwer, L. M., Braun, A., Colette, A., Déqué, M., Georgievski, G., Georgopoulou, E., Gobiet, A., Menut, L., Nikulin, G., Haensler, A., Hempelmann, N., Jones, C., Keuler, K., Kovats, S., … Yiou, P. (2014). EURO-CORDEX: New high-resolution climate change projections for European impact research. *Regional Environmental Change*, *14*(2), 563–578. https://doi.org/10.1007/s10113-013-0499-2

Jones, G. V. (2007). *Climate change: Observations, projections, and general implications for viticulture and wine production*.

Kistner, E. J. (2017). Climate Change Impacts on the Potential Distribution and Abundance of the Brown Marmorated Stink Bug (Hemiptera: Pentatomidae) With Special Reference to North America and Europe. *Environmental Entomology*, *46*(6), 1212–1224. https://doi.org/10.1093/ee/nvx157

Kizildeniz, T., Irigoyen, J. J., Pascual, I., & Morales, F. (2018). Simulating the impact of climate change (elevated CO2 and temperature, and water deficit) on the growth of red and white Tempranillo grapevine in three consecutive growing seasons (2013–2015). *Agricultural Water Management*, *202*, 220–230. https://doi.org/10.1016/j.agwat.2018.02.006

Lavee, S., & May, P. (1997). Dormancy of grapevine buds-facts and speculation. *Australian Journal of Grape and Wine Research*, *3*(1), 31–46.

Malheiro, A., Santos, J., Fraga, H., & Pinto, J. (2010). Climate change scenarios applied to viticultural zoning in Europe. *Climate Research*, *43*(3), 163–177. https://doi.org/10.3354/cr00918

Martínez-Lüscher, J., Kizildeniz, T., Vučetić, V., Dai, Z., Luedeling, E., van Leeuwen, C., Gomès, E., Pascual, I., Irigoyen, J. J., Morales, F., & Delrot, S. (2016). Sensitivity of Grapevine Phenology to Water Availability, Temperature and CO2 Concentration. *Frontiers in Environmental Science*, *4*. https://doi.org/10.3389/fenvs.2016.00048

Martín-Vertedor, D., Ferrero-García, J. J., & Torres-Vila, L. M. (2010). Global warming affects phenology and voltinism of Lobesia botrana in Spain. *Agricultural and Forest Entomology*, *12*(2), 169–176. https://doi.org/10.1111/j.1461-9563.2009.00465.x

Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., & Estrella, N. (2020). *Climate change fingerprints in recent European plant phenology*. *26*(4), 2599–2612. https://doi.org/10.1111/gcb.15000

Milonas, P. G., Savopoulou-Soultani, M., & Stavridis, D. G. (2001). Day-degree models for predicting the generation time and flight activity of local populations of Lobesia botrana (Den. & Schiff.) (Lep., Tortricidae) in Greece. *Journal of Applied Entomology*, *125*(9–10), 515–518. https://doi.org/10.1046/j.1439-0418.2001.00594.x

Morales-Castilla, I., García de Cortázar-Atauri, I., Cook, B. I., Lacombe, T., Parker, A., van Leeuwen, C., Nicholas, K. A., & Wolkovich, E. M. (2020). Diversity buffers winegrowing regions from climate change losses. *Proceedings of the National Academy of Sciences*, *117*(6), 2864–2869. https://doi.org/10.1073/pnas.1906731117

Moreau, J., Monceau, K., & Thiéry, D. (2015). Larval food influences temporal oviposition and egg quality traits in females of Lobesia botrana. *Journal of Pest Science*. https://doi.org/10.1007/s10340-015-0695-6

Moreau, J., Richard, A., Benrey, B., & Thiéry, D. (2009). Host plant cultivar of the grapevine moth Lobesia botrana affects the life history traits of an egg parasitoid. *Biological Control*, *50*(2), 117–122. https://doi.org/10.1016/j.biocontrol.2009.03.017

Moriondo, M., Jones, G. V., Bois, B., Dibari, C., Ferrise, R., Trombi, G., & Bindi, M. (2013). Projected shifts of wine regions in response to climate change. *Climatic Change*, *119*(3–4), 825–839. https://doi.org/10.1007/s10584-013-0739-y

Nelson, W. A., Bjornstad, O. N., & Yamanaka, T. (2013). Recurrent Insect Outbreaks Caused by Temperature-Driven Changes in System Stability. *Science*, *341*(6147), 796–799. https://doi.org/10.1126/science.1238477

Nesbitt, A., Dorling, S., Jones, R., Smith, D. K. E., Krumins, M., Gannon, K. E., Dorling, L., Johnson, Z., & Conway, D. (2022). Climate change projections for UK viticulture to 2040: A focus on improving suitability for Pinot Noir. *OENO One*, *56*(3), 69–87. https://doi.org/10.20870/oeno-one.2022.56.3.5398

Parker, A. K., Garcia De Cortázar-Atauri, I., Chuine, I., Barbeau, G., Bois, B., Boursiquot, J.-M., Cahurel, J.-Y., Claverie, M., Dufourcq, T., Gény, L., Guimberteau, G., Hofmann, R. W., Jacquet, O., Lacombe, T., Monamy, C., Ojeda, H., Panigai, L., Payan, J.-C., Lovelle, B. R., … van Leeuwen, C. (2013). Classification of varieties for their timing of flowering and veraison using a modelling approach: A case study for the grapevine species *Vitis vinifera* L. *Agricultural and Forest Meteorology*, *180*, 249–264. https://doi.org/10.1016/j.agrformet.2013.06.005

Parker, A. K., García de Cortázar-Atauri, I., Gény, L., Spring, J.-L., Destrac, A., Schultz, H., Molitor, D., Lacombe, T., Graça, A., Monamy, C., Stoll, M., Storchi, P., Trought, M. C. T., Hofmann, R. W., & Van Leeuwen, C. (2020). Temperature-based grapevine sugar ripeness modelling for a wide range of *Vitis vinifera* L. cultivars. *Agricultural and Forest Meteorology*, *285–286*, 107902. https://doi.org/10.1016/j.agrformet.2020.107902

Parker, A. K., Garcia De Cortázar-Atauri, I., Van Leeuwen, C., & Chuine, I. (2011). General phenological model to characterise the timing of flowering and veraison of Vitis vinifera L.: Grapevine flowering and veraison model. *Australian Journal of Grape and Wine Research*, *17*(2), 206–216. https://doi.org/10.1111/j.1755-0238.2011.00140.x

Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Ko¨ppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.*, 12.

Ponti, L., Gutierrez, A., Boggia, A., & Neteler, M. (2018). Analysis of Grape Production in the Face of Climate Change. *Climate*, *6*(2), 20. https://doi.org/10.3390/cli6020020

Prevéy, J., Vellend, M., Rüger, N., Hollister, R. D., Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Clark, K., Cooper, E. J., Elberling, B., Fosaa, A. M., Henry, G. H. R., Høye, T. T., Jónsdóttir, I. S., Klanderud, K., Lévesque, E., Mauritz, M., Molau, U., Natali, S. M., … Rixen, C. (2017). Greater temperature sensitivity of plant phenology at colder sites: Implications for convergence across northern latitudes. *Global Change Biology*, *23*(7), 2660–2671. https://doi.org/10.1111/gcb.13619

Ramos, M. C., & Jones, G. V. (2018). Relationships between Cabernet Sauvignon phenology and climate in two Spanish viticultural regions: Observations and predicted future changes. *The Journal of Agricultural Science*, *156*(9), 1079–1089. https://doi.org/10.1017/S0021859618001119

Ramos, M. C., & Martínez de Toda, F. (2022). Influence of weather conditions and projected climate change scenarios on the suitability of Vitis vinifera cv. Carignan in Rioja DOCa, Spain. *International Journal of Biometeorology*, *66*(6), 1067–1078. https://doi.org/10.1007/s00484-022-02258-6

Reineke, A., & Selim, M. (2019). Elevated atmospheric CO2 concentrations alter grapevine (Vitis vinifera) systemic transcriptional response to European grapevine moth (Lobesia botrana) herbivory. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-39979-5

Reineke, A., & Thiery, D. (2016). *Grapevine insect pests and their natural enemies in the age of global warming*. 12. https://doi.org/10.1007/s10340-016-0761-8

Reineke, A., & Thiéry, D. (2016). Grapevine insect pests and their natural enemies in the age of global warming. *Journal of Pest Science*, *89*(2), 313–328. https://doi.org/10.1007/s10340-016-0761-8

Reis, S., Martins, J., Gonçalves, F., Carlos, C., & A. Santos, J. (2021a). European grapevine moth in the Douro region: Voltinism and climatic scenarios. *OENO One*, *55*(2), 335–351. https://doi.org/10.20870/oeno-one.2021.55.2.4595

Reis, S., Martins, J., Gonçalves, F., Carlos, C., & Santos, J. A. (2021b). European Grapevine Moth and *Vitis vinifera* L. Phenology in the Douro Region: (A)synchrony and Climate Scenarios. *Agronomy*, *12*(1), 98. https://doi.org/10.3390/agronomy12010098

Roditakis, N. E., & Karandinos, M. G. (2001). Effects of photoperiod and temperature on pupal diapause induction of grape berry moth Lobesia botrana. *Physiological Entomology*, *26*(4), 329–340. https://doi.org/10.1046/j.0307-6962.2001.00253.x

Rudolf, V. H. W., & Singh, M. (2013). Disentangling climate change effects on species interactions: Effects of temperature, phenological shifts, and body size. *Oecologia*, *173*(3), 1043–1052. https://doi.org/10.1007/s00442-013-2675-y

Sassi, C. de, & Tylianakis, J. M. (2012). Climate Change Disproportionately Increases Herbivore over Plant or Parasitoid Biomass. *PLOS ONE*, *7*(7), e40557. https://doi.org/10.1371/journal.pone.0040557

Semenov, M. A., Brooks, R. J., Barrow, E. M., & Richardson, C. W. (1998). Comparison of the WGEN and LARS-WG stochastic weather generators for diverse climates. *Clim Res*, 13.

Semenov, M., & Stratonovitch, P. (2015). Adapting wheat ideotypes for climate change: Accounting for uncertainties in CMIP5 climate projections. *Climate Research*, *65*, 123–139. https://doi.org/10.3354/cr01297

Singer, M. S., & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: Signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions: Biological Sciences*, *365*(1555), 3161–3176.

Svobodová, E., Trnka, M., Dubrovský, M., Semerádová, D., Eitzinger, J., Štěpánek, P., & Žalud, Z. (2014). Determination of areas with the most significant shift in persistence of pests in Europe under climate change. *Pest Management Science*, *70*(5), 708–715. https://doi.org/10.1002/ps.3622

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An Overview of CMIP5 and the Experiment Design. *Bulletin of the American Meteorological Society*, *93*(4), 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1

Thiery, D. (2008). Les Tordeuses nuisibles à la vigne. *Féret, Bordeaux*, 54.

Thiéry, D., & Desneux, N. (2018). Host plants of the polyphagous grapevine moth Lobesia botrana during larval stage modulate moth egg quality and subsequent parasitism by the parasitoid Trichogramma cacoeciae. *Entomologia Generalis*, *38*(1), 47–59. https://doi.org/10.1127/entomologia/2018/0675

Thiéry, D., Monceau, K., & Moreau, J. (2014). Different emergence phenology of European grapevine moth (Lobesia botrana, Lepidoptera: Tortricidae) on six varieties of grapes. *Bulletin of Entomological Research*, *104*(03), 277–287. https://doi.org/10.1017/S000748531300031X

Thiéry, D., & Moreau, J. (2005). Relative performance of European grapevine moth (Lobesia botrana) on grapes and other hosts.

Oecologia, *143*(4), 548–557. https://doi.org/10.1007/s00442-005-0022-7

Thomson, L. J., Macfadyen, S., & Hoffmann, A. A. (2010). Predicting the effects of climate change on natural enemies of agricultural pests. *Biological Control*, *52*(3), 296–306. https://doi.org/10.1016/j.biocontrol.2009.01.022

Torres-Vila, L. M., Rodriguez-Molina, M. C., Roehrich, R., & Stockel, J. (1999). Vine phenological stage during larval feeding affects male and female reproductive output of Lobesia botrana (Lepidoptera: Tortricidae). *Bulletin of Entomological Research*, *89*, 549–556. https://doi.org/10.1017/S000748539900070X

Tzanakakis, M. E., Savopoulou-Soultani, M., Oustapassidis, C. S., Verras, S. C., & Hatziemmanouel, H. (2017). Induction of dormancy in Lobesia botrana by long day and high temperature conditions. *ENTOMOLOGIA HELLENICA*, *6*, 7. https://doi.org/10.12681/eh.13953

Van Asch, M., Van Tienderen, P. H., Holleman, L. J. M., & Visser, M. E. (2007). Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biology*, *13*(8), 1596–1604. https://doi.org/10.1111/j.1365-2486.2007.01400.x

Vassiliou, A. V. (2009). *Control of Lobesia botrana (Lepidoptera: Tortricidae) in vineyards in Cyprus using the Mating Disruption Technique*. *28*(2), 145–150. https://doi.org//10.1016/j.cropro.2008.09.013

Wang, E., & Engel, T. (1998). Simulation of phenological development of wheat crops. *Agricultural Systems*, *58*(1), 1–24. https://doi.org/10.1016/S0308-521X(98)00028-6

Welch, K. D., & Harwood, J. D. (2014). Temporal dynamics of natural enemy–pest interactions in a changing environment. *Biological Control*, *75*, 18–27. https://doi.org/10.1016/j.biocontrol.2014.01.004

Wermelinger, B., Baumgärtner, J., & Gutierrez, A. P. (1991). A demographic model of assimilation and allocation of carbon and nitrogen in grapevines. *Ecological Modelling*, *53*, 1–26. https://doi.org/10.1016/0304-3800(91)90138-Q

Wolkovich, E. M., García de Cortázar-Atauri, I., Morales-Castilla, I., Nicholas, K. A., & Lacombe, T. (2018). From Pinot to Xinomavro in the world's future wine-growing regions. *Nature Climate Change*, *8*(1), 29–37. https://doi.org/10.1038/s41558-017-0016-6.