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Review

Pest management under climate change: The importance of understanding tritrophic relations

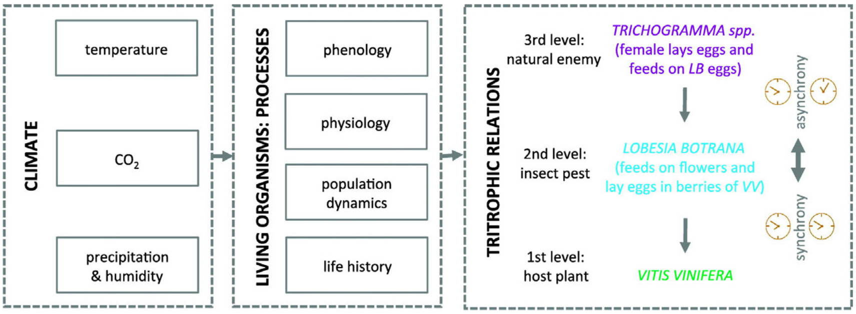
V. Castex [a,*], M. Beniston [a], P. Calanca [b], D. Fleury [c], J. Moreau [d]

[a] *Institute of Environmental Sciences, University of Geneva, Switzerland*
[b] *Agroscope, Agroecology and Environment, Switzerland*
[c] *Department of Environment, Transportation and Agriculture (DETA), Geneva State, Switzerland*
[d] *Université de Bourgogne Franche-Comté, UMR 6282 Biogéosciences, Equipe Ecologie-Evolutive, France*

HIGHLIGHTS

- Climate change might affect trophic interactions in timing and distribution.
- Warmer conditions will enhance shifts in plant and insect phenologies.
- Voltinism might increase in warmer regions previously unsuitable.
- Southern regions could become too warm in the future for optimal IPM.
- Warming conditions may change the latitudinal distribution of insect pests.

GRAPHICAL ABSTRACT



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ABSTRACT

Plants and insects depend on climatic factors (temperature, solar radiation, precipitations, relative humidity and CO_2) for their development. Current knowledge suggests that climate change can alter plants and insects development and affect their interactions. Shifts in tritrophic relations are of particular concern for Integrated Pest Management (IPM), because responses at the highest trophic level (natural enemies) are highly sensitive to warmer temperature. It is expected that natural enemies could benefit from better conditions for their development in northern latitudes and IPM could be facilitated by a longer period of overlap. This may not be the case in southern latitudes, where climate could become too warm. Adapting IPM to future climatic conditions requires therefore understanding of changes that occur at the various levels and their linkages. The aim of this review is to assess the current state of knowledge and highlights the gaps in the existing literature concerning how climate change can affect tritrophic relations. Because of the economic importance of wine production, the interactions between grapevine, *Vitis vinifera* (*1st*), *Lobesia botrana* (2nd) and *Trichogramma* spp., (*3rd*), an egg parasitoid of *Lobesia botrana*, are considered as a case study for addressing specific issues. In addition, we discuss models that could be applied in order quantify alterations in the synchrony or asynchrony patterns but also the shifts in the timing and spatial distribution of hosts, pests and their natural enemies.

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[*] Corresponding author at: University of Geneva - ISE, Boulevard Carl-Vogt 66, 1205 Geneva, Switzerland.
E-mail addresses: victorine.castex@unige.ch (V. Castex), Martin.Beniston@unige.ch (M. Beniston), pierluigi.calanca@agroscope.admin.ch (P. Calanca), Dominique.Fleury@etat.ge.ch (D. Fleury), Jerome.Moreau@u-bourgogne.fr (J. Moreau).

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Contents

1. Introduction

Plants and insects are dependent on heat and sunlight accumulation for their development. Plant phenology (the sequence of developmental stages) is directly influenced by weather and climate (temperature, photoperiod, CO_2, relative humidity, precipitation) (Bale et al., 2002; Bregaglio et al., 2013; Caffarra and Donnelly, 2011; García de Cortázar-Atauri et al., 2010). Insect pests are as well influenced directly (climatic factors) and indirectly (length of the growing season, habitat structure, food quality, overwintering, oviposition) in their development (Moreau et al., 2008; Reineke and Thiery, 2016). Previous studies have shown that changes in climatic conditions over the last three decades have already influenced interactions between plants and insects pests. Concerning future climate change, even stronger impacts on population dynamics, adaptation, limits of development and phenological stages are expected (Caffarra et al., 2012).

The Intergovernmental Panel on Climate Change (IPCC) reports that levels of CO_2 around 280 ppm prior to the industrial period have today exceeded 400 ppm and could attain up to 550 ppm in 2050, depending on emission scenario (Solomon et al., 2007). In line with this, climate models project a further increase in mean temperature for the future. They further indicate shifts in precipitation patterns and higher frequencies of extreme weather events, even if such changes are harder to predict (Edenhofer et al., 2015). As discussed in Rogeli et al. (2016), the 2015 Paris climate agreement (COP-21) aims at limiting emissions to hold global warming below 2 °C (based on the IPCC AR5 Scenario Database). In a more pessimistic scenario, an increase of 4 °C to 6 °C become probable if Paris targets are not reached.

For agriculture, the evaluation of the impacts of a changing climate on plant growth plays a key role in view of the necessity to adapt crop management (Bregaglio et al., 2013). Gregory et al. (2009) point out that integration of pests into such assessment is necessary to develop effective measures of adaptation to future climatic conditions. Higher temperatures are expected to affect not only plants and insects phenology and physiology individually, but also biological interactions between these two trophic levels (Kalinkat et al., 2015). Initially defined by Solomon (1949), the concept of “trophic interactions” refers to the predation risk for the prey. This concept can be extend to include a third level, where natural enemies act as predator of insect pest (Price, 1980). Tritrophic relations are particularly important in the context of sustainable agriculture because they are at the heart of Integrated Pest Management (IPM) (Wajnberg et al., 2016). In fact, IPM aims at using natural predators as biological control agents against insect pests.

The overarching goal of this study is to review current knowledge on how climate change can affect agricultural crops, pests and their natural enemies. Concepts and ideas are developed here referring to pests and pest management in viticulture, more specifically to the three levels of interactions where *Vitis vinifera* acts as host plant (1st level), *Lobesia botrana* as the herbivore (2nd level) feeding on *V. vinifera*, and *Trichogramma* spp., an egg parasitoid of *L. botrana*, as natural enemy (3rd level).

First, this review aims at emphasizing that under climatic change, and at different latitudes, tritrophic relations might evolve in synchrony or asynchrony according to bioclimatic regions. Secondly, considering the important range shifts that have already occurred for a number of taxa with respect to latitude and altitude in the recent past (Chen et al., 2011). It is expected that warming climate might alter tritrophic relations leading to stable, expansion or to extinction of some species, but the knowledge on their timing and distribution in the future is still unclear. This literature review aims at obtaining an overview of validated facts, models, historical and observed data in the objective to model and understand whether the expected range shifts might evolve under global warming conditions.

1.1. Climatic variables and phenology

1.1.1. Grapevine and climate

V. vinifera (*grapevine*), as a perennial plant, can provide valuable information on past climatic variations (observed phenology) allowing predictions to be made concerning future development under changing climatic conditions (Lacombe et al., 2013). In this context, climate is considered as a long-term forcing factor, while weather comprises short-term meteorological variations that are linked to local or regional specificities such as altitude, exposure to sunlight and slope orientation and modulated by the seasonality of grapevine growth (Rusch et al., 2015). All these factors will influence the accumulation of Degree Days (DD) and induce changes in the phenology and physiology (roots system, foliage and aerial system) of *V. vinifera*.

Phenology is the study of development stages of plants as a result of heat (forcing) and cold (chilling) accumulation during growing and dormancy periods. In many wine-growing European regions, the trends recorded in the last decade reveals changes in growing season temperatures and precipitation (Fraga et al., 2013). Seasonality is important as *V. vinifera* accumulates more heat and more rapidly in spring (Moriondo et al., 2013). There is now consensus that climate extremes may increase in frequency as a consequence of global warming (Beniston, 2004; Edenhofer et al., 2015). Extreme events such as prolonged summer drought, heat waves and spring frost episodes have a considerable potential to damage grapevines (Jönsson et al., 2011). In fact, they not only harm crop development directly, but can also promote the emergence of insect pests and diseases (Bale et al., 2002; Reineke and Thiery, 2015; Nagarkatti et al., 2003, Tobin et al., 2003).

1.1.1.1. Temperature. One of the most important factors affecting plant phenology is temperature. A warmer climate will lead to higher heat accumulation and to faster development of the plants. Yet, for *V. vinifera* the attention should not be limited to the growing season, because the occurrence of cold periods is important as well when it comes to chilling requirements. In Chuine (2010), the northern geographic limit for vineyards appears to be mainly related by the inability of the grape to reach full fruit maturation, while the southern limit is governed by the inability to flower owing a lack of chilling temperatures that are necessary to break bud dormancy (Caffarra and Eccel, 2010). Experts agree that current *V. vinifera* growing limits are moving because of global warming and that grapes could be cultivated in northern regions of Europe (ex. Netherlands, Poland) where climate may provide new optimal conditions for winegrowing (Cuccia et al., 2014; Svobodová et al., 2014a, 2014b).

Warmer temperature is expected to be favourable for the quality of berries. Indeed, earlier development stages and shifts in the geographic distribution of the optimum climate for each *V. vinifera* variety can create new opportunities with a slight increase of temperatures and also alter the production quantity and quality when the optimum is reached (Garcia de Cortazar-Atauri et al., 2010; Quenol et al., 2014). Milder temperatures in winter and in spring will lead to an earlier start of *V. vinifera* and a potentially longer growing season. Referring to the recent past, an earlier ripening (maturity of berries) has been observed, inducing changes in phenological, behavioural and genetical adaptation of several varieties to attacks or stress (Price, 1980). Regarding the future, anticipation of budburst by between 3 to 18 days is expected (Duchêne et al., 2010; Garcia de Cortazar-Atauri et al., 2009a; Ollat and Touzard, 2014; Touzard et al., 2016; Webb et al., 2007). Many studies demonstrate that flowering and veraison are more strongly influenced by warming than the other phenological stages (Fraga et al., 2012).

1.1.1.2. CO_2 and photosynthesis. Higher concentrations of CO_2, nitrogen (N), and carbohydrates (C) are capable of influencing *V. vinifera*, essentially by increasing photosynthesis processes (Caffarra and Eccel, 2011; Garcia de Cortazar-Atauri et al., 2009a; Reineke and Thiery, 2016; Zavala and Gog, 2015). Changes in the C:N ratio in the atmosphere will generate higher biomass production allowing a bigger growth of leaves and berries. The response of plant physiology to changes in the physical and chemical characteristics of the atmosphere (Asplen et al., 2015) might impact the leaves nutritional properties and reduce its quality (Reineke and Thiery, 2016; Zavala and Gog, 2015). In Zavala and Gog, (2015), elevated CO_2 also influences the hydraulic and thermal characteristics of leaves by reducing transpiration rates through closure of stomata. According to the impacts on maturity, an accelerated ripening in grapes is expected under elevated CO_2 (Martínez-Lüscher et al., 2016) as it has been observed in laboratory conditions.

1.1.1.3. Precipitation and relative humidity. Precipitation and extreme events (hail, frosts or drought frequency by the intensity and period of occurrence) can affect plant phenology and its physiological behaviour (leaves surface, nutrient content, chemical compounds, etc.) (Zavala and Gog, 2015), especially in the growing and ripening periods (Castex et al., 2015; Fraga et al., 2013; Rienth et al., 2014). Future precipitation patterns are hard to predict. There is, however, evidence that over the past few decades, summers in Southern and Central Europe have already become drier and seasonal patterns more variable (Fraga et al., 2012; Pachauri et al., 2015). The combined effect of higher temperatures and water deficit has negative effects on *V. vinifera* (Reineke and Thiery, 2016) stimulating vegetative development, increasing water needs and transpiration rates. Relative humidity and wind are also important at the micro scale, in particular when looking at local factors such as slope, orientation, habitat heterogeneity, etc. (Quenol, 2004; Rusch et al., 2017) but hard to quantify at larger (regional) scale.

1.1.2. Insects (pest and natural enemies) and climate

In line with plants, climate influences insect life history traits, speed and cycles of development and metabolic rates, making the duration of life stages earlier and shorter (Bale and Hayward, 2010). Insects are ectotherms (also called poikilothermic), which means that their body temperature is correlated to their external environment and highly sensitive to climate variability (Bale and Hayward, 2010; Denis et al., 2013; Gutierrez et al., 2008; Moiroux et al., 2014). A changing climate may lead to shifts in population distribution (displacement to higher latitudes and altitudes), increase in population growth rates and number of generations, extension of the life cycle and increased risk of invasion by exotic pests (Chuine, 2010; Porter et al., 1991; White et al., 2003).

1.1.2.1. Temperatures. Insect metabolism is driven by heat and cold accumulation above a so-called *base temperature* (Tb). Warmer temperatures in winter and spring will affect the overwintering of pupae, increase the survivorship of the insect pests and lengthen growing season (Bale et al., 2002; Moriondo and Leolini, 2015). Warmer conditions may accelerate development rates as heat will be accumulated earlier and faster (Honêk, 1996) and increase voltinism, i.e. the number of generations an insect can achieve in one year.

Multivoltine species like *L. botrana* that initiate diapause (day length and temperature thresholds required to finish a period of dormancy) (Jönsson et al., 2011; Martín-Vertedor et al., 2010; Stoeckli et al., 2012; Tobin et al., 2003, 2008). It is expected that with an increase in temperature, polyphagous herbivores might be able to extend their distribution range, and improve abundance and survival rates, resulting in increased voltinism (Bale et al., 2002; Caffarra and Eccel, 2011; Chuine, 2010; Régnière, 2009; Reineke and Thiery, 2016; de Sassi and Tylianakis, 2012; Thomson et al., 2010).

According to Colinet et al. (2015), fluctuating temperatures that remain within allowable ranges generally improve performance. Insects have good adaptation capacity to fluctuating temperature but their physiology is sensitive with respect to extreme temperature (frost or heat waves) and their timing. Therefore, changes in the seasonality of extreme events can affect development stages both positively or negatively. Faster development rates and increased voltinism suggest that future conditions may change the distribution of insect pests in latitude and altitude (Svobodová et al., 2014a, 2014b).

1.1.2.2. CO_2 and photoperiod. Herbivores are sensitive to CO_2 rise in the atmosphere by their feeding and hosting patterns and also in relation to their oviposition strategies. In Guerenstein and Hildebrand (2008), moth like *L. botrana* have sensing organs (receptor-cell) detecting CO_2 stimuli susceptible to increase their eggs laying rate by night when carbon dioxide concentration are higher (and according to plant assimilation with increased photosynthesis during the day).

Also, photoperiod induced by the changes in distribution range can lead to earlier diapause induction and decrease of the metabolic action period (Bale and Hayward, 2010); (Nagarkatti et al., 2003; Reineke and Thiery, 2016; Stoeckli et al., 2012).

1.1.2.3. Precipitation and relative humidity. Precipitation patterns are likely to change in the future but it is hard to assess the impacts of such changes on development and feeding or reproduction rates of insects. Sensitivity to reduced transpiration rates and water scarcity will influence humidity conditions on leaves and the maturity of berries as food for insects (Zavala and Gog, 2015). It is known that relative humidity affect the duration of early development and that drought shorten the lifespan of eggs and larvae and increase their mortality (Ortega-López, 2014; de Sassi and Tylianakis, 2012). In Gallardo et al. (2009), *L. botrana* for example has an optimal development rate with 70% of relative humidity, where the optimum is indicated as 65% in Briere and Pracros (1998) and Gallardo et al. (2009) (Table 1). Indeed, species needs in temperature and relative humidity can register strong differences according to their geographical areas of origin (Foerster and Foerster, 2009; Reineke and Thiery, 2016).

2. Climate change and trophic interactions between grapevine, insect pests and natural enemies

In this study, trophic relations are discussed with a focus on *L. botrana*, as the pivot of the interaction chain involving *V. vinifera* and *Trichogramma* spp. *L. botrana* damage *V. vinifera* by feeding and hosting on it, but also act as host of *Trichogramma* spp., which feed and lay eggs on *L. botrana*. *Trichogramma* spp. is considered an egg parasitoid (Moreau et al., 2010) and used as a natural enemy for biological control. But this is a delicate balance, depending on the interplay between expected changes in the phenology of *V. vinifera*, as a host plants for *L. botrana*, and changes in *L. botrana* and *Trichogramma* spp. interactions (Battisti and Larsson, 2015; Berggren et al., 2009; Fraga et al., 2016; Reineke and Thiery, 2016).

In the following we review the state of art regarding the levels of interactions between *V. vinifera*, *L. botrana*, and *Trichogramma* spp., focusing on their evolution on the background of recent changes in climatic conditions. Biological and ecological aspects will only be referred to, as appropriate, to understand the possible changes in phenology, feeding rate, growth rate, spatial and temporal distribution range (Moreau et al., 2010; Reineke and Thiery, 2016) but will not be in the scope of a detailed analysis.

2.1. 1st trophic level: Vitis vinifera

V. vinifera is a perennial crop that provides access to long historical records of phenology, allowing for comparison with climatic records. The description of key phenological stages is based on standardized indices like the BBCH (C) and Baggiolini scale (Baggiolini, 1952; Bloesch and Viret, 2008; Hess et al., 1997).

The physiology of *V. vinifera* develops in synchrony with climate conditions, emphasizing its strong adaptability and suitability to different climates (Carbonneau et al., 2007; Fraga et al., 2013). *V. vinifera* budburst (overwintering) is induced by a period of chilling temperatures (dormancy) followed by a period with forcing temperatures (post-dormancy) (Chuine et al., 2003; Fraga et al., 2013).

In the context of a warming climate, mean phenological stages, from budburst to harvest, are projected to undergo significant changes in time, with earlier appearances of these phases in the future as compared to today (Fraga et al., 2016; Rusch et al., 2015; Reineke and Thiery, 2016). In Martín-Vertedor et al. (2010), leaf emergence in Spanish vineyards was found to have advanced by approximately 17 days over the last decades. Information concerning grape harvest dates is unconvincing for comparison with climate records, because as the time of harvest is determined by agronomic factors unrelated to climate (García de Cortázar-Atauri et al., 2010).

For Europe, progressive shifts in grapevine cultivated area to the Northwest of their original ranges are well documented and explained by the expansion of grapevine cultivation into new climatic suitability areas (Moriondo et al., 2013). The ability of *L. botrana* to feed or host

Table 1
Temperature thresholds development for *L. botrana and Trichogramma* spp.
(Inspired from Briere and Pracros, 1998; Cooper et al., 2014; Moreau et al., 2010; Svobodová et al., 2014a, 2014b).

Name	Authors	Upper development threshold (UDT)	Lower development threshold (LDT)	Optimum temperature range (Topt)	Accumulated DD (/generation for insects)	Base temperature (Tb) and To (starting date)
Vitis vinifera (early ripening variety)	(Garcia de Cortazar-Atauri et al., 2009a, 2009b) BRIN	*BB-Flo-tmax* 40 °C	*BB-Flo-tmin* 10 °C	*BB-Flo-tOpt* 30 °C	–	10 °C 1st August
	(Caffarra and Eccel, 2010) FENOVITIS	40 °C	10 °C	–	–	10 °C 1st March
	(Plouffe and Bourgeois, 2012) CIPRA-Canada	40 °C (Marquette as reference)	10 °C	–	Budburst (C): 75 Flowering (J): 345 Veraison (L–M): 687	10 °C 1st March
Lobesia botrana	(Di Lena et al., 2013; Ortega-López, 2014)	28 °C	8 °C	–	1st 125 2nd 500 3rd 950	10 °C
Host for *Trichogramma* Feeds on *V. vinifera*	(Milonas et al., 2001)		6.45 °C	20–25 °C		
	(Gabel and Mocko, 1984)	30 °C	7 °C			
	(Briere and Pracros, 1998)	28 to 30 °C	9 °C (L1–L2) 10 °C (L3, L4, L5 + eggs) 12 °C (pupae)		–	–
	(Gallardo et al., 2009)	30 °C	7 °C	20 °C (70%RH)		
	(Plouffe and Bourgeois, 2012) CIPRA-Canada	–	–	30 °C	1st 190 2nd 687 3rd 1184 4th 1681	8.4 °C 1st March
	(Svobodová et al., 2014a, 2014b)	32 °C	10 °C	16 to 29 °C	430 per G. (Touzeau, 1981)	–
Trichogramma sp. (Cacoeciae-Brassicae-Evanescens)	(Smith, 1996)	36 °C (70%RH)	9 °C (25%RH)	20–29 °C (40–60%RH)	–	–
	(Hommay et al., 2002)	–	–	–	1st g.: 135 2nd g. 584	10 °C
Egg parasitoid feed on Lb eggs	(Furlong and Zalucki, 2017)	30 °C	9.6 °C	25 °C (20–30 °C)	–	–
	(Schöller and Hassan, 2001)	32–34 °C	11–15 °C	25 °C	–	–

on *V. vinifera* in these new areas will depend on variety (Moreau et al., 2006), and the possibility to establish phenological alignment (Martín-Vertedor et al., 2010).

2.2. 2nd trophic level: Lobesia botrana

L. botrana Den. & Schiff belongs to the *Tortricidae* family. It is a polyphagous insect able to feed on more than 20 different plants but with a preference for *V. vinifera* (Zalom et al., 2014). *L. botrana* develops better in warm and dry conditions (El-Wakeil et al., 2009; Thiéry, 2005), its development depending on temperature and photoperiod (Pavan et al., 2006; Svobodová et al., 2014a, 2014b), microclimate (Ioriatti et al., 2011), as well as the quality (maturity) of berries (Amo-Salas et al., 2011; Nagarkatti et al., 2003; Stoeckli et al., 2012; Tobin et al., 2003).

L. botrana larvae feed on *V. vinifera* flowers and berries and their evolution is completed in 3 weeks with different impacts on the *V. vinifera* (Amo-Salas et al., 2011; (Reineke and Thiery, 2016). In northern Europe (Switzerland, Germany or north of France), *L. botrana* usually develops two generations per year, but three generations are observed in southern latitudes (e.g. south of France). In the warmest areas in southern Europe (Spain and Greece) even a fourth generation has been reported (Amo-Salas et al., 2011).

Adults of the first generation emerge from overwintering pupae in spring, fly, mate, and lay their eggs on the buds. Larvae of the first generation damage the inflorescence or flower clusters in May-June. The second generation flies, mates, lays its eggs in green berries and exits the fruit to pupate. Damage is caused when the larvae feed on green berries in July, favouring the appearance of fungal diseases (e.g. *Botrytis cinerea*). The third generation feeds on mature berry in August and causes the greatest damages by feeding inside the berry (Milonas et al., 2001; Thiéry et al., 2014).

It is known that females prefer to lay eggs on the host species in which they developed as larvae (Moreau et al., 2008). Indeed, nutrient obtained in their larval stages, can alter their fitness. For example, a female feeding on poor quality plant may modify her oviposition and generally lay fewer and smaller eggs or regulating its eggs size by adaptation needs to changing conditions (Awmack and Leather, 2002; Guerenstein and Hildebrand, 2008; Moreau et al., 2017). *L. botrana* is also able to resist to extreme cold (−22 °C) conditions by adapting its metabolism (Reineke and Thiery, 2016).

Changes in the phenology of *L. botrana* have already been observed in the recent past. This has been the case in south-western Spain, where an increase of 0.9 °C and 3 °C in the annual and spring mean temperatures (Martín-Vertedor et al., 2010) created the conditions for a shift in *L. botrana* phenology of around 12 days, allowing for a fourth generation in 2006 (Di Lena et al., 2013). For the future, some authors argue that an earlier start of spring (warmer temperature) may allow a faster development and the appearance of more generations (Fraga et al., 2013; Pavan et al., 2006). Yet, other studies suggest that the increase of population in late summer may not be sufficient for the last generation to achieve its development due to earlier harvests (Caffarra et al., 2012; Gallardo et al., 2009; Seto and Shelton, 2015).

Generations do not require the same accumulation of heat (Degree Day) and do not have the same time to complete their development. Thermal requirements and DD thresholds differ according to the development stages (i.e., egg and larva development have different DD requirements than adults) (Briere and Pracros, 1998; Cooper et al., 2014; Gilioli et al., 2016). Also, differences in the thermal needs of hosts and parasitoids can influence the development of both spp. and of population interactions (Hance et al., 2007).

2.3. 3rd trophic level: Trichogramma spp.

Trichogramma spp. is an *Hymenoptera* and belongs to Trichogrammatidae family (Audouin, 1842; Audouin and Catalan, 1865; Zalom et al., 2014). It is a polyphagous insect pest, considered as egg parasitoid of *L. botrana*, but most commonly used in corn, sugar cane, etc. (Holzkämper and Fuhrer, 2015; Kölliker-Ott et al., 2003; Schaub et al., 2016; Smith, 1996). Adult females parasitize their prey by laying their eggs on, or in their hosts. The wasp larvae develop and feed into the host or host egg eventually causing its death. Around 650 species exist, the most common species raised for *V. vinifera* protection being *T. evanescence*, *T. brassicae* or *T. cacaociae* (Sentenac and Thiery, 2009; Smith, 1996; Xuéreb and Thiéry, 2006; Zalom et al., 2014). *Trichogramma* spp. can be grown in laboratory conditions and several species are commercially available, but their parasitism rate is unconvincing with only around 50% of effectiveness (Hommay et al., 2002; Smith, 1996).

Trichogramma spp. are sensitive to climatic variations, the sensitivity depending on species and geographical area of origin. *Trichogramma* spp. are vulnerable (growth, parasitism rates, longevity, sex ratios, etc.) to rapid changes even if their threshold development temperature is wide (Reineke and Thiery, 2016). The optimal development temperature (Table 1) is around 2830 °C, but lower and upper thresholds between 8 and 12 °C and between 32 and 34 °C, respectively (Gutierrez et al., 2010). Those thresholds are important factors to be considered in the present context, as they will determine the range of future temperature that can admit *Trichogramma* spp. under future climatic conditions. In Jalali and Singh (1992), the differential responses of *Trichogramma* spp. vary according to development stages and to temperature ranges, so fecundity and longevity vary with temperature and the length of extreme cold or warm periods.

3. Synchrony in the future

A warmer climate and changes in rainfall patterns and relative humidity can potentially lead to a temporal and spatial mismatch between *V. vinifera* and *L. botrana* and between *L. botrana* and *Trichogramma* spp. (Donnelly et al., 2011; Thiéry et al., 2011). Individually, shifts in the phenology of plants and insects in response to climate change are well documented (Bale et al., 2002; Martín-Vertedor et al., 2010; Reineke and Thiery, 2016; Stoeckli et al., 2012). In the past 30 years, those changes had strong effects on population density of *L. botrana*, with the appearance of an additional generation being now the rule in the warmest regions of Europe (Martín-Vertedor et al., 2010; Thomson et al., 2010; Torres-Vila et al., 1999).

3.1. Thermal requirements for development

Insect development is a non-linear process, and life tables usually describe population behaviour under constants thermal temperature (Furlong and Zalucki, 2017; Roy et al., 2002). Thermal constants like the lower and upper developmental thresholds (LDT and UDT; Table 1) are used to measure developmental rate of insects (Honêk, 1996; Traoré et al., 2006) and take into account critical threshold, above which a temperature increase ceases to be beneficial or even becomes detrimental (lethal threshold). The optimal range (Topt) is used to define the spectrum of temperatures that support highest developmental rates (Furlong and Zalucki, 2017). In Moshtaghi Maleki et al. (2016), *L. botrana* life expectancy (age in days) was found to decrease proportionally with the increase in temperature.

In the literature, the upper and lower temperature thresholds for development can vary according to the trophic level, in spite of the fact that they generally have common ranges (Moiroux et al., 2014). Also, high latitude organisms are generally more tolerant to thermal variations than the one from lower latitudes (Lancaster, 2016).

Nevertheless, if we consider the ranges for optimal development, warming conditions could impact the needs in thermic units per generation and the synchrony between the trophic levels as *L. botrana* 2nd and 3rd generations might develop faster (Pavan et al., 2006). Actual observations on *L. botrana* tend to confirm shorter development cycles due to warmer conditions allowing earlier diapause induction and egg hatch, and more generations due to a prolongation of the season (Martín-Vertedor et al., 2010; Reineke and Thiery, 2016). For optimal development of *L. botrana*, egg hatch has to be in synchrony with *V. vinifera* phenology and maturity (flower clusters and maturity of berries).

3.2. Interaction mechanisms

The synchrony between *L. botrana* and *V. vinifera* phenology is a key point to understand geographical distribution and relative abundance of the trophic networks in actual time and in the future. Climatic factors like temperature increase and drought in the growing seasons might have effects on the maturity of berries directly influencing their quality as food for insects (Moreau et al., 2017). The poor nutritional quality of plant due to a combined increase in photosynthesis, in CO_2 concentration and changes in the C:N ratio in leaves (proteins) could accelerate food intake of *L. botrana* to satisfy its basic requirements and induce more damages to *V. vinifera* (DeLucia et al., 2012; Guerenstein and Hildebrand, 2008; Reineke and Thiery, 2016; Thomson et al., 2010; Zavala and Gog, 2015).

In general, host plant quality can affect herbivorous insects like *L. botrana* and alter its life history traits such as larval growth, diapause induction and larval defense against natural enemies (Moreau et al., 2017). On a poor-quality host plant, for example, a female may either lay few good-quality eggs or a large number of poor-quality eggs (Awmack and Leather, 2002). Indeed, even if phytophagous insects like *L. botrana* have evolved life history strategies to deal with changes in the interaction mechanisms, in a warmer climate conditions may rely on the interspecific competition between parasitoids and modify their abundance, (Hance et al., 2007). However, it remains uncertain how those interactions will evolve in the future, which trophic level could benefit or be impaired from those changes, and when and where conditions will stop or start to be beneficial. Based on current knowledge, one can speculate that *L. botrana* could profit better survival rates in northern regions but suffer from lack of host and food in southern regions.

3.3. Shifts in timing and distribution range

Species heat requirement determined by latitude, altitude and microclimate specificities (Lancaster, 2016) could be modified by the amplitude of thermal variation, generating a shift between the trophic levels in the future. Development will still be possible, even with warmer conditions, but it will depend on the ability of feeding and hosting in the time and space. Changing conditions could promote the emergence of new or invasive species emerging from southern regions and spread into northern regions and higher altitudes, in areas previously unsuitable (Bale et al., 2002; Fraga et al., 2013; Reineke and Thiery, 2016; Thiéry et al., 2011; Tobin et al., 2003). Cuccia et al. (2014) emphasizes that a warming of 1 °C corresponds to a relative northward shift of climatic zones by roughly 180 km and shows that climatic conditions experienced in Europe in the 1970s are those we encounter today 100 km further north and 200 m higher in altitude. According to comparisons between today's climate and that of the 1950s (Beniston, 2014), the velocity of northward-moving isotherms has attained up to 15 km $year^{-1}$. Observed changes from the past to today, but also from south to north (Moriondo et al., 2013) can be considered to be an analogy to climate variability in latitude and altitude (Beniston, 2015; Bonnefoy et al., 2010; Caffarra et al., 2012; Caffarra and Eccel, 2011; Colinet et al., 2015; Seto and Shelton, 2015).

Also, one should expect a decrease of populations in the warmest regions as a result of temperatures that would reach or exceed the upper thermal threshold beyond which population development is inhibited (Gutierrez et al., 2012; Ioriatti et al., 2011; Reineke and Thiery, 2016). Southern regions still enable the growing of *V. vinifera* but insects, being more sensitive to temperature variation might suffer more in those regions, allowing a gap in the suitability of the co-evolution of *V. vinifera* and *L. botrana* with more extreme temperatures. Life history traits of polyphagous insects and distribution of population of natural enemies will likely evolve in synchrony or asynchrony with their prey (Colinet et al., 2015; Fraga et al., 2016; Maher et al., 2006; Price, 1980; Reineke and Thiery, 2016; Thiéry et al., 2014; Torres-Vila et al., 1999). For example, a late harvest taking place in September could allow the larval offspring from another (e.g. the 4th) adult flight that will not find berries on which develop and will not be able to diapause at pupal stage, leading to population decline in the following year (Martín-Vertedor et al., 2010). Results by Caffarra and Eccel (2011) and Caffarra et al. (2012) indicate that an increase in temperature might result in an increased asynchrony, supplied by a lack of host and food in the end of the growing season (Thomson et al., 2010; Reineke and Thiery, 2016; Romo and Tylianakis, 2013).

In general, it is worth noting that there is a research gap and no consensus concerning the possible evolution of the trophic interactions in the future and how warmer temperature and elevated CO_2 will alter trophic interactions in vineyards and facilitate biological control (Eigenbrod et al., 2015; Reineke and Thiery, 2016; Romo and Tylianakis, 2013). In any cases, several studies suggest that the highest trophic levels are more sensitive to climate changes induced in trophic relations than the lower level (Araújo and Luoto, 2007; Barton et al., 2009; Chen et al., 2015; Eigenbrod et al., 2015; Garcia de Cortazar-Atauri et al., 2009b; Gilman et al., 2010; Gutierrez et al., 2010; Hance et al., 2007; Price, 1980; Romo and Tylianakis, 2013; de Sassi and Tylianakis, 2012) mainly due to an earlier start of herbivores development in the season compared to their natural enemies. More heat will be accumulated in the insects pests, faster will be their development and the difference of development rate will increase generating an asynchrony (Moiroux et al., 2014).

In the case of *L. botrana* and *Trichogramma* spp., predator release in crops takes place when *L. botrana* lays its eggs. Generally this occurs around 10–15 days before the females of *L. botrana* begin to lay its eggs, but the timing vary according to temperatures (Hommay et al., 2002) and the release of natural predators has to be adapted to *L. botrana* development stage (Hirschi et al., 2012). Also, as *L. botrana* and *Trichogramma* spp. are both multivoltine, it is important to consider the rate of development of each generations and their heat requirement. *Trichogramma* spp. life cycle is shorter than the one of *L. botrana*. Consequently, prey and predator could in principle develop a different number of additional generations in the future (Zalom et al., 2014).

4. Modelling trophic relations

Phenological models are used to predict development stages and validated with observed data. According to the scale of interest and the specific objectives, models operate with different choices of driving variables and inputs (precipitation, relative humidity, solar radiation, slope orientations) (Amo-Salas et al., 2011; Fraga et al., 2016; Gutierrez et al., 2010; Jones and Davis, 2000; Malheiro et al., 2010; Moriondo et al., 2013; Rusch et al., 2015; Santos et al., 2012; Webb et al., 2007, 2012).

Nevertheless, even if few of them are biologically more realistic by taking into account inter-annual and regional variability (Caffarra and Eccel, 2010; Cuccia et al., 2014; Le Roux et al., 2015; Parker et al., 2013), the issue of spatial and temporal robustness of the models is particularly important (Chuine, 2010; Fila et al., 2014; Garcia de Cortazar-Atauri et al., 2009b), especially in relation to the reliability of projections of climate change impacts.

4.1. Approaches and methodology for modelling

Models can generally be classified as deterministic or stochastic, dynamic or static, process-based or empirical (Thornley and France, 2007). In addition, depending on the type of functional dependence, it is possible to distinguish between linear models, such as the classic Growing

Degree Days (GDD) models, and non-linear models, e.g. mechanistic models that take into account both biotic and abiotic factors (Caffarra and Donnelly, 2011; Caffarra and Eccel, 2010; Chuine et al., 2003). They are driven by weather data to predict site-specific dynamics or the dynamics across a landscape.

Many models adopt the so-called Bioclimatic Indices (Table 2), usually measured in terms of Degree Days and estimated as the accumulation of daily mean temperatures during the growing season above a given Tb (Bellia et al., 2007; Bonnefoy et al., 2010; Gallardo et al., 2009; Jones and Davis, 2000; Milonas et al., 2001; Murray, 2008; Santos et al., 2012). A Tb of 10 °C is generally accepted for grapevine as the buds has to be exposed to temperatures below 10 °C during a certain period to break its dormancy and start to budburst (Carbonneau, 1992; Garcia de Cortazar-Atauri et al., 2009a; Winkler et al., 1974). Sometimes Tb is parameterised as 0 °C (Parker et al., 2011). Insects are generally in line with their host and assume the same Tb.

Some authors consider that the accumulation of forcing units begins on 1st January (Bindi et al., 1997; Gutierrez et al., 2012) implicitly assuming that at the beginning of a new year, the preceding pre-dormancy period was completed and dormancy was already broken. Other authors, however, start accumulating forcing units on March 1, assuming that it's the end of winter (Caffarra and Eccel, 2010). Worth noting is also the fact, that *V. vinifera* budburst defines the beginning of the growth cycle and any delay at this stage has impacts on the whole cycle. Therefore, accurate calculations of the budburst date are of utmost importance for a successful modelling of the phenology of *V. vinifera* (Garcia de Cortazar-Atauri et al., 2009aa; Reineke and Thiery, 2016; Thomson et al., 2010).

4.2. Phenological models for grapevine

The most recent models developed to predict grapevine phenology are so-called Grapevine Flowering Veraison (GFV) models. They are generic phenological models that focus on predicting the dates of flowering and veraison of *V. vinifera*.

The General GFV Model was developed by Parker et al. (2011). It is a Single Process Based Model using GDD with FU and CU specified for different varieties of *V. vinifera* that can therefore be employed to study conditions for viticulture under different scenarios. From daily mean temperatures, it generates predicted phenological stages in the BBCH and Baggiolini (1952) scale that can be confirmed with observed data from the past, and simulate future data when submitted to sensitive analysis.

Another GFV Process Based Model (PBM) is FENOVITIS, developed by Caffarra and Eccel (2010). It is a non-linear model adapted to Chardonnay that sums temperature from a defined date and above a minimum temperature threshold (Chilling and Forcing critical temperatures) until the appearance of the next phenological stage (50% appearance).

4.3. Phenological models for insects (ecological models)

Insect pests modelling can be used to study tritrophic relations in all of their facets, including population dynamics, prey-predator and parasitoid-host relations (Gilioli et al., 2016; Moiroux et al., 2014; Ponti et al., 2015). Despite the fact that temperature is the main driver of species phenology, biotic and abiotic interactions is necessary for modelling their distributions and fitness, and to study their relationships with climate and host plants (Araújo and Luoto, 2007; Chuine, 2010; Régnière, 2009; Roy et al., 2002).

The most common models are Ecological Niche Models (ENMs), predicting phenology and distribution. They explore and exploit correlations at a particular point in time, which makes them difficult to use for application to climate change studies (Gutierrez et al., 1999, 2012). A prominent example of ENM is CLIMEX (CLIMatic indeEX), a climate-driven modelling program designed to provide insight of a species respond to climate by using its geographical distribution, its seasonal phenology and relative abundance in different locations (Beddow et al., 2010; Tonnang et al., 2017).

4.4. Demographic Models

Physiologically Based Demographic Models (PBDM) explore the distribution and abundance of a species assuming that physiological, phenological and demographic responses as well as ecological niches can be expressed as a function of abiotic and biotic factors and modeled on a per capita basis (Gilioli et al., 2016; Gutierrez and Baumgaertner, 1984).

The PBDM for *L. botrana*, developed in the work by Gutierrez et al. (2012), includes mechanistic biology, coupled to an extended PBDM for grapevine phenology, growth and development. This model assess the distribution and relative abundance of *L. botrana* under the effects of +2° and +3 °C warmer climate scenarios on relative abundance in the prospective range of the moth in California.

4.5. Overlapping models

Phenological models have been developed with the aim of improving the timing of insecticide applications (Gallardo et al., 2009; Milonas et al., 2001) or the efficacy of parasitoid-based pest control

Table 2
Bioclimatic indices commonly used for modelling phenology.

Indices	Description	Formula
Huglin, HI (Huglin, 1958)	Heliothermic index measuring the relation between climate and phenological stages (tb = 10 °C)	Sum of the daily mean and maximum temperatures from April to September, subtracting 10 °C on each day from both variables where Tm = Tmean, Tx = Tmax, k = day length coefficient (from 1,02 to 1,06 between Lat. 40 to 50): $HI = \sum[(Tm - 10) + (Tx - 10) / 2] * k$
Winkler, WI (Winkler et al., 1974)	Degree Day Index measures the needs of heat for the plant phenology and provides climatic classes from the coldest to the warmest in a long term perspective and precocity of development stages	Sum of daily mean temperatures (from March 30 to April 1) and subtracting tb (usually 10 °C) on each day: $GDD = \sum(\text{daily Tmin} + \text{daily Tmax} / 2) - \text{Tbase}$
Cool Night Index (CI) (Tonietto, 1999; Tonietto and Carbonneau, 2004)	Minimum temperatures preceding the harvest and dryness Index developed to estimate soil water availability	
Indice Risk Alteration, IRA (Brodeur et al., 2013)	Measures the probability of shifts in synchrony between insect pest and its natural enemies modified by climate changes	For $T \leq T_{inf}$ ou $T \geq T_{sup}$: $D = 0$ For $T_{inf} < T < T_{sup}$: $D = Dmax(\frac{Tu-}{Tu-TDmax})(\frac{T}{TDmax})^{\frac{TDmax}{Tu}} - T^{Dmax}$ T: temperature D: development rate at T Dmax: max development rate at TDmax TL: Estimated min temperature threshold TDmax: Maximum temperature threshold Tu: Estimated max temperature threshold

(Wajnberg et al., 2016). The focus of such operational applications is flight predictions (Amo-Salas et al., 2011; Severini et al., 2005).

In the past, attempts have been undertaken to forecast voltinism under climate change conditions by linking models of the relationships between hosts and pests (Tobin et al., 2003). Little has been done, however, to model tritrophic relations, with the aim of implementing biocontrol. Moving forward in this direction is of paramount importance for studying how IPM can be adapted to climate change.

As illustrated in the chart-flow (Fig. 1), by comparing models of climate and phenology (ecological models and GFV models) and applying a sensitivity analysis for the simulation of future climate scenarios, it would be possible to identify critical shifts in the synchrony or asynchrony of the different trophic levels and the ensuing overlap periods (Gilioli et al., 2016; Hirschi et al., 2012; Hoover and Newman, 2004; Stoeckli et al., 2012).

5. Conclusion

This review has highlighted that climatic factors have a strong effects on the phenology of plants and insects. Indeed, warmer conditions are expected to favour the emergence of parasitoids and correspond to more generations. Although, it is worth noting that the physiological development of ectotherm organisms, mainly driven by temperatures, exhibits a different response to changes assuming different thermal tolerance and optimums (Brodeur et al., 2013; Singer and Parmesan, 2010).

In practice, complex interactions between pests and their natural enemies will not only reflect the quantity of accumulated degree-days but, rather, the quantity at the right time (Fraga et al., 2016; Moriondo et al., 2013). In fact, parasitoids seems more likely to be affected by climate changing conditions as their development depends on the adaptation capacity of the lower trophic level (Hance et al., 2007). In other words, the highest trophic levels (natural enemies) are more vulnerable to changes as their adaptive capacity to frequent and intense climatic variations is apparently less than that of herbivores (Romo and Tylianakis, 2013; Wajnberg et al., 2016). In the future, herbivores might benefit from those changes, thereby reducing the effectiveness of biocontrol through the suppression of hosts (Romo and Tylianakis, 2013).

However, there is no consensus in the literature concerning the potential effectiveness of IPM under climate change conditions, especially because some authors postulate better parasitism of *L. botrana* by *Trichogramma* spp. as warmer conditions could suppress overwintering of *L. botrana* and slow its developmental rate during the cold period of the year (Foerster and Foerster, 2009). Those uncertainties highlight the needs for more detailed investigations of the impacts of climate change on tritrophic relations.

In this specific context, the question is not so much where there will be synchrony/asynchrony between *L. botrana* and *Trichogramma* spp. (Wajnberg et al., 2016; Caffarra et al., 2012; Zavala and Gog, 2015) but when it would be observed. In Southern parts of Europe (From South of Spain and Mediterranean areas) a shift may not necessarily allow an optimised IPM, whereas new regions might become optimal for biological control (Northern parts of Europe).

This review also considered the role of models for advancing our understanding of tritrophic relations. PBM seems more adapted as they are able to consider different drivers and explain emerging interactions in a physical way. Yet, some important factors like host-plant quality and availability but also physiological defenses have been largely neglected in studies of the phenology of phytophagous insects (Thiéry et al., 2014). Other factors such as thermal tolerance (lethal thresholds), the photoperiod (day length) and the diapause induction should be considered more systematically in these models and the interpretation of their results (Bale et al., 2002; Colinet et al., 2015; Moriondo and Leolini, 2015).

A more realistic modeling of the potential synchrony or asynchrony of pests and their natural enemies as well as of the future spatial and temporal evolution will allow anticipating the future role of IPM and help identifying possibilities for developing sustainable agriculture under altered climate conditions.

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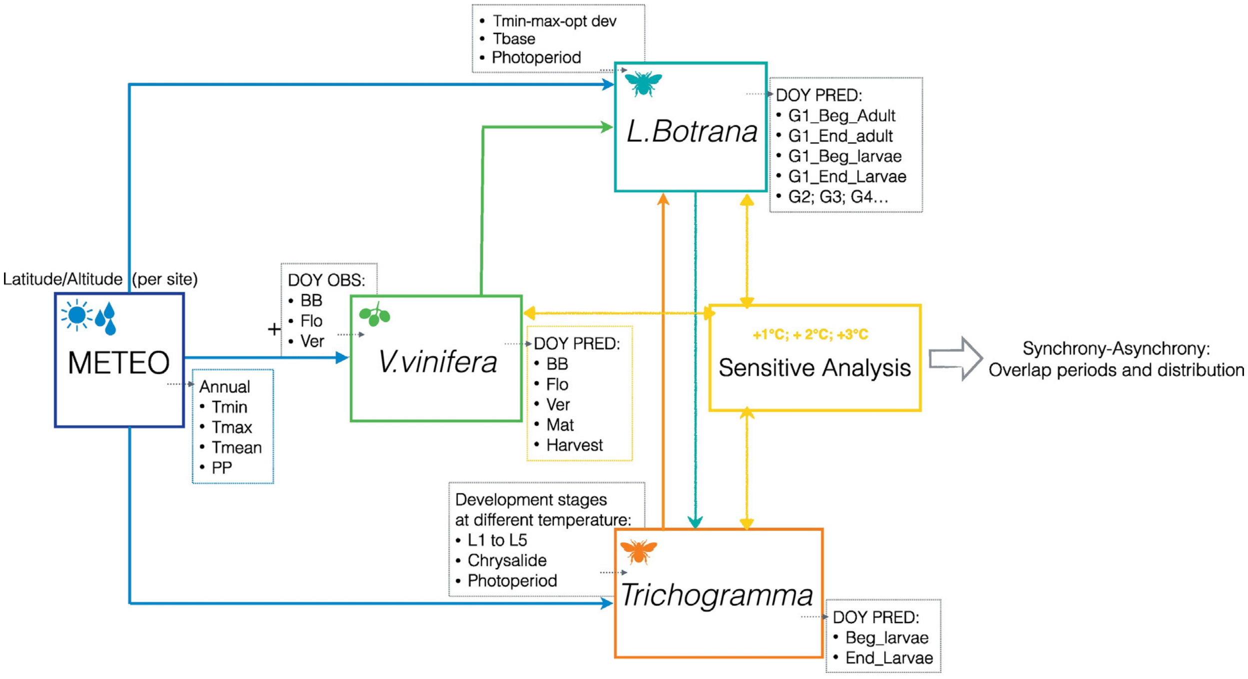

Fig. 1. Chart-flow model for overlap period identification after applying a sensitive analysis at different temperature.

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