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REVIEW

Grapevine insect pests and their natural enemies in the age of global warming

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Abstract We review direct and indirect effects of climate change on both the grapevine plant as a host for phytophagous insects, as well as on grape insect pests, their natural enemies and corresponding future grape plant protection strategies. Phenology, voltinism and distribution ranges are well known traits of many arthropods influenced by temperature as the key abiotic factor and thus by current and future climate change scenarios. Case studies of grapevine pests based on data from three decades point to clear changes in phenology of grape berry moths, shifts in distribution ranges of leafhoppers as vectors of grapevine diseases and range expansion of grapevine mealybugs. These case studies also illustrate the need to include data on putatively changed tri-trophic interactions in vineyards when predicting impacts of climate change on grapevine pest insects. Hence, future pest management strategies should be based on a sound set of field data obtained for both pests and antagonists under changed abiotic conditions, which can also build the basis for refining and extending currently existing models for forecasting population levels of respective insect pests.

Keywords Climate change · Viticulture · Trophic interactions · Biological control · Insect phenology

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Key message

- Climate change will have significant impacts on grapevine as a host plant for phytophagous insects as well as on trophic interactions in the vineyard.
- Effects of climate change on grapevine pest insects and their antagonists are already evident, e.g. in changes in phenology or distribution ranges.
- Future pest control strategies and modelling approaches will require a detailed knowledge of the effects of climate warming on both the grapevine plant, the respective insect species and its natural enemies.

Introduction

In the vineyard, grapevines are in the centre of complex communities and interact in trophic networks with a range of organisms both below- and above-ground. Some of these organisms are fairly detrimental to grape production such as microbial pathogens or phytophagous arthropods, others are rather beneficial, such as rhizobacteria, mycorrhizal fungi, or entomophagous arthropods ensuring the natural control of grape pests and pathogens (Walton et al. 2012). All members of these complex communities are influenced by the prevailing environmental conditions, in particular by temperature and precipitation. The latest reports published by the Intergovernmental Panel on Climate Change (IPCC) illustrate that global atmospheric carbon dioxide (CO_2) levels have substantially increased since the Industrial Revolution and are expected to surpass the 700 ppm level by the end of this century (IPCC 2014). The accumulation of CO_2 and other greenhouse gases in the atmosphere is forcing an elevation of global temperature: Over the past century, a rise of ~0.61 °C in mean global surface temperature has been recorded and further increases of 0.6–5.0 °C are projected for this century (IPCC 2014). During the same period, precipitation has increased significantly in some parts of the world (e.g. eastern parts of North and South America, northern Europe and northern and central Asia), whereas it has declined in others (e.g. the Mediterranean, Southern Africa and parts of Southern Asia). In addition, more frequent and longer lasting heat waves in summer as well as reduced winter chill hours have been observed recently as a consequence of global warming in many temperate areas of the world (Fischer and Knutti 2015; Horton et al. 2015). Such alterations in the prevailing climatic conditions will have direct effects at the level of an individual species (grapevine plant, microorganisms and insects) and at the same time will considerably affect the relationships within biotic communities in vineyards (Fig. 1).

The focus of this review is how climate change over the last three decades has affected grape insect pests and their natural enemies and, in turn, how future grape plant protection strategies have to be adjusted accordingly. It is often accepted that climate change and related global warming will have detrimental effects on crop production by favouring their pests. However, arthropod pests, their competitors, and natural enemies can each be affected positively or negatively by such changes which makes future trends of arthropod pest pressure in vineyards hard to predict. Here, we will present evidence for direct and indirect effects of climate change on both the grapevine plant itself as a host plant for phytophagous insects, as well as on distribution ranges and developmental rates of grape insect pests and their natural enemies. Finally, some future management strategies and research needs addressing grape pest management under climate change scenarios will be discussed.

Effects of climate change on grapevine's suitability as a host plant for arthropods

Grapevines are hosts of various arthropod pests, attacking different parts of the plant such as roots, buds, berries or leaves. Damage caused by phytophagous mites, leafhoppers, piercing-sucking insects or by leaf-eating or cluster-feeding Lepidoptera can be either direct due to feeding activities or indirect via the transmission of pathogens such as bacteria or viruses (Bostanian et al. 2012). In general, any direct or indirect consequences of changes in abiotic factors which differentially affect the growth or fitness of grapevines will alter its suitability as a host plant for phytophagous insect pests. Increases in atmospheric levels of CO_2 can alter plant photosynthesis rates as well as the chemical composition of plant tissues (Gutschick 2007). Plants grown under elevated CO_2 levels typically show an increase in photosynthesis rates and biomass production,

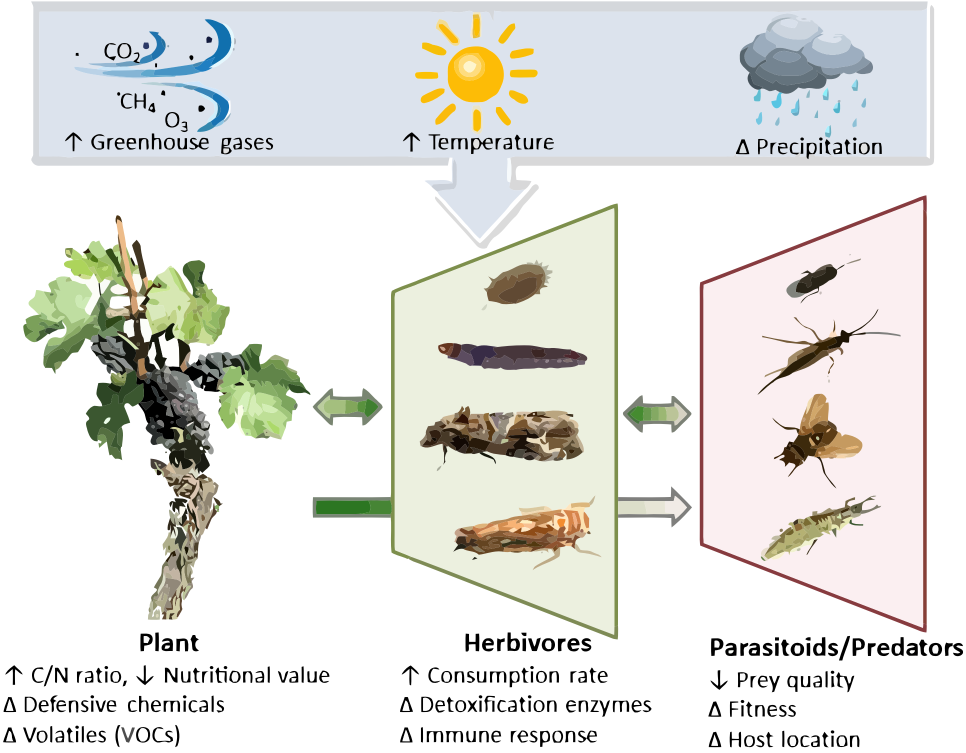

Fig. 1 Schematic outline of examples of putative effects climate change has on tri-trophic interactions between grapevines, associated herbivores and their natural enemies. *Arrows pointing up-* or *downwards* represent an increase or decrease of respective traits. For traits marked with a delta, variable responses (increase or decrease) are observed

known as the so-called fertilization effect. Stimulation of photosynthesis under elevated CO_2 levels results in lower levels of total nitrogen, while carbohydrates accumulate in foliage of plants, generating a higher carbon to nitrogen (C:N) ratio (Coviella and Trumble 1999; Korner 2006; Long et al. 2006; Zavala et al. 2013). At the same time, an increased C:N ratio in leaves reduces the nutritional quality of the plant for herbivorous insects, which might in turn respond to this reduced food quality by accelerating food intake (DeLucia et al. 2008, 2012; Guerenstein and Hildebrand 2008; Zavala et al. 2013). For grapevines, CO_2 enrichment treatments in a free air CO_2 enrichment (FACE) facility carried out in an Italian vineyard (Bindi et al. 2001) revealed that grapes grown under increased CO_2 levels accumulated fruit and vegetative biomass at a higher rate. However, this CO_2-fertilization effect may be reduced by negative effects of other climatic factors or abiotic conditions that are expected under future climate change scenarios. Leibar and colleagues (2015) grew grapevines under various abiotic stressors such as elevated temperature, elevated atmospheric CO_2 concentration and/or water stress, thus examining putative effects of a combination of multiple stress factors on plant performance. For example, photosynthetic activity of grapevines grown under a combination of elevated CO_2, elevated temperature and well-watered conditions increased. However, these positive effects were abolished under the presence of a water deficit.

Alterations in the chemical composition of plant tissues as a result of changes in abiotic factors might also affect physical and chemical defence mechanisms of grapevines against phytophagous insects. Chemical defence reactions based on the production of secondary defensive compounds by grapevines against arthropods are not well understood so far and have only just recently been the subject of a couple of studies (Melo-Braga et al. 2012; Nabity et al. 2013; Timm and Reineke 2014), but are well described in other plant–insect systems (Barah and Bones 2015; Kerchev et al. 2012; Kliebenstein 2014; Wu and Baldwin 2010). Studies on the effects of climate change scenarios on defence mechanisms in plants have indicated that exposure to elevated CO_2 suppresses the plant defence hormone jasmonic acid (JA) while stimulating production of salicylic acid (SA) (DeLucia et al. 2012). The JA pathway is regarded as the key driver of resistance against chewing insects, while SA is relevant for defence mechanisms against microbial pathogens. Accordingly, this shift in plant hormone levels could result in an increased susceptibility of plants to insect damage, while resistance to pathogens is enhanced at the same time. Moreover, environmental factors such as light intensity, atmospheric CO_2 concentration, temperature, relative humidity and nutrient status of the plant can greatly influence biosynthesis, emission profiles and timing of emission of plant biogenic volatile compounds (BVOCs) (Constable et al. 1999; Dudareva et al. 2006; Loreto and Schnitzler 2010). BVOCs are important in plant adaptation processes, as semiochemicals in inter- and intraspecific communication as well as in plant defence reactions and their production, emission and stability is known to be greatly affected by abiotic factors (Yuan et al. 2009). A meta-analysis by Robinson and colleagues (2012) pointed to an overall significant decrease in total terpene concentration due to elevated CO_2 in different plants species which might in turn result in a reduced synthesis of some BVOCs. However, prediction of a modulated BVOC production under climate change scenarios is highly complex and not fully understood so far and should also consider possible adaptation mechanisms in both plants and insects (DeLucia et al. 2012; Zavala et al. 2013).

Elevated CO_2 levels have the tendency to also induce alterations in plant structure, which might manifest itself in an increased leaf area, leaf thickness or higher number of leaves (Pritchard et al. 1999; Robinson et al. 2012). Such modifications in grapevine plant architecture may affect visual clues known to be important during location of host plants by arthropods. In addition, density and quantity of susceptible plant tissues as well as the plant's microclimate can be affected resulting in an increased leaf surface wetness and leaf surface wetness duration (Calonnec et al. 2013). For pathogens, changes in the plant's microclimate will enlarge the risk of infection by certain foliar pathogens such as downy mildew *Plasmopara viticola* (Kennelly et al. 2007) or powdery mildew *Uncinula necator* (Carroll and Wilcox 2003). However, at the same time, phytotron studies have indicated that an increase in CO_2 levels did not affect powdery mildew incidence (Pugliese et al. 2010), which is in accordance with simulations of disease severity for the same pathogen rather pointing to a decrease in future disease severity levels (Caffarra et al. 2012). Relative humidity is important for the development of insect populations, but plant surface water is supposed to be a less critical parameter (Pangga et al. 2013). Moreover, any alterations in the structure of grapevine canopies due to abiotic factors might influence the presence of pest or beneficial arthropods. For spider mites, it has been shown that distribution patterns in the vine canopy are influenced by plant vigour (Hanna et al. 1996). Yet, spatial and temporal dynamics of arthropods in zones of the vine canopy are not well understood so far, albeit the fact that grapevine pruning substantially offers avenues of altering the plant's architecture and thus it's suitability as habitat for arthropods.

Direct effects of climate change on grapevine insect pests

Alterations in temperature, precipitation and other climatic factors are expected to have substantial impacts on grape insect pests as well as on the severity of the epidemics they cause on their host plant. For many insect species, temperature is the key abiotic factor having direct effects on life-cycle duration, voltinism, phenology and range distribution (Bale et al. 2002). Examples for effects of climate change on these traits are given below. Under climate change scenarios, global mean temperatures are predicted to increase, with an accumulation of extreme events like heat waves during summer months and a rise in temperature and precipitation extremes during winter (Fischer and Knutti 2015; Horton et al. 2015). In particular, high summer temperatures beyond the species-specific optimal zones and tolerance limits as well as the interaction between mean temperature and temperature variability can negatively affect developmental rates, reproduction or survival of arthropods (Berg et al. 2010; Colinet et al. 2015). At the same time, the considerable degrees of phenotypic plasticity expressed by many insect species might allow a rapid adaptation to the physiological challenges associated with global warming (Bale and Hayward 2010). Several members of the lepidopteran family Tortricidae are adapted to resist cold and dry winters and are known to be able to survive at low winter temperatures. For example, the supercooling points of diapausing and non-diapausing grape berry moth *Lobesia botrana* individuals were around −24 and −22 °C, respectively, with survival at low temperatures increasing as the duration of acclimation period increased (Andreadis et al. 2005). Temperate and wet winters when combined are catastrophic in particular to those insects overwintering as pupae since an increase in winter mortality due to a higher virulence of entomophagous fungi or bacterial antagonists can be envisaged (Bale and Hayward 2010). Moreover, natural antagonists of pest insects may react differentially to changing abiotic conditions affecting multitrophic interactions and community compositions (Fig. 1). Such shifts in microbial communities might likewise affect, e.g. the disease-suppressive quality of soils, which has important implications for the biological control of soil borne pest insects (Eisenhauer et al. 2012).

Recent analysis of long-term datasets, modelling studies and experiments conducted both in the laboratory as well as under field conditions are pointing to a few major general features, in which the influence of climate change on insect pests is already evident and which are presented below.

Insect phenology

Climate warming is expected to alter the dates of recurring natural phenomena and analysis of available long-standing records of some phenological events that have provided indications of a change in the natural calendar over the past (Chuine et al. 2004). For several insect species, such shifts in phenology in response to climate warming are well documented, for example, in various lepidopteran species, which show a significant advance in the dates of their first appearance in spring (Parmesan 2006; Penuelas and Filella 2001; Stoeckli et al. 2012). For the European grapevine moth *L. botrana,* a significant advance in phenology by more than 12 days has been observed for Spanish populations (Martin-Vertedor et al. 2010), with a similar trend being visible in other grapevine growing regions as well (see example for Germany below). It is also important for herbivorous insects to synchronize their development with that of their host plant. In *L. botrana*, the influence of grape phenology on oviposition behaviour and fitness is well documented (Maher et al. 2006; Thiéry et al. 2014; Torres-Vila et al. 1999). A combination of phenological models of both the host plant grapevine and the pest species *L. botrana* revealed that an increase in temperature might result in an increased asynchrony between larvae-resistant growth stages of grapevine and *L. botrana* first generation larvae, having negative impacts on grape yield (Caffarra et al. 2012). On the other hand, grapevine harvest dates might advance as well, limiting putative damage due to an earlier appearance of late-season generations or an increased number of *L. botrana* generations. Phenological changes for grapevine during the last five decades as a result of climate change are well documented for different locations and varieties. Overall, grapevines respond to global warming by an earlier bud break, bloom, véraison and harvest and shorter intervals between these events (Jones and Davis 2000; Jones et al. 2005; Schultz and Jones 2010). This might have consequences for the synchronous development of grapevine plants and respective pest insects. Changes in climatic conditions can also completely disrupt the synchronization in phenology between the different trophic levels as have been proved for egg hatching of the winter moth *Operophtera brumata* and bud burst of its primary host plant oak (*Quercus robur*) (van Asch and Visser 2007; Visser and Holleman 2001).

Voltinism

Voltinism, the number of broods or generations of an insect per year, might increase as a direct effect of rising global temperatures. Thus, voltinism is often considered as one of the most spectacular traits affected by global warming. In this scenario, multivoltine species might have one or more additional generations per year, as temperature is the primary factor driving developmental time (Bale et al. 2002). Naturally, voltinism has a major effect on the population dynamics of a given insect pest species by adding successive generations which will globally increase the species' population density at the end of the year. The abovementioned phenological advance in *L. botrana* populations in Spain due to warming also contributed to an increased voltinism in the respective years by promoting an entire additional generation (Martin-Vertedor et al. 2010). However, as harvest time is influenced by different factors, a harvest occurring before *L. botrana* larvae leave grape bunches for pupation might reduce population levels, since larvae are removed during harvest. Also, in warmer climates, grape harvest takes place earlier in the year, thus counter-acting possible advantages gained by the pest insect due to increased voltinism. In addition, short day lengths in late summer are utilized by many insects to regulate their diapause induction (a developmental arrest) long before temperatures actually drop (Denlinger 2002). While for some insect species, photoperiodic cues may not change in response to climate warming, for others genetic shifts in the photoperiodic response and the timing of diapause have already been demonstrated even within very short periods of time (Bradshaw and Holzapfel 2001; Gomi et al. 2007). In addition, consequences of having additional generations per year can be compensated by adverse effects breaking the optimal synchrony with the resource as it has been observed in Southern European vineyards in the case of *Scaphoideus titanus* (Chuche and Thiéry 2014). This illustrates that putative changes in insect voltinism are complex and difficult to predict for future global warming scenarios.

Shifts in distribution ranges

Temperature is one of the fundamental abiotic factors that limit an organism's distribution range. In particular, the range of many herbivorous insects is limited by low winter temperatures. Thus, increasing winter temperatures as predicted under climate change scenarios are expected to be the chief factor affecting range shifts of insects, by increasing survivorship of overwintering stages (Bale et al. 2002; Garrett et al. 2006). As a consequence, thermophilic arthropods are favoured in their current area of distribution due to global warming and might be able to extend their range to new, currently not colonized areas if their host plants are present. However, distribution ranges of insects are not only determined by the individual species responses to the prevailing climatic conditions, but are also greatly affected by interactions with other species, or by the presence of suitable host plants at the new location (Jenkinson et al. 1996). Hannah et al. (2013) present predictions for global geographic shifts in suitability for viticulture, with a decline projected for traditional wine-producing regions such as Bordeaux in France and Tuscany in Italy (but see statement by van Leeuwen et al. (2013) on the same topic) and an increase for northern regions of North America and Europe as well as for areas at higher elevations. White et al. (2006) estimate a decline in the premium wine grape production area in the United States and stress the importance of extreme temperature events for suitability of current and future viticultural areas.

Recent range shifts attributed to climate change have been observed and are well recognized for a number of insect species (Gevrey and Worner 2006; Musolin 2007; Parmesan et al. 1999; Williams and Liebhold 2002). For grape insect pests, we can expect that species which are currently restricted, e.g. to Mediterranean environments or are of tropical and subtropical origins, can expand their potential range into temperate regions under predicted future climatic conditions. A simulation of climatic conditions in the year 2055 indicated a climate-driven northward shift in distribution ranges of 11 degrees N for the European grapevine moth *L. botrana* (Svobodova et al. 2014). Furthermore, global trade, which is considered as a major factor contributing to recent invasions (Monceau et al. 2014; Perrings et al. 2005), has increased substantially during recent decades. This extends the risk that alien invasive species could inadvertently be transported into new areas therefore favouring long-distance spread of herbivorous insect pests, pathogens and pathogen vector species (Hunter 2005; Jeger and Pautasso 2008). In this regard, several recent examples of incidences of sudden shifts in distribution ranges of grapevine insect pests are given by the presence of the European grapevine moth *L. botrana* in Californian vineyards (Gutierrez et al. 2012) or by the introduction of the spotted wing drosophila *Drosophila suzukii* from Asia to Europe and the United States (Cini et al. 2012; Hauser 2011).

Effects on natural enemy activity and biological control

Climate change will influence tri-trophic interactions between plants, herbivores and antagonists in various and complex ways (Thomson et al. 2010). Viewing the interactions between pest insects and their natural enemies as a race, one question arising is who is going to win the race in the context of a changing climate? The main limiting factor in attempting to answer such a question is that although historical data concerning pest damages in vineyards exist, those concerning biocontrol regulation rates are critically missing for longer periods.

Parasitoids or predators of tortricids in vineyards have long been known, for example, *Campoplex capitator* (also called *Campoplex majalis* because of being very active in May) (Audouin 1842) or members of the *Trichogramma* family (Marchal 1912). The Ichneumonid *C. capitator* has already been described as the most efficient larval parasitoid of *L. botrana* in 1842 (Audouin 1842) and is still today (Moreau et al. 2010; Thiéry et al. 2011; Xuéreb and Thiéry 2006). In that regard, its efficiency as natural control agent of *L. botrana* has probably not changed that much over the last century and a half. However, historical population dynamic data for these natural enemies are not available preventing any accurate comparison of antagonistic efficiency in time.

Life history traits of parasitoids and predators of grape insect pests as well as their geographical distribution range can be affected by climatic changes. *Trichogramma* species as grape berry moth egg parasitoids are present worldwide in vineyards and are good examples of variable reactions to changes in temperature and relative humidity with strong differences according to species or geographical area of origin (Foerster and Foerster 2009; Gross 1988). Not only constant or alternating temperatures but also daily short-term heat shocks affect traits such as growth and parasitism rates, longevity, sex ratio and in several cases traits related to foraging behaviour (e.g. locomotion activity and searching behaviour) (Firake and Khan 2014; Reznik et al. 2009). All these traits can affect reproduction rates and thus parasitism success (Kalyebi et al. 2006).

As for pest insects, distribution ranges of parasitoids and predators may change, and reductions or extensions of geographical areas are being expected. The tachinid fly *Phytomyptera nigrina* is an example of a recent geographic range extension in European vineyards. This efficient larval ectoparasitoid of *L. botrana* classically occurred in Spanish vineyards and extended its distribution range to the Southern French vineyards during the last two decades (Thiéry et al. 2006; Vogelweith et al. 2013).

A fair part of the biological control against grape pest insects is also achieved by generalist predators acting in autumn/winter such as harvestmen spiders or earwigs. It is thus likely that warm autumn conditions will affect their activity and thus their predation capacity, but so far very little is known concerning the climatic requirements of such species.

Among the factors affecting parasitism efficiency, resistance of the host, especially through its immune system, recently received increasing attention (Haine et al. 2008; Hammill et al. 2010; Siva-Jothy et al. 2005; Vogelweith et al. 2013). Temperature may directly affect the immune system of the juvenile host (Bauerfeind and Fischer 2014; Hoffmann et al. 2003) and change the sensitivity of the pest to natural enemies (fungal, viral or bacterial infection or parasitoids). Several results indicate that increasing temperature positively influences immunity (Adamo and Lovett 2011; Mandriolo 2012) which is reversely paid by fitness costs in most cases (Vogelweith et al. 2014). For example, activity of the phenoloxidase, an enzyme involved in melanization and encapsulation of parasitoid's eggs, is increased by warming (Adamo and Lovett 2011). Variations in the immune system are also related to the host food quality (Ponton et al. 2011; Vogelweith et al. 2011), on which climatic factors indirectly act.

Examples on effects of global warming on grape insect pests

Here, we present case studies supporting our hypothesis that global change has already influenced the interactions between grapevines and insect pests. Case studies are based either on our own long-term observations and datasets or on available modelling studies from the literature forecasting responses of grape insect pests to climate change.

Phenological changes in grape berry moths

Tortricid moths were historically considered among the key insect pests of grapes. The red worms attacking grape clusters described as a divine scourge in the Bible were most likely *Eupoecilia ambiguella* (R. Roerich quoted in Thiéry (2005)). The leaf rolling tortrix (*Sparganothis pilleriana*) was the main grape pest in France during the eighteenth century (Audouin 1842) and is now restricted to limited local areas in France, Germany and Spain. Among the tortricid species commonly considered as attacking grape bunches *L. botrana*, *E. ambiguella* and *Argyrotaenia pulchellana* are present in Europe, while *Endopiza (=Paralobesia) viteana* is distributed throughout the Eastern United States and South-eastern Canada (Roehrich and Boller 1991). All these species are multivoltine, with damage inflicted by first generation larvae feeding on buds and flowers as well as by subsequent generation larvae feeding on berries. The economic importance of grape berry moth damage therefore depends strongly on the developmental stage of grapevine. Larval feeding on berries directly reduces yield and increases infestation of berries with fruit flies. It also creates infection sites for fungal rot organisms such as *Botrytis cinerea* or sour rot (Cozzi et al. 2006; Fermaud and Giboulot 1996). These multivoltine species can have one additional generation per year, depending on the climatic factors and food quality, and are thus particularly responsive to future climate change. The number of generations of tortricid moths is determined by several interacting factors, including temperature, humidity and food quality and differs geographically (Gallardo et al. 2009; Thiéry et al. 2014). All three species overwinter as diapausing pupae, with the induction of this facultative diapause being determined by decreasing day length (photoperiod) when individuals are in the egg or young larval stage (Nagarkatti et al. 2001; Roditakis and Karandinos 2001). Adult emergence from overwintering pupae in spring is clearly temperature-dependent which has motivated the development of forecasting models based on degree-days above a minimum threshold temperature.

Since monitoring of developmental progression in the field is pivotal for optimum timing of control strategies against grape berry moths, sex pheromone delta traps are widely used to monitor flight of males in each generation (Anshelevich et al. 1994; Ortega-Lopez et al. 2014) which may be complemented by food traps for females (Thiéry et al. 2006). As a result, data of emergence of the first moths in spring have been recorded for a given region over a long period of time, and provide a clear fingerprint of the effects of climate change on phenology of grape berry moths. Pheromone traps (Biotrap® Temmen GmbH, Germany) with species-specific synthetic lures (either (E,Z)-7,9-dodecadienyl-1-acetate for *L. botrana* or (E)-9-dodecenyl acetate for *E. ambiguella*) were installed in the middle of a commercial vineyard in the Rheingau region, Geisenheim, Germany (49°59′N, 7°56′E) and were checked weekly for captures of *L. botrana* and *E. ambiguella* males during the beginning of April and the end of October of the years 1983–2014. Trap catches were linked to local data for air temperature obtained from the German meteorological service (Deutscher Wetterdienst). Both *L. botrana* and *E. ambiguella* males showed a tendency for a slightly earlier, but non-significant appearance since beginning of the records in 1983 (Fig. 2). Adult moths emerge from overwintering pupae about 13 days earlier for *L. botrana* and 11 days earlier for *E. ambiguella* compared with 30 years ago (trend for the period of 1983–2014). A plot of the mean temperature during winter and early spring months (November–April) against date of first flight of *L. botrana* and *E. ambiguella* males shows a strong correlation between higher winter temperatures and earlier emergence of males from pupae in the field (Fig. 3). Thus, the observed advanced appearance of adult grape berry moths in European vineyards throughout the last three decades is most likely due to an increase in winter and early spring temperatures. As a consequence, if moths appear earlier in spring, they will have an extended period of time available to interact with their host plant, given that grapevine is also responding to climate warming in a similar manner, i.e. shifting to earlier bud burst and blooming, which is in fact the case (Schultz and Jones 2010).

Modelling studies have recently used phenological models of grapevine and/or grapevine moths and applied these to future climate change scenarios. Tobin et al. (2008) point out that for the American grape berry moth *E. viteana,* milder winters and warmer spring temperatures will have pronounced effects on voltinism, since generation duration and thus number of generations in this insect are driven by the quantity of degree-days accumulating prior to a diapause-inducing photoperiod. Using a phenology model, the authors further demonstrate that increases in mean surface temperatures of >2 °C can have dramatic effects on voltinism in this species, by shifting the timing of second generation oviposition to a significantly earlier date. This increases the risk of a late *E. viteana* summer generation with direct economic impacts for growers. However, for the same species, a recent study conducted by Chen et al. (2015) highlights the importance of characterizing the influence of changes in the diurnal temperature range in addition to effects of an increase in mean temperature alone. In a study focussing on the Italian Alps, Caffarra et al. (2012) predict a loss in grapevine yield due to increasing temperatures, which will result in an increased asynchrony between larvae-resistant growth stages of grapevine and phenology of *L. botrana* larvae. The potential geographical distribution and relative abundance of *L. botrana* in California and the continental U.S.A. were modelled by linking a holistic physiologically based demographic model for *L. botrana* to a mechanistic model of grapevine phenology and development (Gutierrez et al. 2012). Future climate change scenarios were included in this model by increasing observed mean temperatures by 2 and 3 °C, respectively. Accordingly, *L. botrana* abundance is expected to increase in northern California and other agricultural areas but is likely to decrease in hotter areas of southern California where summer temperatures might approach the upper thermal limit of this species. However, eradication of this insect in many areas in California as it is attempted by an elaborate action plan (Cooper et al. 2014) might make model predictions obsolete.

Range extension of leafhoppers as vectors of grape diseases

Threats posed by active and/or passive spread of a number of grapevine pathogens and their vectors into new grapevine growing areas are an important issue that has to be considered when assessing potential risks of global warming on pest and disease pressure in viticulture. In particular, intercontinental trade of a large quantity of planting material (including canes, grafts, scions and rootstocks) produced and exchanged commercially poses a very high risk for global spread of grapevine pathogens and/or insect pests. Recent examples for range extensions of grapevine pests due to global trade include various

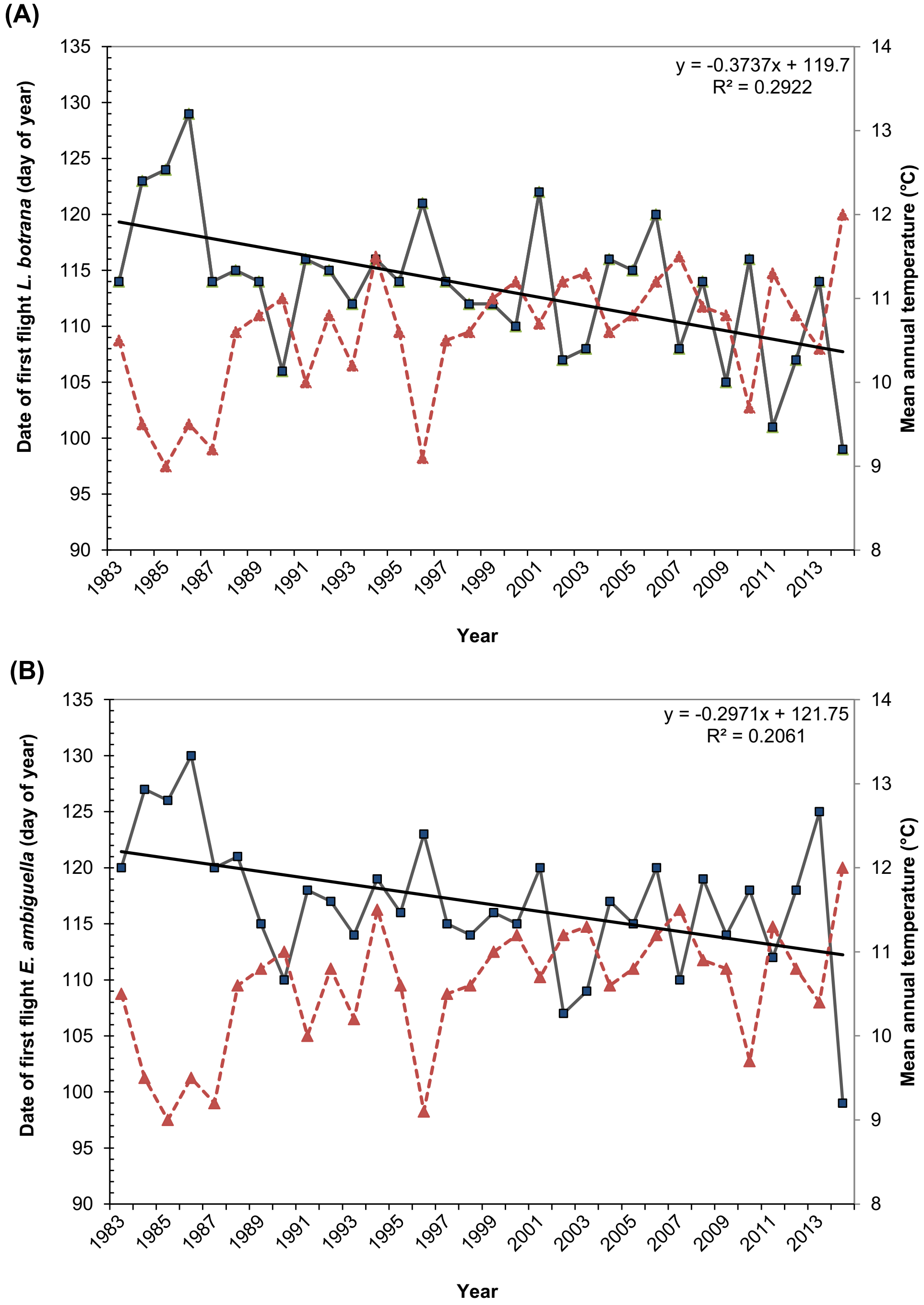

Fig. 2 Julian day of year of first *Lobesia botrana* (**a**) and *Eupoecilia ambiguella* (**b**) males emerging from overwintering pupae and trapped in pheromone-baited traps (*solid grey line*, left *y*-axis) and mean annual temperatures (*red dotted line*, right *y*-axis) in the Rheingau region, Germany between 1983 and 2014. The trends refer to appearance of males, which are 13 days earlier for *L. botrana* (**a**) and 11 days earlier for *E. ambiguella* (**b**)

leafhoppers, known for their potential to function as vectors of a certain group of prokaryotes, the phytoplasmas. These phloem-limited, insect-transmitted, plant pathogenic bacteria are responsible for hundreds of plant diseases worldwide (Christensen et al. 2005). In grapevines, phytoplasmas belonging to different taxonomic groups all cause fairly similar symptoms, including growth reduction, leaf discolouration, downward rolling of leaves, reduced quality and quantity of fruit and finally plant death. The most important and destructive phytoplasma disease of grapevines is Flavescence dorée (FD), known to occur mainly in France, Italy and Spain. Within the past 15 years, the yellows disease Bois noir (BN) has also become a main and commercially significant disease of grapevine all over Europe (Johannesen et al. 2008) and was recently identified in North American vineyards as well (Roll et al. 2007). Phytoplasma diseases of grapevine also occur elsewhere in the world including America, Canada and Australia and are usually referred to as grapevine yellows (Constable et al. 2004; Olivier et al. 2007).

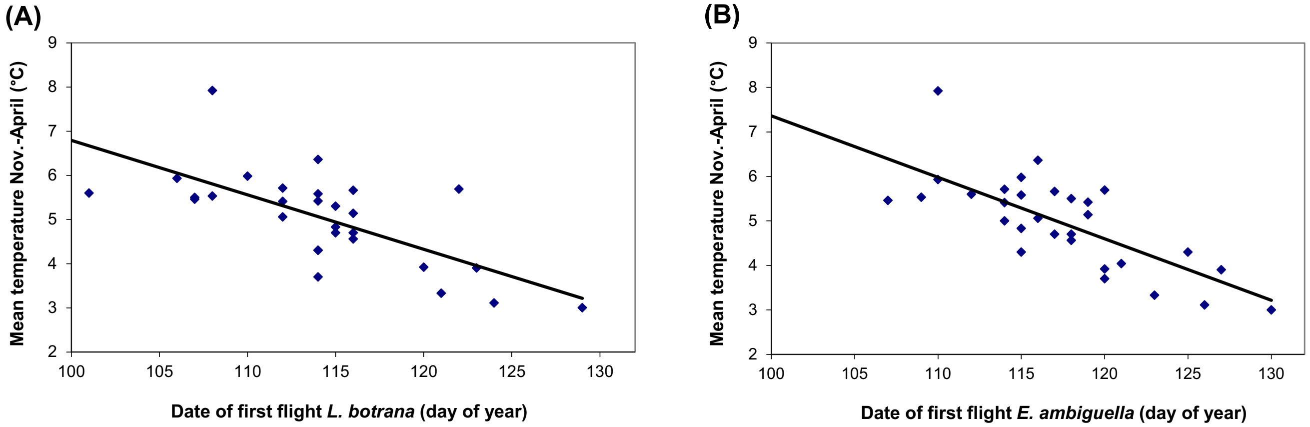

Fig. 3 Correlation curves for day of year of first *Lobesia botrana* (**a**) and *Eupoecilia ambiguella* (**b**) males emerging from overwintering pupae and trapped in pheromone-baited traps in the Rheingau region, Germany and the mean temperature from November to April in the same region. Data refer to the period of time between 1983 and 2014 and are significantly correlated (Pearson's correlation coefficients $r = -0.724$ for *L. botrana* and $r = -0.779$ for *E. ambiguella*)

Flavescence dorée and *Scaphoideus titanus*

Transmission of FD is currently assumed to be limited to the phloem-feeding nearctic leafhopper *Scaphoideus titanus* Ball (Cicadellidae), which is found only on cultivated grapes (*Vitis vinifera*) in Europe. This species originates from the north-eastern part of North America and was introduced as a single event in France without the FD phytoplasma probably with plant material as diapausing eggs under the bark of grapevine plants (Bertin et al. 2007; Papura et al. 2009, 2012). A French Cicadellidae inventory done in 1927 did not mention *S. titanus* (Ribaut 1952) and occurrence of *S. titanus* on grapes in France was first reported in 1958 (Bonfils and Schvester 1960). However, *S. titanus* could have been missed before because of it being present only in a small spatial area and at low population levels (Chuche and Thiéry 2014). Historically, a massive import of American grapes and multiplication in a few nurseries occurred during the grapevine phylloxera period and may have also introduced *S. titanus*. At first, area extension of *S. titanus* was rather slow, reaching Italy and Slovenia in the 1980s (Belli et al. 1985; Seljak 1987). Yet, geographical range expansion of this insect to most Southern European vineyards dramatically increased during the last three decades (Chuche and Thiéry 2014).

Scaphoideus titanus has one generation per year and overwinters in the egg stage under the bark of 2 year or older shoots. The climatic requirements of this leafhopper are consistent with its geographical origin from the northern part of America, thus being well adapted to cold winters: exposure of eggs to temperatures at or below 5 °C (regarded as a cold winter) induced an earlier hatching of larvae from eggs and thus an earlier termination of diapause of overwintering eggs than found in regions with milder winters (Chuche and Thiéry 2009). At the same time, egg hatchability is at an optimum at 22 °C (Falzoi et al. 2014), and warm summer temperatures are required for *S. titanus* to complete its life-cycle (Chuche and Thiéry 2009, 2014). However, winter temperatures differentially affect egg incubation time in males and females (Chuche and Thiéry 2012). Thus, warm winters could be expected to have negative effects on the population dynamics of *S. titanus* by altering future proportions of adult males to females.

Currently, *S. titanus* is present up to the 45th degree of latitude in Europe, but it is progressively extending the northern border of its range. Even under current climatic conditions, but particularly with summer temperatures increasing, this insect will certainly have the potential to get established in wine-growing regions north of the 46th degree of latitude (Maixner 2005). Thus, the simultaneous presence of FD infected vines and its vector *S. titanus* will induce a rapid progression of this disease into currently unaffected areas. Since grapevine FD phytoplasmas are listed as an A2 quarantine pest in the region of the European and Mediterranean Plant Protection Organization (EPPO 2007), a couple of European countries have conducted a pest risk assessment for FD (and its vector) concerning the potential of entry, establishment, spread and economic damage within the given areas (Steffek et al. 2007). Such assessments point to the fact that the highest risk of introduction of *S. titanus* arises from the extensive trade of propagation material as well as from the passive or active spread of the vector, with current and especially future climate in middle and northern European wine-growing regions not limiting its permanent establishment. For North American, Australian and South African wine-growing regions FD is regarded as a serious threat and importation of rootstocks from certain European countries is regulated and controlled by import requirements.

From the perspective of climate change, some alternative insect vectors of grapevine phytoplasmas considered yet as anecdotic in the epidemiological process could increase in population densities or vector potential. A monitoring of such species would thus be important in future years.

Pierce's disease and *Homalodisca coagulata*

In the United States, another leafhopper nowadays poses a severe threat to much of the United States' wine and table grape production. The xylem-feeding leafhopper *Homalodisca coagulata* (Say) (glassy-winged sharpshooter, Hemiptera: Cicadellidae) is an efficient vector of *Xylella fastidiosa*, a plant pathogenic bacterium that reproduces in the xylem and plugs the water-conducting tissue of grape wines, leading to Pierce's disease (PD) (Redak et al. 2004). *Homalodisca coagulata* is native to the South-eastern United States and Northern Mexico, but increased numbers of this insect were first detected in California in the beginning of the 1990s (Martensson 2007). During 1997–2000, *H. coagulata* triggered very severe and devastating outbreaks of Pierce's disease in Californian vineyards, causing serious concerns to the viticultural as well as other horticultural industries (Hopkins and Purcell 2002). A couple of sharpshooter species native to California can also function as a vector for *X. fastidiosa*, yet PD outbreaks before the end of the 1990s differed in pattern and severity from epidemics involving *H. coagulata*. For example, cases of PD in California before that time were typically showing a gradient in terms of plants infected within a vineyard, with higher number of plants being infected at vineyard margins decreasing rapidly with distance from the border (Martensson 2007; Redak et al. 2004). Differences in recent PD epidemics are attributed to characteristics of the biology of the invasive vector species *H. coagulata*, like its polyphagous nature and association with, e.g. citrus plants and a variety of other plants frequently bordering vineyards. Moreover, winter activity of *H. coagulata* and its high dispersion capacity result in longer distances and greater speed of PD spreading compared to other PD insect vectors (Blua and Morgan 2003). Hence, *H. coagulata* is a well-suited vector transmitting strains of the bacterium *X. fastidiosa* very efficiently to grapevine as well as other cultivated plant species such as almond, citrus and stone fruits and exemplifies the biological risks associated with the introduction and/or range extension of an exotic species into new areas.

The geographic pattern of reported PD incidences together with the fact that diseases caused by *X. fastidiosa* are mainly restricted to plants grown in tropical or subtropical environments suggests that climate, particularly winter temperatures, appears to be a key factor in the epidemiology of PD (Redak et al. 2004). Feil and Purcell (2001) proved experimentally that *X. fastidiosa* populations inside a grapevine plant decline when temperatures within xylem vessels are below 5 °C for a given period of time ("cold curing"). A mathematical model for predicting the effect of "cold curing" of grapevines inoculated with *X. fastidiosa* was recently developed (Lieth et al. 2011). However, different *X. fastidiosa* strains apparently show a different ability to cope with low winter temperatures (Martensson 2007). In addition, severity of PD disease has increased in certain regions in the South-western US within a period of time of just 6 years as a result of warmer winter temperatures (Anas et al. 2006). For the insect vector *H. coagulata*, different minimum threshold winter temperatures for overwintering adults are reported, ranging from −7 °C (Martensson 2007) to an accelerated mortality of *H. coagulata* at temperatures ≤10 °C (Johnson et al. 2007). The latter authors showed that the insects did not display any feeding activity at temperatures below 10 °C and hence died. This suggests that threats due to the presence of *H. coagulata* may vary with the severity of local winter temperatures. Taking future climate warming scenarios into account, models predict an increase in distribution ranges and severity of glassy-winged sharpshooter and *X. fastidiosa* infections in California (Gutierrez et al. 2011).

To assess the invasion risk posed by both *X. fastidiosa* and *H. coagulata* to currently unaffected areas of worldwide viticulture, climate modelling programmes were applied to biological parameters for both the bacterium and its insect vector (Hoddle 2004; Rathe et al. 2012). According to these models, under the prevailing climatic conditions, *H. coagulata* could get permanently established in the major wine grape growing regions of New Zealand, Australia, the Bordeaux region of France, as well as in the central and southern grape growing areas of Italy and Spain. Climate models for *X. fastidiosa* further forecast that cold stress will at the same time exclude this bacterium from most of New Zealand's and few viticultural areas of Australia, from all of France, as well as from the northern and central areas of Spain and Italy (Hoddle 2004). Presence and establishment of *X. fastidiosa* have been recently reported for Southern Italy (Cariddi et al. 2014) with devastating effects on local olive production (EFSA 2015). Survival and establishment of both the pathogen and its vector would certainly be possible in some grape-producing areas of Chile and the Western Cape Province in South Africa. Accordingly, most of these countries regard the *Homalodisca-Xylella* complex as a serious threat and are considering various quarantine and/or phytosanitary regulations to prevent potential introductions and subsequent disease outbreaks. As lower winter temperatures are the main factor limiting the current geographic range of both organisms, global warming, and especially milder winter temperatures in grapevine growing areas, will certainly support potential establishment of both the insect vector and the pathogen of PD in currently unaffected areas.

Geographic distribution of vine mealybug Planococcus ficus and its natural enemies

The vine mealybug *Planococcus ficus* (Signoret) (Homoptera: Pseudococcidae) is a phloem-feeding insect able to feed on all parts of the grapevine plant, which is regarded as a key pest in many countries around the world with grapevine cultivation (Daane et al. 2012). Damage is caused mainly through feeding of mealybugs on leaves which may inhibit photosynthesis and can result in defoliation. In addition, excretion of honeydew often leads to sooty mold growth, defoliation, and in prolonged cases, vine weakening (Daane et al. 2006). Economic damage caused by *P. ficus* is enhanced by the fact that this insect may also act as a vector for grapevine leafroll-associated virus (GLRaV), one of the most economically destructive grapevine viruses (Almeida et al. 2013). Recently, *P. ficus* was introduced into California and has since quickly spread, highlighting concerns of range expansion both in the USA and other countries. Seasonal development of vine mealybug is temperature-dependent. Based on region and climatic conditions, three to seven generations are completed under field conditions (Daane et al. 2012). In order to predict further spread of this species under different climate change scenarios, Gutierrez et al. (2008a, b) modelled the current and putative future geographic distribution of *P. ficus* in different locations in California. Interestingly, the authors also included the major natural enemies of *P. ficus*, namely a coccinellid predator (*Cryptolaemus montrouzieri*) and two parasitoid wasp species (*Anagyrus pseudococci* and *Leptomastidea abnormis*). For the regions studied, their model predicted an increase in *P. ficus* densities under future climate change scenarios because of a failure of biological control. This failure will be mainly due to an increasing search for shelters against heat stress by vine mealybugs which are inaccessible to natural enemies, despite the fact that both densities and range of its main respective antagonists will as well as increase under rising temperatures. Thus, this study highlights the need to include tri-trophic interactions when predicting future distribution ranges of grapevine pest insects.

Future management and research needs

Currently, knowledge on how insect pests as well as their interactions with grapevines and natural enemies present in the vineyard are actually influenced by climate change is limited. Exact predictions regarding future grape yield losses, quality changes or which vineyards or countries with viticulture will be most affected by climate change are thus somewhat speculative. However, the few examples presented here illustrate the complexity of the implications of climate change on plant protection strategies in global viticulture. Growers have to face the establishment of new pests and diseases in their area, as well as anticipate a change in population densities of autochthonous and already well-established insect pests in the vineyard. Adaptations of growers to mitigate climate-related risks in terms of plant protection strategies thus have to take into account effects of climate warming on grapevines, the respective pest insect species and its natural enemies. Most data available on the effect of climate change on grapevine plants and interacting organisms are, however, generated in growth chambers or under laboratory conditions (Pugliese et al. 2010; Rogiers et al. 2011; Salazar-Parra et al. 2012; Salazar Parra et al. 2010). Yet, field studies also show indirect effects via modifications of plant quality or via climate change related adaptations in vineyard management practices, e.g. that vineyard irrigation can reduce leafhopper populations (Daane and Williams 2003). Overall, for understanding environmental stress physiology of grapevines, responses have to be studied from the gene to the whole plant and vineyard level (Schultz and Stoll 2010). This is also relevant for studying the interactive effects of elevated CO_2 and other stress factors on the complex interactions between grapevines, insect pests and their natural enemies, which are best studied in free air CO_2 enrichment (FACE) facilities (Long et al. 2004). For grapevines, FACE studies are scarce with the exception of the studies performed by Bindi et al. (2001).

Further gaps of knowledge concern life history traits of the main parasitoids and natural enemies of key grape insect pests like *L. botrana* or *E. ambiguella*. Rearing of parasitoids as a prerequisite for generating sound life history data is sometimes challenging to achieve under laboratory conditions and field data are difficult to obtain. However, as pointed out above, an understanding of modified tri-trophic interactions is important for a robust prediction of future outbreaks and population dynamics of grape insect pests and should thus not be neglected.

An important trait in the life of moth species is the sex pheromone produced by females which amount and volatility conditioning their reproductive success. Climate change may have profound effects on semiochemical communication and this should be carefully and intensively studied in future years. Also, the ecologically friendly control method based on pheromones, mating disruption, will undoubtedly be affected in an unknown way by temperature, wind and hygrometry changes. Research should be encouraged in this area.

In addition, existing population models have to be adequately linked to various climate change scenarios (Seem 2004). The model of Gutierrez et al. (2008a, b) on the current and putative future geographic distribution of the vine mealybug *P. ficus* and its natural enemies is an excellent example of the need to include organisms from several trophic levels. While this aspect makes modelling approaches much more complex, existing models for forecasting population levels of insect pests have to be refined and extended, for example, to tri-trophic interactions related to grapevine plants.

Author contribution statement

AR and DT conceived the manuscript structure, collected literature and wrote the manuscript. AR analysed data on *Lobesia botrana* and *Eupoecilia ambiguella* phenology. Both authors read and approved the manuscript.

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Compliance with ethical standards

Ethical Statements This article is a review paper and does not contain any experiment with animals performedby any of the authors.

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