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REVIEW ARTICLE

Biological protection against grape berry moths. A review

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Abstract

Grape is a major crop, covering 7.5 M ha worldwide, that is currently being confronted with three main challenges: intensive pesticide use that must be reduced, invasion by new pests/diseases, and climate change. The biological control of pests and vectors would help address these challenges. Here, we review the scientific literature on the biological control of grape moths by macroorganisms (excluding nematodes). Two components, biological control with an active human role, mainly using biocontrol agents through inundation or inoculation, and conservation biological control, are considered. The major points are the following. (1) Tortricid grape moths seriously damage grapes worldwide, causing yield losses and quality reduction. The more geographically widespread species, *Lobesia botrana*, continues to extend its range, invading South American and, more recently, North American vineyards. (2) Parasitoids and predators (including arthropods, birds, and bats) that can control grape pests are very diverse. (3) Different methods exist to assess pest control efficiency in the field but some of them remain to be developed. (4) Environmental factors, including host plants, landscape, grass or floral covers, and organic practices, affect the natural control of grape moths. (5) Pest resistance to parasitoids strongly depends on their immune system, which is controlled by the host plant. Future climate changes may modify this tritrophic interaction and thus affect biological control strategies. We conclude that biological control has a great deal of potential in viticulture and that addressing these key factors would improve the efficiency levels of biological control strategies. This would help growers and stakeholders to significantly reduce insecticide use in vineyards.

Keywords *Lobesia botrana* · *Eupoecilia ambiguella* · Biodiversity · Agroecology · Viticulture · Agricultural practices · Landscape architecture · Parasitoids · Predators

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1 Introduction

Crops worldwide are the targets of more than 10,000 insect species (Dhaliwal et al. 2010), which are responsible for huge annual losses of between 20 and 50% of total production (Thacker 2002; Oerke 2006). Given the rate of human population growth, protecting crops from damage caused by pests is a major challenge to ensuring an adequate food supply in the future (Thomas 1999; Tilman et al. 2011). The extensive use of chemical products to control crop pests is now widely criticized because of their negative effects on the environment and trophic chains, from plants to humans (Hallenbeck and Cunningham-Burns 1995; Desneux et al. 2007; Geiger et al. 2010). Moreover, owing to the past irrational use of pesticides, some insect pests have acquired forms of resistance, making them less susceptible to biochemical products (Roush and Tabashnik 1990; Boyer et al. 2012). For the past few decades, the scientific community and governmental agencies have recommended the use of alternative, less invasive and more environmentally friendly methods of control to make agriculture more sustainable. Controlling pests through biological control and integrated pest management strategies are potential ways to address current ecological and societal concerns (Kogan 1998; Thomas 1999; Way and Van Emden 2000; Brewer and Goodell 2012).

Biological control and integrated pest management aim at optimally managing insect pests using different techniques, like the use of chemical mediators to disrupt mating (i.e., insect pheromones), autocidal control (based on the release of sterile males), and auxiliary macroorganisms (Thacker 2002; Walter 2005), without disturbing ecosystem functions (Ehler 2006; Naranjo and Ellsworth 2009; Abrol and Shankar 2012). At least two strategies based on the activity of auxiliary macroorganisms can be developed: (i) biological control based on endogenous biodiversity from crops and the adjacent seminatural habitat and (ii) natural enemy releases. To maximize their efficiency, such control methods must consider the ecology of targeted pests and natural enemies, as well as the relationships among trophic levels, including host plants (Ferguson et al. 2005; Pérez-Staples et al. 2012).

Here, we focus on grape, which is a major crop worldwide, with a vine area of 7.52 million ha that is targeted by numerous pests and diseases, resulting in very high levels of pesticide treatments (e.g., in 2010, the treatment frequency ranged from 10 to 25 times per year in France; Butault et al. 2010) with total amounts of active substance in kilograms per hectare in average 21.4 (EU) and, respectively, 49.6 (Portugal), 32.6 (France), 31.1 (Germany), 20.3 (Greece), and 17.8 (Italy) (Endure 2006). Among the numerous insect pests of grapes, the two tortricid Lepidoptera, the European grapevine moth *Lobesia botrana* (Den. & Schiff.) and the grape berry moth (GBM) *Eupoecilia ambiguella* (Hubn.), have been worldwide harmful pests for years in viticulture and often cause high levels of damage to grape bunches (Thiéry et al. 2011a) (Fig. 1). These two main species have very similar traits and will be grouped further in this review as GBMs. Surprisingly, no accurate quantitative economic impact is available for GBMs. One *L. botrana* larva is capable of damaging between 2 and 10 berries, depending on the cultivar and the grape phenology, and up to 20 to 30 larvae per cluster may occur in heavily attacked vineyards (Delbac and Thiéry 2016). In addition to direct predation on the berry, the presence of larvae encourages bunch rot development (causal agents being *Botrytis cinerea*, *Aspergillus carbonarius*, and *Aspergillus niger*), which results in severe qualitative and quantitative damages (Cozzi et al. 2006; Delbac and Thiéry 2016). Currently, these pests are mainly controlled by synthetic insecticides, which can be neurotoxic (e.g., pyrethrinoids and indoxacarb); insect growth regulators, like flufenoxuron; and recently, muscle contraction inhibitors, like emmamectin. Thus, viticulture must be adapted to the new challenges of pest management, and the development of biological controls against these pests is promising (Thiéry 2011). Alternative treatments against GBMs have already been produced, and they mainly rely on natural insecticides including sprays of *Bacillus thuringiensis* (Bt) toxin (see Pertot et al. 2017 for a recent review) and on mating disruption by sex pheromones (recently reviewed in Ioriatti et al. 2011). Biological control based on macroorganisms (parasitoids and predators) could also be developed as a valuable alternative to chemical pest control in viticulture in combination with these two methods (Mills and Danne 2005; Moreau et al. 2009; Thiéry 2011).

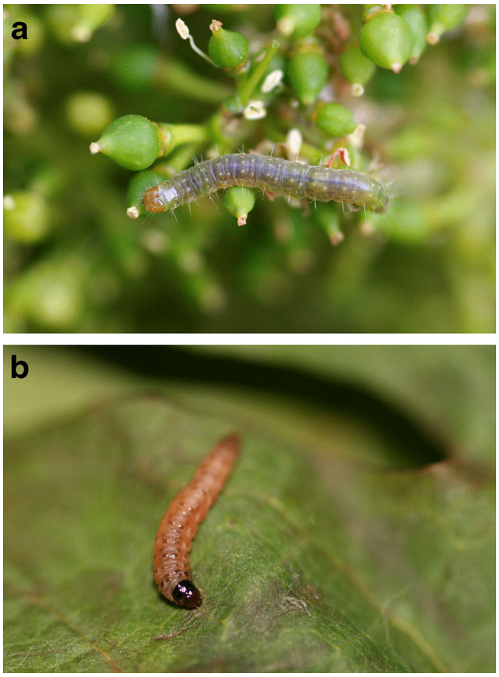

Fig. 1 Fully grown (5th instar) larva of **a** *Lobesia botrana* (picture F. Vogelweith) and **b** *Eupoecilia ambiguella* (picture F. Vogelweith), on vine leaves. Larva length is c. 1 cm

Despite the numerous studies carried out in ecological chemistry, physiology, and behavior to improve the effectiveness of grape pest management (Thiéry 2008; Ioriatti et al. 2011), GBMs continue to proliferate in vineyards, which suggests that control methods have not been optimized.

The objective of this review is to synthesize the literature regarding the biological control of GBMs. It will focus on the biological control of GBMs by beneficial macroorganisms, including arthropods, birds, and bats, and will consider the biological and ecological factors that may affect the efficiency levels of such biological control strategies. The key factors identified in this review should help increase our understanding of the context dependency and the variability associated with biological control strategies and thus aid in their future development to protect grapes from GBMs.

2 Grape berry moths in vineyards

The two GBMs, *L. botrana* and *E. ambiguella*, are polyphagous and plurivoltine, producing two to four generations per year under European vineyard conditions (Thiéry 2008) (Fig. 2). While the larvae develop on more than 30 different food plants, these polyphagous species occur mainly on grape varieties and almost exclusively develop on flowers and berries. Therefore, grape provides an important and continuous resource from spring to autumn, allowing the establishment of high population levels, which can reach over 15–30 larvae per grape cluster in some places (Thiéry et al. 2014; Schellhorn et al. 2015; Delbac and Thiéry 2016). They undergo diapause in the winter as pupae under grape stock bark or inside the nonharvested grape bunches, and then adults emerge in early spring for nuptial flights. Interestingly, *L. botrana* and *E. ambiguella* belong to the Olethreutini subfamily, a group of species that oviposit individual eggs unlike most moths, which lay egg clusters (Moreau et al. 2016). This trait is interpreted as an oviposition strategy for limiting exposure to egg parasitoids and predators, which have a discrete and cryptic host/prey resource. Neonatal larvae can penetrate berries within the few hours after hatching. Fully grown larvae rarely move from one bunch to another (Torres-Vila et al. 1997), and when the adult density is high, high larval populations may also occur, with up to 30 larval *L. botrana* per *Cabernet sauvignon* bunch (Thiéry et al. 2014). Thus, the spatial distributions of eggs and larvae are mostly the result of the oviposition behavior performed by the females (Gabel and Thiéry Gabel and Thiéry 1992, 1996). During their development in June, the larvae of these two moth species build individual nests, called "glomerulae," with their silk (Delbac and Thiéry 2016). The nests provide shelter and protection against adverse conditions (i.e., insulation from temperature variation and a barrier against predators and parasitoids). In July and August, the larvae of these two species are berry borers.

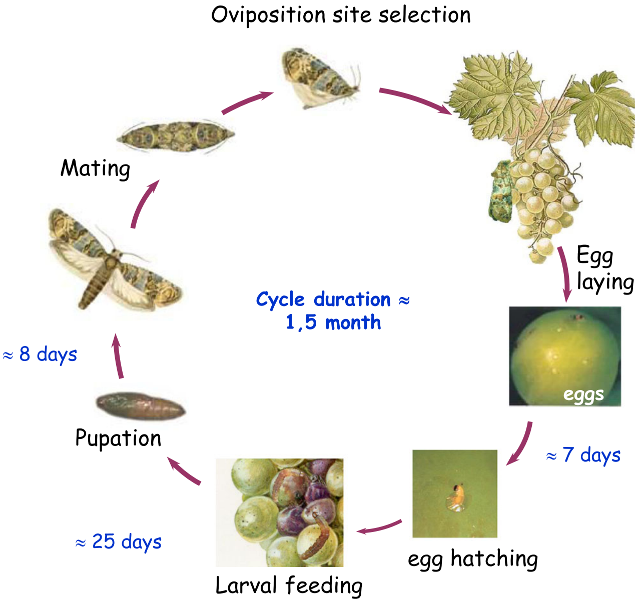

Fig. 2 Life cycle of grape berry moths, as represented for *L. botrana* showing the main stages. Duration is indicative and varies as a function of external temperature. Durations provided are those recorded in vineyards for the spring generation in south west France (1 month in summer). The two species *L. botrana* and *E. ambiguella* have very similar life cycle. In SW France, *Lb* accomplishes three or four generations per year, *Ea* two or three cycles (D. Thiéry and N. Maher)

3 Grape pests' natural enemies in vineyards

Globally, both the species richness and evenness of natural enemies increase the capabilities of natural pest control services in agrosystems (Letourneau et al. 2009; Crowder et al. 2010). This is the result of nonexcluding mechanisms, either a complementarity effect or a sampling effect (Straub et al. 2008). The complementarity effect predicts that pest suppression resulting from different natural enemy species is equal or greater than the sum of the suppression induced by each species alone. This relationship can be explained by resource complementarity owing to niche partitioning or facilitation (Straub et al. 2008). The sampling effect hypothesis states that a larger number of species in a given assemblage increase the probability of including an effective predator that contributes more than the other to the pest control function (Loreau and Hector 2001; Straub et al. 2008). Promoting the abundance and diversity of natural enemies is therefore expected to optimize natural pest control services in vineyard landscapes. However, the exact roles of several species and functional groups found in vineyards are not known.

Contributions to the biological control of GBM can come from either natural populations of arthropod predators or parasitoids and also from avian and mammalian predators (Thiéry et al. 2001; Sentenac 2011; Vincent et al. 2012; Rusch et al.

2015 for a recent issue). Increasing attention is currently being placed on arthropod biodiversity, which may have potential owing to their natural predation and parasitism capabilities. As examples, impressive numbers of carabid beetle species (124 in Goulet et al. 2004; 39 in Rusch et al. 2016) and 97 spider species (Bolduc et al. 2005) have been found in vineyards. Larval or egg parasitoids are also very abundant and diverse in vineyards (Thiéry et al. 2006; Thiéry et al. 2011b; Moreau et al. 2009; Sentenac 2011). To date, these studies have only established the occurrence of a large diversity of natural enemies, but their control potential has not been evaluated.

3.1 Parasitoids

Current vineyards are far from being "no parasitoid lands." In lectures or training courses, students and growers are always surprised by a list of parasitoids found in most vineyards, with more than 70 species that are mainly found in Hymenoptera (Thiéry 2008; Loni et al. 2016) (see Table 1 for an abbreviated list). Recently, in a study conducted in Australian vineyards, 20–30 parasitoid species were found (Paull and Austin 2007). In addition to the host density, which is a main driver of parasitoid populations, viticulture practices, such as organic viticulture or the use of interrow grass covers and floral strips, also favor a complex parasitoid community (Genini 2000). Globally, recent research indicates that landscape and climatic conditions also affect the diversity of parasitoids that naturally occur in a vineyard (Moreau et al. 2009; Loni et al. 2016). Clearly, understanding how such factors contribute to the variation in biodiversity requires further study.

Some species of parasitoids are rather cosmopolitan and found worldwide, such as the Ichneumonid *Campoplex capitator* or the Pteromalids *Dibrachys* spp., possibly because they are more plastic in their ecological requirements (Moreau et al. 2010). Other species are less frequently observed and are limited to certain vineyards or vine production regions. An example is *Exochus tibialis*, which was exclusively found in Switzerland (in the Valaisan vineyards, Switzerland) and Alsace (France) in a large field survey performed by Moreau et al. (2009).

The Ichneumonid *C. capitator* (previously named *Campoplex majalis* for its strong occurrence in spring) was probably the first well-studied larval parasitoid (Audouin 1842; Jolicoeur 1894). This species is described as a specialist parasitoid that has a large expected foraging distance (Xuéreb and Thiéry 2006). Because it is able to undergo diapause in its host, it has the advantage of good synchrony with the pest and is thus very active in the first spring generation.

In addition to Hymenoptera, the tachinids from the order Diptera can be important parasitoids, and *Phytomiptera nigrina* is suspected to increase its geographical area in the context of climate change (Reineke and Thiéry 2016). *P. nigrina* is an efficient parasitoid in warm vineyards (Thiéry et al. 2006) and will represent an interesting larval parasitoid against *L. botrana* in future years.

Trichogramma sp. has been known egg parasitoids in viticulture for more than a century. For instance, *Oophtora semblidis* (current name *Trichogramma semblidis*) was found in *L. botrana* and *E. ambiguella* eggs from several vineyards (Marchal and Feytaud 1911). To date, only the release of *Trichogramma* sp. has been attempted in viticulture on a large scale. The main reasons being that the moth eggs are easily mass produced and inexpensive, and the resulting larvae provide an efficient level of biocontrol against other moth pests (e.g., the European corn borer). They were first used in 1980 against GBM eggs (Barnay et al. 1999; Reda Abd el Monsef 2004; Hommay et al. 2011; Walton et al. 2012), the American grape berry moth *Endopizza viteana* (Nagarkatti et al. 2003), and also against the light brown apple moth *Epiphyas postvittana* in Australian vineyards (Glenn and Hoffmann 1997). Several species of *Trichogramma*, such as *T. brassicae* Bezdenko, *T. cacoeciae* Marchal, *T. dendrolimi* Matsumura, and *T. minutum* Riley, have been used with significant but varying pest reduction results. Currently, the use of *Trichogramma* sp. against GBMs is still very marginal in viticulture, mainly because of the varying and inconsistent efficiency levels (Barnay et al. 1999; Walton et al. 2012). Even though the use of sulfur applications is suspected as deleterious for *Trichogramma* sp., we did not identify a scientific report stating that specific conclusion. Thus, the main factors for explaining these varying parasitism rates are the amounts of *Trichogramma* sp. released per surface area and the number of release points, which affects the size of the protected area (Hommay et al. 2011). Hommay et al. (2002) reported better results against the GBM when releasing *Trichogramma evanescens* at 800 instead of 400 points per hectare.

To increase the efficiency of *Trichogramma* sp. releases, several experiments investigated the roles of kairomones in the attraction of *Trichogramma* sp. The egg odors of *L. botrana* and *E. ambiguella* have been analyzed and rely mainly on C16–C18 fatty acids and esters (Gabel and Thiéry 1992; Thiéry et al. 1995). They are well detected by conspecific females, and the arrestment of *T. brassicae* has been described in response to oleic acid (Frenoy et al. 1992). Some evidence also exists that host females (pheromone and wing scales) may attract *Trichogramma* sp. (Fatouros et al. 2008; Milonas et al. 2009). Thus, the marking of the alternative host *Ephestia kunhiella* eggs with *L. botrana* scales in the laboratory increased the oviposition rates by *T. cacoeciae* (Barnay et al. 1999). This suggests that several *Trichogramma* sp. can use such kairomones to optimize their foraging behaviors in vineyards and that such semiochemicals may be useful for improving the efficiency of biological control programs. Surprisingly, such research efforts on *Trichogramma* sp. against grape moths have not been sustained in vineyards for the last few years. The three following reasons could help in

Table 1 Nonexhaustive list of parasitoids (alphabetic order) reported from the literature as natural enemies of grape moths in vineyards in west European countries. This list is selected and implemented from Thiéry (2008) and Sentenac (2011). Only species reported by at least 2 references in the former list are presented here

Species	Family	Host orders	Reported hosts in vineyards	Parasitized instars (when known)
Agrothereutes abbreviatus (F.)	Ichn	Lepidoptera	EA, LB	Pupae
Ascogaster quadridenata (Wesm.)	Ichn	Tortricidae	LB	Larvae, pupae
Brachymeria minuta (Wesm.)	Chal	Lep, Dip	EA	
Campoplex capitator (Aub.)	Ichn	Tortricidae	EA, LB	L3-L4
Diadegma fenestrale (Holm.)	Ichn	Lepidoptera	LB, SP	Larvae
Dibrachys affinis (Masi)	Chal	Lepidoptera and other insects	EA, LB, SP	L4-L5
Dibrachys cavus (Walk.) (syn *boucheanus*)	Chal	Lepidoptera and other insects	EA, LB, SP	L4-L5, pupae
Dicaelotus inflexus (Thom.)	Ichn	Lepidoptera	LB	Pupae
Dicaelotus resplendens (Holm.)	Ichn	Lepidoptera		
Elachertus affinis (Masi)	Chal	Tortricidae	EA, LB, SP	Larvae
Exochus tibialis (Holm.)	Ichn	Lepidoptera	LB	Larvae, pupae
Gelis areator (Panz.)	Ichn	Lep, Hym	EA, LB	Larvae
Goniozus claripennis (Först.)	Beth	Lepidoptera	PS	Larvae
Ischnus alternator (Grav.)	Ichn	Lepidoptera	LB	Pupae
Itoplectis alternans (Grav.)	Ichn	Lep, Hym	LB, SP	Pupae
Itoplectis maculator (Fabr.)	Ichn	Lep, Hym	EA, LB, SP	Pupae
Itoplectis tunetana (Schmied.)	Ichn	Lep, Hym	EA, LB	Pupae
Phaeogenes melanogonos (Gmel.)	Ichn	Lepidoptera	EA, SP	Pupae
Phaeogenes planifrons (Wesm.)	Ichn	Lepidoptera	SP	Pupae
Phytomyptera nigrina (Meig.) (= *nitidiventris*)	Tach	Lepidoptera	LB	Larvae
Pimpla spuria (Grav.)	Ichn	Lepidoptera	LB	Pupae
Pimpla turionellae (L.)	Ichn	Lepidoptera	EA, LB, SP	Pupae
Pteromalus spp. (>8 species)	Ichn	Lep, Dip, Col, Hym	EA, LB, SP	Larvae, pupae
Scambus elegans (Woldst.)	Ichn	Lep, Hym	LB	Larvae
Tranosemella praerogator (L.)	Ichn	Lepidoptera	EA, LB, SP	Larvae
Trichogramma Minutum (Riley)	Chal	Lepidoptera	EA, LB, SP	Eggs
Trichogramma cacoeciae (Marchal)	Chal	Lepidoptera	EA, LB, SP	Eggs
Trichogramma evanescens (West.)	Chal	Lepidoptera	EA, LB, SP	Eggs
Triclistus sp.	Chal	Lepidoptera	LB	Larvae, pupae

EA, *Eupoecilia ambiguella*; *LB*, *Lobesia botrana*; *SP*, *Sparganothis pilleriana*; *Beth*, Hym. Bethylidae; *Chal*, Hym. Chalcidoidea; *Ichn*, Hym. Ichneumonidae; *Tach*, Tachinidae. *Pteromalus* and *Trichogramma* spp. regroup several species

explaining this occurrence: (i) The recent development of insect growth regulators and muscle inhibitors, which are easy to use, efficient, and cheap, in viticulture probably reduced the competitivity of parasitoid release methods; (ii) to a minor extent, mating disruption with sexual pheromones against *L. botrana* and *E. ambiguella* also negatively affected the development of such inundation or inoculation biological control techniques; and (iii) for larval parasitoids, to our knowledge, no commercial product is available for use in vineyards. *C. capitator* has been reared (Xuéreb and Thiéry 2006), as were the two species of *Dibrachys* (*cavus* and *affinis*) (Chuche et al. 2006) but only for research purposes. We hope that the commercial production of such biocontrol agents will become feasible relatively soon.

3.2 Arthropod predators

Owing to the variable habitats occupied by tortricid moths over their life span (eggs and larvae in vegetation, flying adults and nymphs wintering under the bark or in the soil), they are exposed to numerous vertebrate and invertebrate predator species. The arthropod predators of GBMs have been classified into occasional and regular predators; however, knowledge regarding their biology and impacts on pest populations comes from other crops (Sentenac 2011). Arthropod predators that are involved in the top-down control of grape moths encompass a large range of species, including spiders (each vineyard in the Bordeaux region can shelter several dozens of species; Muneret, PhD thesis unpublished data), harvestmen, true bugs

(Miridae, Anthocoridae, Nabidae, and Reduviidae), lacewings (*Chrysopa perla*, *Chrysoperla carnea*, *Chrysoperla lucasina*, *Chrysoperla affinis*, *Dichochrysa flavifrons*, and *Dichochrysa prasina* have been found in vineyards in France), and syrphids (only one species, *Xanthandrus comtus*) (Sentenac et al. 2011). To our knowledge, the identities of the more effective predators of tortricids in vineyards have been poorly investigated, and for the majority of these groups, limited data exists on their distributions in vineyard landscapes. For instance, harvestmen have been detected as tortricid larvae consumers in French vineyards (unpublished data). Recent studies on the codling moth in apple orchards showed that ground spiders are mainly involved in the predation of emergent nymphs during spring, while carabid beetles are involved in the predation of pupae during autumn (Boreau de Roincé et al. 2012). In addition, heteroptera, ants, and earwigs are involved in egg predation (Glen 1977; Glen and Milsom 1978; Frank et al. 2007). Additionally, 15% of earwigs, 8% of carabids, and 8% of spiders have ingested the tortricid codling moths (Unruh et al. 2016). Such data can be reasonably extrapolated to the vineyard system, which is similar to the orchard system. Spiders are rather diverse in vineyards (see Table 2 for the species detected in Bordeaux vineyards) and may be considered the key predators for controlling grape moths (Hogg and Daane 2010).

3.3 Predation by birds and bats

The predation of insect pests by birds and bats has been observed in several case studies (Bael et al. 2008; Karp et al. 2013; Maas et al. 2013). However, using birds and bats for biocontrol is currently being debated. Several observations indicate that birds may have adverse effects because they may also consume the grapes (Skopura and Hothem 1985; Watkins et al. 2000) and also arthropod's natural enemy (Jedlicka et al. 2014). Bats, however, would probably be very efficient, but we miss published reports in grapes and how to actively manage and use bats is less clear, especially since their spatial foraging range is not clearly known. For instance, the combined exclusion of birds and bats around cacao trees caused a significant increase in phytophagous insects and a decrease of 31% in crop yield (Maas et al. 2013). Similarly, in a coffee system, birds reduced phytophagous infestations by approximately 50% (Karp et al. 2013). These results highlight the key roles of birds and bats in the biological control of pests in perennial systems. Avian predation of the grape moth is currently motivating important research efforts (see for example Barbaro et al. 2017). The bird predation of moth larvae was affected by the interaction of bird functional community structure with habitat heterogeneity. However, to date, limited scientific literature is available on this topic. Moreover, Jedlicka et al. (2011) investigated the effects of conservation measures, such as providing nest sites for birds in vineyards. This measure strengthened pest control services to vineyard growers. The presence of nest boxes increased the species richness of avian insectivorous by 50% as well as the predation rates of *L. botrana* by 2.4 times compared with controls. These results in vineyards are in agreement with the literature on the potential positive roles of birds in pest control. However, birds can also have negative effects on overall pest control services through the predation of other natural enemies (e.g., spiders and parasitoids) (Martin et al.

Table 2 Main arachnid species collected in pitfall traps from the east Bordeaux vineyard (Entre Deux Mers and Libourne, Bordeaux vineyards). Family ranked by alphabetic order. Data source: Lucile Muneret PhD unpublished data. Identification by morphological criteria (Roberts 2009 and https://arachno.piwigo.com/)

Families	Species
Agelenidae	*Eratigena agrestis*
Gnaphosidae	*Callilepis nocturna*
Gnaphosidae	*Civizelotes civicus*
Gnaphosidae	*Drassodes lapidosus*
Gnaphosidae	*Drassyllus praeficus*
Gnaphosidae	*Gnaphosa lucifuga*
Gnaphosidae	*Haplodrassus dalmatensis*
Gnaphosidae	*Micaria coarctata*
Gnaphosidae	*Micaria pulicaria*
Gnaphosidae	*Setaphis carmeli*
Gnaphosidae	*Trachyzelotes fuscipes*
Gnaphosidae	*Zelotes aeneus*
Linyphiidae	*Agyneta rurestris*
Linyphiidae	*Diplostyla concolor*
Linyphiidae	*Erigone dentipalpis*
Linyphiidae	*Mermessus trilobatus*
Linyphiidae	*Oedothorax apicatus*
Linyphiidae	*Tenuiphantes tenuis*
Liocranidae	*Agraecina lineata*
Lycosidae	*Arctosa perita*
Lycosidae	*Hogna radiata*
Lycosidae	*Pardosa agrestis*
Lycosidae	*Pardosa hortensis*
Lycosidae	*Pardosa prativaga*
Lycosidae	*Pardosa proxima*
Lycosidae	*Pardosa vittata*
Lycosidae	*Trochosa robusta*
Lycosidae	*Xerolycosa miniata*
Salticicdae	*Neaetha membrosa*
Salticicdae	*Salticus scenicus*
Tetragnathidae	*Pachygnatha degeeri*
Theridiidae	*Asagena phalerata*
Thomisidae	*Ozyptila sanctuaria*
Thomisidae	*Xysticus erraticus*
Thomisidae	*Xysticus kochi*
Zodariidae	*Zodarion italicum*

2013; Jedlicka et al. 2014). The specific roles of birds in the control of specific pest species, such as grape moths, in vineyards are still debated and further applied research on management options to optimize avian predation services is needed.

The predation of flying moths by bats is already known and is currently gaining research interest in vineyards (Rydell et al. 1996). Bats are nocturnal, like adult grape moths, and observations of bats flying at a 5–10-m range above the vines match the flying behavior of *L. botrana* (our unpublished data). However, very few publications have focused on the predation activity of bats in vineyards. Predation, or at least contact with prey, can be recorded by typical ultrasonic vibrations, and recent observations in Burgundy (Sentenac, unpublished data) confirm that the predation of tortricid moth by bats could be considered as a potential factor in biological control. This ongoing study has presently recorded more than 15 species of bats in Burgundy vineyards (Table 3), with the most active species being *Pipistrellus pipistrellus*, *Pipistrellus kuhlii*, and *Eptesicus serotinus*.

Predation should, however, be checked carefully. First is by confirming the amount of grape moth adults of each species predated by analyzing DNA traces in bat guano (see also Section 4). Additionally, the feeding range of bats has to be carefully studied to allow their nesting behavior to be adapted to the control of grape moths. Interestingly, dispensers of *Thaumetopoea pityocampa* pheromones placed in pine forests positively influenced bat activity (Charbonnier et al. 2014). Even though the sonic detection by GBM has not been described to date, the capacity to escape bats should, however, be considered (Speakman and Rydell 2000). The escaping flight strategies of grape moths could be a component of the zigzagging or circular flight patterns observed in males and females, respectively. This type of flight has been observed in *L. botrana* (Gabel and Thiéry 1994) but may not be related to a bat escape behavior.

4 Evaluation of pest control efficiency in the field

As detailed above, vineyards are characterized by a high, sometimes unexpected, biodiversity that contains a large number of grape moth enemies. To estimate the potential natural pest control services in a vineyard, the effective predators and parasitoids that efficiently control GBM should be identified, and the predation and parasitism rates should be quantified in the field (see Birkhofer et al. 2017 for a complete review of methods to quantify biological pest control in the field). However, assessing the level of pest control in an agroecosystem is challenging because it requires a combination of different techniques for an accurate measurement (Birkhofer et al. 2017).

The most employed methods to assess parasitism rate in the field, and thus the potential control of pests by the parasitoid community, are based on a huge sampling of hosts as larvae (e.g., Moreau et al. 2009) or the use of sentinel methods (for example, the exposure of eggs to parasitoids) (Rusch et al. 2017a). The identification of parasitoid species is mainly based on morphological traits and requires accurate skills in systematics (MacFadyen et al. 2009; Sentenac 2011; Rusch et al. 2015). Such techniques are, however, time consuming and necessitate the good handling of collected pest larvae, which have to be raised until emergence (Agusti et al. 2005; Traugott et al. 2006). It also often leads to the underestimation of biological control potential because of sample death, and these techniques are often not compatible with the rapid detection of the parasitoid (Jourdie et al. 2008; Hrcek et al. 2011; Papura et al. 2016). To counteract these problems, more recent molecular methods that enable the detection of prey-specific DNA in the host body (for parasitoids), including grape berry moths, have been developed (Birkhofer et al. 2017). Two main complementary approaches are currently used in this very fast-moving field: diagnostic PCR that uses species-specific primers and DNA barcoding that uses next-generation sequencing and universal primers. Such methods allow the assessment of parasitism rates of several species simultaneously inside collected moth larvae (Wirta et al. 2014; Papura et al. 2016). Such techniques should, however, be improved by making them simpler and cheaper so that they can be used by technicians and vineyard advisors.

Additionally, using artificial prey, such as dummy caterpillars made of plasticine, is a useful technique to evaluate predation rates by vertebrates and invertebrates (Howe et al. 2009). Such techniques allow the predation rate of a given prey to be estimated by determining the number of predation marks as well as the identities of the predator groups based on distinctive bite marks. Distinctive marks can be attributed to chewing arthropods, small rodents, reptilians or birds (Barbaro et al. 2016).

In a more holistic way, it is often more informative to measure the potential biological control of a natural enemy community (parasitoids and predators) using different methods at the same time. To do this, researchers have used cage experiments and applied differential exclusion treatments (Rusch et al. 2013). Such approaches have the ability to evaluate the overall level of biological control in a given field over a given time period. Recently, a method using sentinel prey has been used to quantify the total biological control of natural enemies in vineyards (Rusch et al. 2017b). The exposure of grape moth eggs to parasitoids and predators is a rather easy technique that requires an insect stock culture with sufficient egg production. Fresh grape moth eggs can thus be exposed either on waxed paper or plastic sheets, but a more sophisticated procedure is to force females to oviposit on grape cuttings (either foliar or fructiferous) and to install such plants within the grape rows.

Table 3 Main bat species observed in Burgundy vineyards with recorded sonic casting flight or buzz. Observations and records by Gilles Sentenac (unpublished data)

Species	English common name	Casting flight	Buzz
Pipistrellus pipistrellus	Common pipistrelle bat	x	x
Pipistrellus kuhlii	Kuhl's pipistrelle bat	x	x
Eptesicus serotinus	Serotine bat	x	x
P. kuhlii/nathusii	Kuhl's/Nathusius' pipistrelle bat	x	x
Nyctalus leisleri	Leisler's bat	x	x
Myotis myotis/blytii	Greater/lesser mouse-eared bat	x	
Nyctalus noctula	Common noctule bat	x	x
Plecotus sp.	Brown/gray long-eared bat	x	
Barbastella barbastellus	Western barbastelle bat	x	x
Myotis nattereri	Natterer's bat	x	
Myotis sp.		x	
Myotis mystacinus	Whiskered bat	x	x
Miniopterus schreibersii	Schreibers' bent-winged bat	x	
Myotis emarginatus	Geoffroy's bat	x	
Myotis bechsteinii	Bechstein's bat	x	

Finally, some interesting in situ field video recordings were attempted in Australia to determine how habitat strata, and thus natural enemy communities, control another important polyphagous grape moth pest in Australian viticulture, *E. postvittana* (Frank et al. 2007). Similar techniques could be developed to measure the strength and efficiency of each member of such communities, and to evaluate the connectivity between the natural enemy habitat strata of predators and the grape clusters to be protected.

5 Key factors that induce variation in the biological control of grapevine moths

5.1 Effect of the host plant (including grape cultivar)

Phytophagous insect pests have evolved within a multitrophic environment, and many aspects of their physiology, behavior, and ecology have been shaped by interactions with other trophic levels (Poppy 1997; Karimzadeh and Wright 2008) (Fig. 3). Mainly, host plants directly affect the growth and adult fertility rates of phytophagous insects and indirectly the level of successful parasitism (Karimzadeh and Wright 2008). For example, a nutrient deficiency or/and toxic defensive compounds of the host plant slow-down the development of phytophagous insects, which extends the window of attacks for natural enemies (Benrey and Denno 1997). In grape moths, the egg size, the hatching success, and the larvae's developmental time depend on the grape variety. For instance, grape moths feeding on Gewürztraminer grapes have larger eggs, higher hatching success, and longer developmental times compared with moths feeding on other grape varieties (Moreau et al. 2006a, b). Moreover, the grape variety also influences the egg and larval parasitism rates (Moreau et al. 2009, 2010). Overall, the egg parasitism is higher on cultivars on which *L. botrana* laid larger eggs, but some grape varieties, such as Pinot, appear to be somehow repellent to parasitoids (Moreau et al. 2009). Looking deeper into the trophic interactions in a vineyard is a promising way to improve the efficiency of biocontrol programs because it aids in understanding biological control failures.

The efficiency of the natural enemies depends on their ability to bypass the sophisticated defenses used by grapevine moths (Greeney et al. 2012). The first line of defense that is particularly efficient against larval parasitoids involves escaping, twisting, and dropping (Greeney et al. 2012; Vogelweith et al. 2014). Once this barrier is passed by the natural enemies, the cuticles represent a very efficient way to fight against these natural enemies. Indeed, an individual with a thick and resistance cuticle will be less likely to be parasitize by a parasitoid (Vogelweith et al. 2014). Once morphological and behavioral defenses are bypassed, the last and most efficient defense against natural enemies, such as parasitoids, is the immune system (Greeney et al. 2012) (Fig. 4). In insects, the immune system relies on constitutive and inducible mechanisms (Lavine and Strand 2002; Siva-jothy et al. 2005). The constitutive defenses mostly involve the coordinated actions of the immune cells (the hemocytes) and the enzyme phenoloxidase (PO). Hemocytes insure most immune processes, such as the recognition and encapsulation of parasitoids and pathogens (Lavine and Strand 2002; Cerenius and Söderhäll 2004; Siva-jothy et al. 2005), while PO mediates the melanization of foreign bodies (Fig. 3). Then, the induced response mainly consists of the production of specific antimicrobial peptides by the hemocytes and the fat bodies a few hours after an infection (Haine et al. 2008) (Fig. 3). This production of

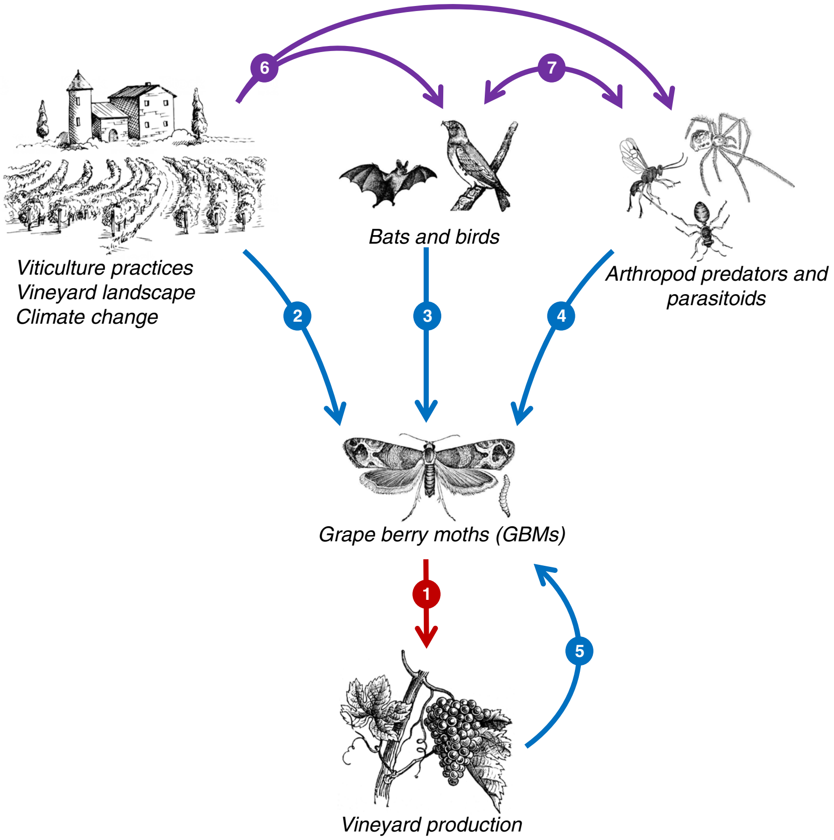

Fig. 3 Identified key ecological relations in vineyard relevant to improve the biological control management of the grape berry moths (GBMs) at different related scales, from plants, pests and natural enemies, to landscape and global environment. 1—Direct damages to grapes by GBs under efficient biological control management (Sections 1, 2, and 4 in the text); 2—effects of the vineyard environment including natural and anthropogenic factors on the susceptibility of GBMs to biological control (Sections 5.2, 5.3, and 5.4 in the text); 3 and 4—control of GBM populations by natural enemies in vineyards, through predation and parasitism pressures (Section 3 in the text); 5—relevant feedback of the effect of the plants on the susceptibility of GBMs to natural enemies, especially through the immune response of GBMs faced with parasitoids (Section 5.1 in the text); 6—indirect effects of the vineyard environment on the ability of natural enemies to control GBMs in the field; 7—interactions between upper trophic levels that may reduce the efficiency of the biological control program

antimicrobial peptides is often associated with a decrease in the PO enzyme system (Moret and Schmid-Hempel 2000; Vogelweith et al. 2011). Nutrition is recognized as a critical factor in immune defense and in resistance to natural enemies (Lazzaro and Little 2009; Ponton et al. 2011; Vogelweith et al. 2013) because the diet's quality and quantity might affect single or multiple immune parameters. For example, the grape variety has a strong effect on the larval immune system (in *L. botrana* and *E. ambiguella*), both in the laboratory and in the field (Vogelweith et al. 2011, 2013, 2015, 2016; Muller et al. 2015). In the laboratory, *E. ambiguella* larvae reared on Gewurztraminer possess more hemocytes but lower antimicrobial activity levels compared with larvae reared on other varieties (Vogelweith et al. 2011). These results suggest a trade-off between constitutive and induced pathways that are modulated by the grape variety (Vogelweith et al. 2011). This immune trade-off appears to result from the components of each grape variety more than from the elicitation of the immune system by bacteria growing on the berries (Vogelweith et al. 2015). Grapevine moths would, therefore, highly invest in their constitutive pathway in response to *B. thuringiensis*. It would then be easier for parasitoids to develop into larvae because they had already invested their energy to defend against the pathogens. However, this trade-off was not found in all grape varieties (Vogelweith et al. 2011), meaning that the biological control should be dependent on the grape variety considered. For instance, larvae reared on Gewurztraminer appear to be more efficient in their defense against parasitoids (higher hemocyte concentrations). Thus, releasing pathogens instead of parasitoids in vineyards containing the Gewurztraminer cultivar might be a more efficient way to control grapevine moths. Conversely, when larvae are developed on a cultivar that requires a higher investment in antimicrobial activity, releasing parasitoids might be the best way to control the grapevine moth population. However, cultivars may be mixed in a vineyard, which could limit this method. That is why the use of larval defenses should be a complement to other methods.

In addition, these defensive techniques are costly, and individuals are expected to invest differently in these defenses depending on their species and on the environmental threat. For

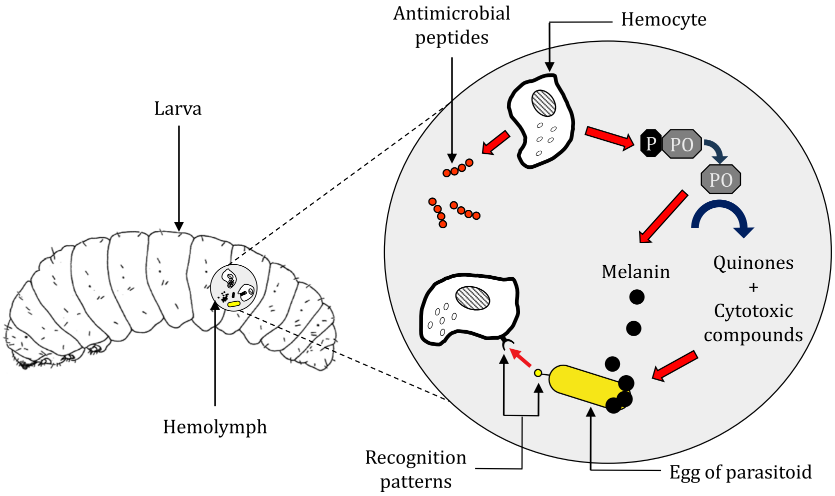

Fig. 4 Summary diagram of the immune response of an insect larva after the injection of a parasitoid egg (F. Vogelweith). Once the parasitoid egg is injected, hemocytes will immediately recognize the foreign body via the recognition patterns at the surfaces. The immune reaction will start with the recruitment of other hemocytes to cover the egg. Hemocytes will also allow the activation of the PO-PPO cascade which will release melanin to cover the egg and produce cytotoxic compounds to kill it. Few hours after the infection, antimicrobial peptides will be produced by the hemocyte to kill the remaining pathogens in the hemolymph

example, *E. ambiguella* invests more in physical defenses (thick and resistant integument) and less in behavioral defenses (e.g., twisting and dropping) and respond quickly to an immune challenge relative to *L. botrana* (Vogelweith et al. 2014). In the field, both the parasitism rate and successful parasitism are lower in *E. ambiguella* compared with *L. botrana* (Vogelweith et al. 2014), indicating that parasitoids might be more efficient in controlling *L. botrana* than *E. ambiguella* populations.

In the field, the larval immune system of *L. botrana* also depends on parasitism pressure (Vogelweith et al. 2013). Indeed, in populations experiencing a high parasitism pressure, larvae invest in higher immune parameter levels compared with populations under low parasitism pressure (Vogelweith et al. 2013). In populations with high levels of immune defenses, biological control might be difficult because their immune defenses could be adapted to the local high pressure from natural enemies.

These studies clearly show the value of increasing and applying our knowledge of tritrophic interactions between the host plant, the pests, and their natural enemies to improve the biological control of these insect pests. However, biological control was thought to be similar for *L. botrana* and *E. ambiguella* when co-occurring in vineyards. Based on their different defense-related investments, it could be important to integrate these results into biological control programs to select the most efficient natural enemies for each grapevine moth species.

5.2 Viticulture practices and biological control

Habitat manipulation is important for enhancing the biological control of arthropod pests. It is now well demonstrated that increasing vegetation diversity and/or structural complexity within fields or in the close vicinity can decrease pest attacks, increase the influence of natural enemies, and reduce crop damage (Letourneau et al. 2011; Tonhasca and Byrne 1994). These effects can be explained by the natural enemy and the resource concentration hypotheses (Root 1973). The former suggests that natural enemies are more abundant and/or diverse, as well as more effective, in suppressing herbivore populations in more diverse plant communities (Andow 1991). This effect is attributed to the higher attractiveness of diverse habitats to predators as a result of an increased availability of resources. The latter suggests that reduced herbivore populations and plant damage levels in more diverse habitats occur because of the lower probability of herbivores to find their host plants (Otway et al. 2005; Plath et al. 2012). This effect is attributed to the chemical stimuli masking host plant odors, visual camouflage, and/or physical barriers limiting the movements of individuals (Finch and Collier 2000 and the references therein). For instance, releasing "odor-masking" substances by nonhost plant species confers some protection to the associated host plant in a diversified plant community (Thiéry and Visser 1986; Finch and Collier 2000).

Several studies have found that such processes operated in grapevine agroecosystems. First, cover crop management affects natural enemy communities and biological pest control. Increasing the within-field plant diversity enhances natural enemy abundance and/or diversity (Letourneau et al. 2009; Shields et al. 2016). Using indigenous grass cover crops within vineyards benefits natural enemies, such as generalist predators and parasitoids, and increases the biological control of tortricids (Danne et al. 2010). In a recent study, Rusch et al. (2017b) found that full grass cover within vineyards strongly limited the attack rates of tortricids compared with vineyards with partial grass cover, despite the effect of landscape context on biological control. Altieri and Nicholls (2002) found higher infestation rates of two grape herbivores, including *L. botrana* in monocultures, when comparing different cropping systems (traditional vineyards based on agroforestry and modernized simple monoculture). They also found that monoculture vineyards exhibited lower numbers of predator and parasitoid species. Moreover, the provision of floral resources within vineyards by manipulating the ground cover increases the longevity and fecundity of parasitoids, which may result in higher parasitism rates of tortricids (Berndt et al. 2002; Begum et al. 2006; Berndt et al. 2006). For instance, buckwheat (*Fagopyrum esculentum*) and alyssum (*Lobularia maritima*) have beneficial effects on tortricid parasitoids (Begum et al. 2006). Similarly, mulching (e.g., covering the soil surface with a layer of organic material) enhances the abundance and/or diversity of carabids, hymenopteran parasitoids, dipteran parasitoids, hemipterans, and spiders without increasing insect pest abundance in vineyards (Thomson and Hoffmann 2007; Bruggisser et al. 2010). Second, contrary to such beneficial practices, tillage (e.g., reducing habitat complexity) has a negative effect on beneficial arthropods in vineyards (Sharley et al. 2008) as in other systems (Thorbek and Bilde 2004). In addition, pesticide applications also explain the variability in the efficiency of tortricid biological control by impacting natural enemy communities. For instance, Nash et al. (2010) found an effect of season-long pesticide applications on arthropod community structure and showed that high pesticide metric scores negatively impact the activity levels of beneficial taxa, reducing the potential for biological control.

Beyond specific farming practices, organic systems promote the abundance and diversity levels of weeds and natural enemies (Bengtsson et al. 2005; Garratt et al. 2011; Tuck et al. 2014). Studies comparing organic and conventional farming in viticulture showed contrasting effects on natural enemies and biological pest control. For instance, Bruggisser et al. (2010) showed that organic farming promoted neither diversity nor abundance at any trophic level (plants, grasshoppers, and spiders) in Swiss vineyards. However, in intensive agricultural landscapes, organic farming favors a local plant species' richness (Nascimbene et al. 2012), and higher abundance and diversity levels of spiders and carabids have been found in organic farming compared with conventional farming (Gaigher and Samways 2010, 2014; Caprio et al. 2015). Despite a limited number of studies and some contradictory results, 6 out of 11 studies found on the Institute for Scientific Information's Web of Knowledge (currently Clarivate Analytics' Web of Science) reported that organic farming, compared with conventional farming, in vineyards tended to enhance the abundance and diversity levels of natural enemies (Caprio et al. 2015; Franin et al. 2016; Froidevaux et al. 2017; Geiger et al. 2010; Peverieri et al. 2009; Puig-Montserrat et al. 2017).

However, further research is needed to understand the context-dependent effects of organic farming. For instance, relatively few studies have simultaneously examined the effects of organic and conventional farming on pest communities and crop damage, and nothing is known about the effective level of pest control between organic and conventional farming. Thus, even if pest species benefit from organic farming, they would exert a higher pressure on grape production even if the level of natural pest control is higher. In Bordeaux vineyards, for instance, grape moths were less parasitized in organic farming systems than in conventional ones (Rusch et al. 2015). This apparently counterintuitive result indicates that more studies examine the local and landscape effects of organic farming on natural enemies, biological control, and pest damage.

5.3 Vineyard landscapes and natural biological control

Landscape context, both in terms of composition and configuration, as well as trophic interactions, in agricultural systems affects population and community dynamics (Tscharntke et al. 2007; Rusch et al. 2010). Recent meta-analyses highlighted that landscape simplification through the loss of seminatural habitats affects the abundance and diversity levels of natural enemies as well as the biological control level (Chaplin-Kramer et al. 2011; Rusch et al. 2016). The positive effect of seminatural habitats on natural enemies and biological pest control is that they provide key resources and functions for natural enemies, such as overwintering sites and refuges from disturbances, alternative hosts or prey, as well as sources of nectar or pollen (Rusch et al. 2010). For instance, several natural enemies overwinter in woody or grassy habitats (Sarthou et al. 2014). Therefore, the spatial distribution between overwintering habitats and crops determines the distribution of individuals in the landscape (Rand et al. 2006). These results strongly suggest that conservation biological control will benefit from a landscape perspective.

Several studies found that maintaining seminatural habitats within vineyard-dominated landscapes benefits natural enemies and the biological control of tortricid moths (Thomson and Hoffmann 2009, 2013; Thomson et al. 2010; Barbaro et al. 2017; Pithon et al. 2016). The mean abundance of natural enemies within a vineyard declines with the distance from woody vegetation, leading to the higher parasitism and predation levels of tortricid moths in vine rows closer to woody habitats (Thomson and Hoffmann 2013). This distance effect was detected up to 40 m from the woody vegetation, thus providing guidelines for landscape management to increase pest control services. In a recent study, Barbaro et al. (2017) found that habitat heterogeneity at both local and landscape scales influences avian insectivory in vineyards by interacting with the avian community structure. Foliage-gleaning insectivores were found to be more abundant in landscapes that supported more seminatural habitats, suggesting an increase in their contribution to pest control along the gradient of landscape complexity.

In conclusion, local and landscape complexity levels, as well as their interactions, are key drivers of natural enemy communities and the biological control of tortricid moths in vineyard-dominated landscapes. However, we still lack a good mechanistic understanding of the relationships between the structure of natural enemy communities (e.g., taxonomic or functional) and the level of biological control. Thus, further studies combining data and molecular analyses are needed to identify the roles of trophic assemblages and to highlight the optimal structure of the food web that promotes the biological pest control of tortricid pests.

5.4 Effects of climate changes on tritrophic interactions and natural biological control

As ectotherms, insect pests are greatly sensitive to environmental temperature, which regulates metabolic reactions (Kingsolver 2009) and influences many physiological processes, such as growth (Angilletta et al. 2004), development (Zuo et al. 2012), reproduction (Fischer et al. 2003), and immune functions (Murdock et al. 2012). Such a temperature dependency is tightly linked to the ecology and evolution of life histories (Ragland and Kingsolver 2008) and, therefore, must be considered when attempting to develop sustainable biocontrol strategies against grapevine moths, especially in a changing environment. Global warming and the expected 0.3–4.8 °C increase in mean global surface temperature at the end of this century underscore the importance of this idea (Intergovernmental Panel on Climate Change 2014). This rapidly changing climatic context can be linked to the "hotter-is-better" hypothesis to predict how GBMs will impact vineyards under warmer environmental conditions. Indeed, this hypothesis postulates that ectothermic species adapted to warm conditions display the highest maximal fitness level and reach this optimum at high environmental temperatures (Kingsolver 2009; Knies et al. 2009). Thus, global warming benefits GBM by bringing the environmental temperature closer to their thermal optimum, especially in areas where thermal conditions remain colder than their thermal optimum (for instance, northern areas of the distribution range) (Deutsch et al. 2008). Thus, global warming may result in high GBM growth rates (Knies et al. 2009) and greater damage levels to crops. In addition to a direct thermal effect on GBM, global warming might also indirectly affect their performance by influencing two associated trophic levels: grapevine (Jones and Davis 2000) and natural enemies, like parasitoids (see Hance et al. 2007; Reineke and Thiéry 2016 for reviews). We summarize here several impacts of climate change on the physiology of grapevine moths and its consequences in terms of yield losses and pest management strategies.

Like many insects, *L. botrana* exhibits a higher developmental rate when exposed to warmer conditions (Torres-Villa 1996; Martín-Vertedor et al. 2010). Additionally, temperature is an environmental factor that triggers the termination of diapause in this species (Roditakis and Karandinos 2001). As a consequence, mild early springs promote a significant advance in the first emergence wave of adults from overwintering pupae and impact the voltinism of this species (Martín-Vertedor et al. 2010; Reineke and Thiéry 2016). For instance, in 2006, warmer conditions allowed the emergence of a fourth generation of *L. botrana* in Mediterranean areas, even though this species is usually trivoltine (Martín-Vertedor et al. 2010). This additional generation likely intensified the pressure exerted on crops (see Caffarra et al. 2012 and references therein). However, grapes also respond to global warming by shifting to an earlier phenology (e.g., earlier bud burst and blooming), which results in a significant advance in harvest dates and a shortened crop life cycle. This is observed in France where winegrowers are currently collecting grape bunches almost 1 month earlier than during the last 50 years (Jones and Davis 2000; Seguin and de Cortazar 2005; Schultz and Jones 2010). By doing so, they remove the resources that potentially allow the complete development of the late-season generation of the pests and their overwintering as diapausing pupae (Martín-Vertedor et al. 2010; Caffarra et al. 2012; Reineke and Thiéry 2016). Despite these potential benefits of global warming for the control of GBM populations, harvest dates are not just determined by temperature but also by grapevine variety, which influences plant phenology (Jones and Davis 2000). Consequently, it could be hypothesized that early ripening varieties, like Chardonnay, would be less prone to the detrimental effects of an additional GBM generation than late ripening varieties that would be exposed to the late pest generation before harvest (Caffarra et al. 2012). The detrimental effects of an additional generation on vine production could, therefore, be modulated by grape cultivars and the corresponding plant phenology.

Faster GBM development may influence their interactions with enemies naturally present or released in vineyards (see Section 3) and the associated consequences on biological control strategies that rely on these natural enemies. Temperature is a decisive factor modulating the ability of pests to fight against parasitoids through behavioral or their immune responses. To our knowledge, no study to date has investigated the direct effects of contrasting thermal conditions on the ability of GBMs to resist parasitoid pressure. However, recent results suggest that GBMs' immune functions can be modulated in the field by temperature (Vogelweith et al. 2013). In the scenario of a rising global temperature, the increased immune functions of grapevine pests would be problematic because they enhance the pests' ability to resist natural enemies, especially parasitoids, which decreases the effectiveness of biocontrol programs.

6 Perspectives and conclusions

The body of knowledge we have reviewed highlights several key factors operating at multiple spatial scales that influence the biological control of grapevine moths. We particularly show that host plant, farming practices at the field scale, and landscape context, as well as climate change, are driving grapevine moth population dynamics through direct effects on pest populations or indirect effects mediated by their natural enemies. This review also provides a framework for understanding the context dependency of the efficiency of biological control programs targeted against these insect pests.

6.1 Challenges for research

Several research avenues addressing the biological control of grapevine moths clearly need further investigation. This includes the diversity of macroorganisms that participate in the biological control of grape pests. In addition to parasitoids, spiders and harvestmen are clearly important components of predator webs. However, their biology, behavior, and more generally, life history traits should be further investigated. Progress in barcoding techniques should also allow deeper investigations into the functional ecology of food webs and into who eats whom and at what intensity level. Our understanding of these parameters is increasing in several agrosystems, including vineyards, in which there is a particular focus on predators of grape berry moths. This research should provide rapid progress that is accessible to grape growers. Understanding factors that influence host/prey quality is also crucial for avoiding unsuspected failures in biological control. Research on the roles played by the pest host plant should therefore be intensified for the induction of pest resistance, including the immune system expression, to biocontrol agents. Additionally, in our opinion, the possible attraction and arrestment roles of maternal pheromones (see Section 3) should receive more attention. The regulation of natural enemies by landscape factors, including plant biodiversity and especially floral interrow plantings, is now being studied in vineyards. These efforts should be intensified, especially identifying which types of flowers provide the best fitness gains for parasitoids and predators.

6.2 Challenges for growers and crop protection advisors

The main new finding that can be quickly implemented to help protect grapes from grape moths is the installation of grass or flower strips in vineyards to favor natural enemy activity. The reduction of insecticide use is now in progress in most European grape-producing countries, and this will favor the use of biological controls. Control practices, like the use of mating disruption or *B. thuringiensis*, should also be developed because limited harmful effects on biodiversity have been reported. Very recent results also indicate that the organic production of grape favors increased biodiversity and the capability of natural control (Muneret et al. 2017). These practices could be quickly implemented in viticulture.

All of the studies we reviewed illustrated that many factors influence the efficiency of biological control. Additionally, the impact of global warming on *L. botrana* is complex and thus hard to predict, being dependent on coevolutionary plant–pest and pest–parasitoid mechanisms in the context of tritrophic interactions. Deeper insights into these coevolutionary mechanisms in the face of climate change will be needed to improve our predictions of the future impact of pests and, subsequently, the use of biocontrol strategies. In addition, we emphasized the need for improved knowledge of trophic relationships between natural enemies and GBM in vineyards to predict the level of tortricid control. Determining the roles of the different species involved in grape moth regulation, as well as considering the whole community, is a major challenge in enhancing biological control in actual and future vineyard systems. The reduction of insecticide consumption in European viticulture requires that obstacles to biocontrol be addressed and that several biological control strategies be developed.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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