



European grapevine moth, *Lobesia botrana*

Part I: Biology and ecology

Giovanni Benelli^{1,*}, Andrea Lucchi¹, Gianfranco Anfora², Bruno Bagnoli³, Marcos Botton⁴, Raquel Campos-Herrera⁵, Cristina Carlos⁶, Matthew P. Daugherty⁷, César Gemeno⁸, Ally R. Harari⁹, Christoph Hoffmann¹⁰, Claudio Ioriatti¹¹, Rodrigo J. López Plantey¹², Annette Reineke¹³, Renato Ricciardi¹, Emmanouil Roditakis^{14,15}, Gregory S. Simmons¹⁶, Wee Tek Tay¹⁷, Luis M. Torres-Vila¹⁸, John Vontas^{19,20}, and Denis Thiéry²¹

- 1 Department of Agriculture, Food and Environment, University of Pisa, Via del Borghetto 80, 56124 Pisa, Italy
- 2 Centre Agriculture Food Environment (C3A), University of Trento, Via Edmund Mach 1, 38098 San Michele all'Adige, Italy
- 3 Department for Innovation in Biological, Agro-food and Forest Systems, University of Tuscia, Via San Camillo de Lellis s.n.c, 01100, Viterbo, Italy
- 4 Brazilian Agricultural Research Corporation (Embrapa), Bento Gonçalves, Brazil
- 5 Instituto de Ciencias de la Vid y del Vino (ICVV, Gobierno de La Rioja, Universidad de La Rioja, CSIC), Finca La Grajera Ctra Burgos Km 6 salida 13 Lo-20, Logroño 26007, La Rioja, Spain
- 6 CITAB – Centre for the Research and Technology of Agro-Environmental and Biological Sciences, Agronomy Department, UTAD – University of Trás-os-Montes and Alto Douro, Quinta de Prados, 5000-801 Vila Real, Portugal
- 7 Department of Entomology, University of California, Riverside, USA
- 8 Department of Crop and Forest Sciences, University of Lleida, Av. Alcalde Rovira Roure 191, 25198 Lleida, Spain
- 9 Department of Entomology, Agricultural Research Organisation, The Volcani Center, Bet Dagan 50250, Israel
- 10 Julius Kühn-Institute, Institute for Plant Protection in Fruit Crops and Viticulture, Geilweilerhof, 76833 Siebeldingen, Germany
- 11 Research and Innovation Centre, Fondazione Edmund Mach (FEM), Via E. Mach 1, 38010 San Michele all'Adige (TN), Italy
- 12 Universidad Nacional de Cuyo, Facultad de Ciencias Agrarias, Cátedra Zoología Agrícola y Cátedra. Instituto de Biología Agrícola de Mendoza (IBAM-CONICET). Almirante Brown 500, Chacras de Coria, M5528AHB, Mendoza, Argentina
- 13 Department of Crop Protection, Hochschule Geisenheim University, Von-Lade-Straße 1, 65366 Geisenheim, Germany
- 14 Department of Agriculture, School of Agricultural Sciences, Hellenic Mediterranean University, Stavromenos P.C., 71410, Heraklion, Greece
- 15 Institute of Agri-Food and Life Sciences, Hellenic Mediterranean University Research Centre, 71410, Heraklion, Greece
- 16 United States Department of Agriculture, Animal Plant Health Inspection Service, Plant Protection and Quarantine, Science and Technology, Salinas, CA 93905, USA
- 17 Black Mountain Laboratories, CSIRO, Canberra, ACT 2601, Australia
- 18 Servicio de Sanidad Vegetal, Consejería de Agricultura DRPyT, Avda. Luis Ramallo s/n, 06800 Mérida, Badajoz, Spain
- 19 Institute of Molecular Biology and Biotechnology (IMBB), Foundation for Research and Technology (FORTH), Nikolaou Plastira Street 100, 70013, Heraklion, Crete, Greece
- 20 Pesticide Science Laboratory, Department of Crop Science, Agricultural University of Athens, Iera Odos 9 75, 11855, Athens, Greece
- 21 UMR INRAE 1065 Santé et Agroécologie du Vignoble, INRAE, 71 Avenue Edouard Bourlaux, 33882 Villenave-d'Ornon, France

* Corresponding author: giovanni.benelli@unipi.it

With 1 figure

Abstract: Though the European grapevine moth, *Lobesia botrana* (Denis & Schiffermüller) (Lepidoptera: Tortricidae) can feed on more than forty plant species, grapevine is the preferred crop worldwide. This moth is a western palearctic species that has recently spread to Chile, Argentina, and California. The possible further expansion in other regions of the Americas is greatly feared and should be monitored carefully in the near future. In this framework, we provide an updated review of the current knowledge on its taxonomy, morphology, biology, ecology, genomics, geographic distribution, and invasiveness. Then, in the last section, we develop a research agenda pointing out significant challenges for future investigations on bio-ecology and invasion biology, which are tightly connected with the prevention and management strategies.

Keywords: pest distribution; chemical ecology; climate change; invasiveness; life cycle; morphology and taxonomy; sex pheromone; Tortricidae; vineyard pest

1 Introduction and history

The European grapevine moth (EGVM) *Lobesia botrana* (Denis & Schiffermüller) (Lepidoptera: Tortricidae) is among the most economically important pests in European vineyards (Bournier 1977; Ioriatti et al. 2011). The EGVM is a western palearctic species not reported in Scandinavia and northern Russia (Razowski 2003), that has recently spread to Chile, Argentina, and California (USA). In California eradication was declared in 2016 (Simmons et al. 2021a); a post-eradication phase is ongoing to confirm eradication or to detect its reintroduction.

Despite its wide host range, grapevine is the preferred crop, whereas the spurge flax *Daphne gnidium* L. (Thymelaeaceae) is the major wild host (Maher & Thiéry 2006; Lucchi & Santini 2011).

EGVM was first described in 1775 by Denis & Schiffermüller, anonymously, on specimens collected near Vienna, Austria, and was found in Austrian vineyards for the first time around 1800 (Bovey 1966). It was firstly detected in Germany in 1854, then causing heavy damage in the Palatinate region in 1889 (Zschocke mentioned in Stellwaag 1928). In a comprehensive book on grapevine pests, Audouin (1842) mentioned EGVM as an anecdotic pest only occurring on vines. In Switzerland, according to Linder et al. (2016), the first damage of EGVM on vine was observed in 1910, despite having been recorded in Valais before 1880. In France (Southern Alps and Bordeaux wine growing regions) the presence of EGVM dates to 1890 (Feytaud 1920), and first severe outbreaks in Bordeaux occurred in 1911 (Marchal 1912). In Spain EGVM was first recorded in 1879, achieving pest status in the early 20th century (Ruiz Castro 1965).

Due to the severe impact of EGVM on grape yields, wine quality and the fungal toxins it may generate in warm vineyards, many studies have been carried out since the beginning of the 20th century to gain a better knowledge on the moth. Notably, a 5-year scientific mission was deployed all over French vineyards gathering noted entomologists, such as Paillot, Picard, Feytaud, and Marchal (Marchal 1912; Feytaud 1913a, b).

EGVM presence in Italy was first suggested by Dei in 1873 in Northern Italy, in the province of Trieste. In Trentino

vineyards, between 1909 and 1913, EGVM populations were larger than those of the other common tortricid *Eupoecilia ambiguella* (Hübner) (Catoni & Schwangart 1914). The two species co-occurred in Piedmont as well, with alternating predominance depending on the area, though EGVM was generally considered more harmful than *E. ambiguella* (Voglino 1914). Probably the alternation between the two moths may be explained by the different humidity requirement of each species (Bovey 1966). The main research available on their climatic preferences, as well as on their crepuscular mating and egg laying activity, has been carried out in Germany by Stellwaag and Götz (Stellwaag 1943).

Despite the long history of this important pest of grapes, a comprehensive synthesis is still lacking. In the present review, we focus on EGVM taxonomy, biology, ecology, and genomics, as well as on its geographic distribution and invasiveness. In the final section, a research agenda highlighting specific challenges to be faced in forthcoming studies dealing with EGVM bio-ecology and invasion biology is presented.

2 Taxonomy, morphology, biology, ecology, and genomics

2.1 Taxonomy

EGVM was first described by Denis & Schiffermüller (1775) as *Tortrix botrana*. Later, it was reported by other authors under different names, including *Tortrix vitisana* (Jacquin 1786), *Tortrix romaniana* (Costa 1840), *Eudemis rosmarinana* (Millière 1866), *Coccyx botrana* (von Praun 1869), *Polychrosis botrana* (Ragonot 1894), and *Polychrosis botrana flavosquamella* (Dufrane 1960). A complete list of other scientific names together with international and local common names is given in Torres-Vila (2000). Today, this species belongs to the genus *Lobesia*, which includes more than 110 species worldwide (Gilligan, 2022), some of which with several synonyms. At present, three synonyms have been defined for EGVM, i.e., *L. flavosquamella*, *L. rosmarinana* and *L. vitisana* (Gilligan, 2022) and the EGVM mitochondrial genome has been fully described (Piper et al. 2016).

2.2 Morphology

2.2.1 Adult

EGVM adults are about 6 mm long at rest, with a wingspan of 11–13 mm (Bovey 1966). Adult size is mainly influenced by larval feeding (Torres-Vila et al. 1999). The forewings show a variegated marble coloration (Fig. 1A). No identification features are noticeable on the abdomen (Figs. 1F and 1G), although in females it takes a convex shape (Silvestri 1912; Bovey 1966). The morphology of the male's genital valve plays a significant taxonomic role (Gilligan et al. 2011); they are relatively simple and have a well-differentiated sacculus and a rounded apex; the uncus is bifid, and the vinculum is U-shaped and strongly sclerified. In females, the last urotergite ends in two lobiform expansions (anal papillae) covered with short, dense sensilla (Fig. 1G). The copulatory bursa is long, claviform, clearly bilobed at the apex and has an elongated and ridged signum (Gilligan et al. 2011). In the female, as in many other lepidopterans, the sex pheromone gland is located between the VIII and IX urotergite, just beneath the intersegmental membrane.

2.2.2 Egg

The egg is lenticular, plano-convex and slightly elliptical in shape, 0.65–0.90 mm long and 0.45–0.75 mm wide (Lucchi 2018). It is uniformly coloured over its entire surface, which appears almost smooth due to the polygonal lattice of the chorion (Silvestri 1912; Bovey 1966). The attachment of the egg to the substrate is ensured by a sticky substance secreted by the colleteric glands. Egg convexity increases as the embryo develops and affects the entire upper surface, except for the edge, which remains flat. The egg shows a pale straw-yellow colour when freshly laid, and then it gradually turns to transparent light grey with bright iridescent reflections (Fig. 1B). During embryonic development, the translucent chorion reveals the growing larva which eventually shows two red-spots where the head will be, while the body, folded upon itself, is of lighter colour than the surrounding yolk (Feytaud 1924) (Fig. 1C). At the end of the embryonic development the egg darkens on the side where the black head of the larva is located.

2.2.3 Larva

The newly hatched larva measures about 1 mm in length and shows a prognathous head, of about the same width as the prothorax, with the rest of the body being thinner. Thorax and abdomen have relatively long bristles, especially in the posterior region of the body. The ketotaxis of the newly hatched larva is identical to that of the mature larva (Hinton 1946; Carter 1984). The head is blackish in colour, while the rest of the body, including the pronotum, is creamy white. The dermoskeleton of the dorsal and ventral surface of the body, except for the head and the pronotum, is rough due to the presence of tiny tubercles ending in short, thin bris-

les (Silvestri 1912; Bovey 1966). The mature larva (instar V, sometimes VI, as noted by Pavan et al. 2013) can be 8–15 mm long. The head is slightly elongated, hazel-brown in colour, sometimes green or gray, with short, retractile, tri-articulated antennae in the anterior region of the head, with the second article blackish in colour (Varela et al. 2010). It bears a very long, marginal bristle, about 2/3 longer than the article itself; and the third article ends in a sub-conical

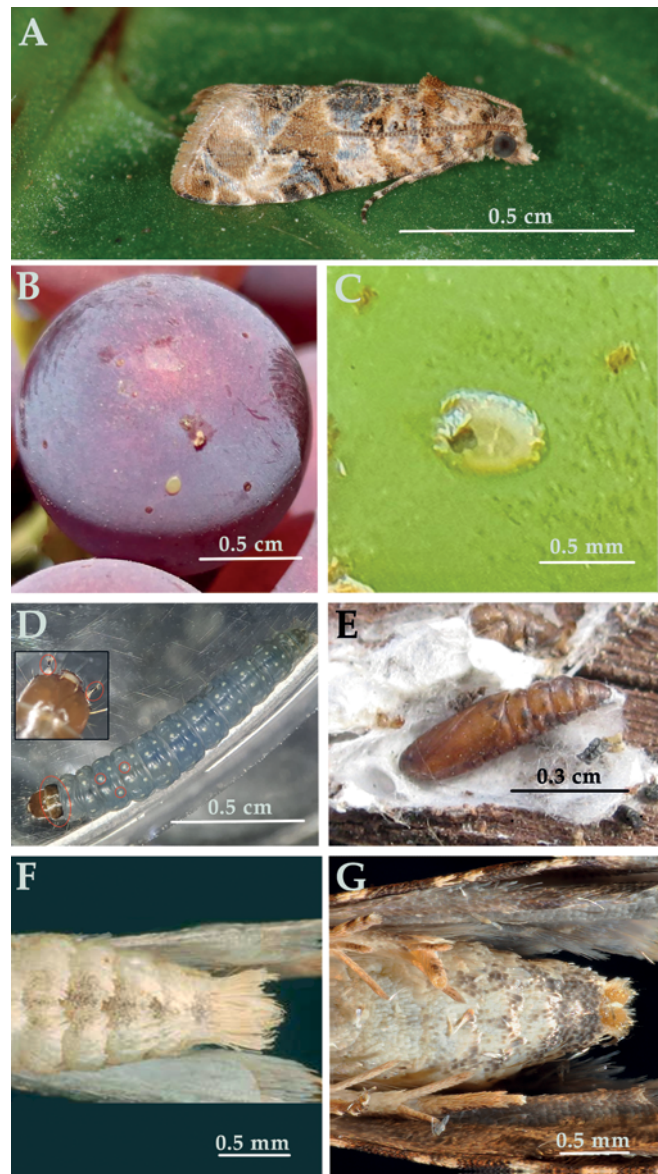


Fig. 1. *Lobesia botrana* developmental stages and some distinctive features: **A**) adult, **B**) newly laid egg, **C**) egg showing the black cephalic capsule of the larva, **D**) fifth instar larva indicating (with marked through red circles) the second black antennal segment, the pale-white setiferous areas and the prothoracic sclerite with a brownish-black posterior margin, **E**) chrysalis profile, **F**) detail of the male abdomen and **G**) detail of the female abdomen showing the two anal papillae (both ventral view).

process bearing a short bristle (Silvestri 1912; Bovey 1966). There are 6 ocelli on each side of the head, five arranged in an arc and the sixth in front of the anterior penultimate. The mandibles, strong and sub-pyramidal in shape, are pentadentate, with the second tooth more developed outwards. Head capsule width (Savopoulou-Soultani et al. 1990; Delbac et al. 2010) as well as mandible length (Pavan et al. 2010) serves to discern larval stages. The jaws have a short lobe with four short apical sensilla and a short palpus. The prothoracic scutum is brown, generally like that of the head, but in some cases, particularly in the third generation larvae, it can assume a blackish colouration, mainly in its proximal end (Varela et al. 2010) (Fig. 1D). The setiferous areas of the thorax and abdomen are significantly lighter in colour than the surrounding dermoskeleton. The position (ketotaxis) and length of thoracic and abdominal bristles, as well as those of the head, are of considerable systematic importance (Hinton 1946; Carter 1984). The six legs are strong and relatively small. Pseudo-legs are present on abdominal urites III, IV, V, VI and X. All of them are short and have a crown of regularly alternating hooks of different lengths which amount to 30–40 for the pseudo-legs of urites III–VI and about 25 for those of urite X. The anal comb bears 6–8 teeth (Silvestri 1912; Bovey 1966). Through the application of echoentomography (ultra-high frequency ultrasonography, UHFUS), an advanced diagnostic technology in the clinical and pre-clinical field, the heartbeat of a 5th instar larva in a quiet state was reported as 55 bpm (Ricciardi et al. 2022).

2.2.4 Pupa

The pupa is obtecta (chrysalis), 4–6 mm long, slender (especially in males), with the cranial portion rounded and the caudal portion pointed and equipped with hooks. Female pupae are generally larger than male pupae. They differ from each other by the position of the genital sprouts, which are in the IX and VIII abdominal sternites in males and females, respectively (Lucchi 2018). The pupa is greenish at first, but it turns dark brown as it matures. The morphological character that allows an easy and reliable discrimination lies in the apex of the last abdominal segment (cremaster), which in EGVM ends with a fan-shaped surface and is equipped with 8 large, hooked bristles, 4 dorsal and 4 lateral-dorsal. The chrysalis is contained in a fusiform, non-rigid cocoon, composed of tightly packed white silky threads (Silvestri 1912; Bovey 1966) (Fig. 1E).

2.3 Biology and ecology

2.3.1 Host plants

EGVM is a polyphagous species whose host range includes more than 40 wild and cultivated plants belonging to at least 27 botanical families (Silvestri 1912; Bovey 1966; Stoeva 1982; Coscollá 1997; Torres-Vila 2000; Thiéry 2005; Ioriatti et al. 2011). Cultivated species include grapevine (*Vitis vinifera* L.), currant (*Ribes uva-crispa* L.), black currant (*Ribes*

nigrum L.), cherry (*Prunus avium* L.), plum (*Prunus domestica* L.), kaki (*Diospyros kaki* L.), pomegranate (*Punica granatum* L.), kiwi (*Actinidia chinensis* Planchon), and olive (*Olea europea* L.). EGVM cannot usually complete its entire annual life cycle on some of these hosts due to their phenology or fruit features (Stoeva 1982; Torres-Vila 2000; Thiéry & Moreau 2005; Torres-Vila & Rodríguez-Molina 2013). It can develop in the laboratory on crops such as *Medicago sativa* L. (lucerne) and *Solanum tuberosum* L. (potato) (Bovey 1966), but these are rarely attacked in the wild (Torres-Vila 2000). Several other plants can be used for laboratory rearing of the larvae (e.g., apples, cherries, etc.), but oviposition on apples was hardly observed. The grape ivy, *Parthenocissus tricuspidata* (Siebold & Zucc.) Planch., has been reported as toxic for larvae (Torres-Vila et al. 1992).

EGVM colonised European vineyards coinciding historically with the phylloxera crisis in the late 19th and early 20th centuries (Bovey 1966; Thiéry 2005; Torres-Vila & Rodríguez-Molina 2013). The flax-leaved daphne, *D. gnidium* L., a shrub that typically populates Mediterranean shrublands (Lucchi & Santini 2011; Torres-Vila & Rodríguez-Molina 2013), was a reported host before vineyard colonisation (Millière 1875), and it was proposed as the ancestral host from which EGVM moved to grapevines (Marchal 1912; Grassé 1928). Although this hypothesis was questioned in the past (Bovey 1966) and direct scientific evidence is lacking, daphne is currently considered the native EGVM wild host (Maher & Thiéry 2006).

2.3.2 Life history

The biology and ecology of EGVM have been described elsewhere (Marchal 1912; Silvestri 1912; Stellwaag 1928; Bovey 1966; Roehrich & Boller 1991; Coscollá 1997; Torres-Vila 2000; Ioriatti et al. 2011). Main adult activities (flight, calling, mating and egg-laying) take place in the vicinity of dusk, although they occasionally occur at daybreak or at any time on cloudy days. Flight activity of females (based on circadian activity in the laboratory) has been shown to be concentrated in the 6 hrs around onset of scotophase (Hurtrel & Thiéry 1999). Larval diel activity (locomotion, feeding, pupation, etc.) has not been reported in the wild. However, under laboratory conditions using artificial diet and a simulated 1-h dusk, larvae were more active during the night period (Iltis et al. 2021). Adults usually do not actively disperse more than 80–100 m during their lifetime, and flight distances over 300 m are infrequent (Roehrich & Carles 1981; Schmitz et al. 1996), although they could cover much longer distances in passive flight if dragged by advective air currents (Torres-Vila et al. 2006). EGVM is a polyvoltine species exhibiting facultative diapause. The number of generations and voltinism in a given area is determined by day length and temperature, acting on diapause induction and development rate, respectively. Short photophases (8–12 h long) during at least half of the egg-larval stage induce diapause in larvae that will be later dis-

played by pupae (Komarova 1949; Roehrich 1969; Roditakis & Karandinos 2001; Baumgärtner et al. 2012). In southern Europe, diapause induction normally occurs in the second half of August. The accumulated thermal integral determines the number of generations per year. EGVM larvae can produce supernumerary instars to ensure the best fit of the life cycle to diapause-inducing environmental conditions (Pavan et al. 2013). In Europe, EGVM usually shows two generations in the northern latitudes and three in southern temperate ones, although the latitudinal gradient may be locally modified by altitude, continentality or microclimatic conditions. The number of generations ranges from one in Romania to three-four in Spain, Greece, Crete, Italy, and the former Yugoslavia, and even five in Turkmenistan (Coscollá 1997; Torres-Vila 2000). The current trend is towards an increase in EGVM voltinism given the global warming scenario (Martín-Vertedor et al. 2010). When EGVM develops on vine, the typical trivoltine life cycle is described as follows.

The first flight of the year consists of overwintered individuals, usually starts in late March or early April and lasts for 4–6 weeks. Males emerge on average some days earlier than females (protandry) and egg laying starts 1–3 days after mating (pre-oviposition period depending on temperature), at around phenological grapevine stage 17 (Eichhorn & Lorenz 1977). Protandry is mostly independent from the host plant (Moreau et al. 2006; Thiéry et al. 2014a), however it was not observed in adults from larvae reared on two grape varieties (Cabernet Sauvignon and Red Bacco) (Thiéry & Moreau 2005). Females of the 1st flight lay eggs on the bracts, flower buds and, very rarely, on the rachis of inflorescences, on shoots, and leaves of vine plants. The smooth surface of flower buds stimulates egg laying (Marchal 1912), with olfaction, taste and vision also playing a role (Tasin et al. 2011a). Females lay eggs singly and more rarely in groups of 2–3 eggs, as is typical of the subfamily Olethreutinae. Eggs hatch 7–10 d after oviposition (65–75°C-day, with a 10°C development threshold, Touzeau 1981) and go through five phases of embryonic development: visible embryo, visible eyes, visible mandibles, brown/darkened head, and black head (Feytaud 1924). The larva pierces the egg at one of the poles with the mandibles and leaves the chorion, which is usually not consumed and remains on the substrate. Neonate larvae walk for up to 24 h (depending on sun irradiation and temperature) in search of a suitable location to settle, the so-called ‘erratic stage’ (Marchal 1912). Once installed they drill into the flower buds, where they feed mainly on the staminal primordia and gynoecium. Symptoms are not evident at this initial stage, but about a week later individual larvae tie several flower buds with silk threads forming the so-called glomerulus (or nest), which is visible to the naked eye, and feed inside, relatively protected from sun irradiation, desiccation, rain, or natural enemies. Larvae may build one to three glomeruli during their development, walking or ballooning to new ones, as the flowers are consumed, to avoid conspecific competition (Torres-Vila et al. 1997a;

Thiéry et al. 2014b). Frass may remain adhered externally to the glomeruli. Fifth instar mature larvae stop feeding and leave the inflorescences, spinning a whitish fusiform silky cocoon and pupating preferentially on the leaves (Causse et al. 1984) or in the soil. Sexes may be identified at the pupal stage by the relative position of the genital primordia. Pupal age can be estimated from the coloration and transparency of the integument (Lalanne-Cassou 1977). When the adult is ready to emerge, the pupa exits the cocoon head first, aided by characteristic abdominal movements, dorsal spines and caudal hooks. The new imago excretes a greenish white meconium, which is usually more abundant in males than in females. The pupal exuvia remains attached in the cocoon in a position characteristic of many Tortricidae. The duration of the larval stage is 20–28 days and that of the pupal stage is 12–14 days (170°C-day and 130°C-day respectively, with a 10°C development threshold, Touzeau 1981).

In the second flight, the first adults emerge in late June and the females lay eggs on green berries at phenological stages 31–33 (Eichhorn & Lorenz 1977), usually in the most shaded area of grape clusters. Neonate larvae exhibit the same erratic locomotion behaviour as the first-generation larvae. Initially they feed externally on unripe berries and then penetrate them next to the peduncular insertion or at the point of contact between two berries, stimulated by their thigmotropism. Larval installation on shoots or leaves is rare (Lucchi et al. 2011). Larvae then continue their development boring into the grape pulp, piercing several berries sometimes securing them with silk threads to prevent falling off, often taking refuge inside an excavated berry. Scattered groups of attacked berries (foci) turn purple and then dark brown with visible frass and silk and are the clearest symptom of larval damage on unripe berries. When weather conditions are suitable, damaged grapes may be colonised by fungal species, including *Aspergillus* spp., and especially the grey rot *Botrytis cinerea* (Persoon: Fries) (teleomorph: *Botryotinia fuckeliana* Whetzel) which may cause severe qualitative and quantitative damage (Ferraud 1990). Larval survival and damage is usually higher on varieties with denser grape bunches because they promote both larval installation and fungal colonisation. Larval development in the second generation requires a greater thermal integral than in the first generation (255°C-day, with a 10°C development threshold, Touzeau 1981), due to the lower nitrogen content of grapes in comparison with flowers. Mature EGVM larvae pupate in mid-July on the bunches, on the leaves, or in the soil, following the same pattern of the first generation. The thermal integral required for pupal development is similar to that of the first generation.

The third flight usually starts at the end of July-early August. Oviposition takes place on ripening berries (around veraison) at phenological stages 35–37 (Eichhorn & Lorenz 1977), and larvae develop during August and September. Larvae pierce the grapes more superficially than in the second generation, mainly feeding on the berry skin. Such

behaviour intensifies grey rot disease (Ferraud 1990). Fermentation of the sweetened dripping juice attracts vinegar flies (*Drosophila* spp.) whose larvae in turn greatly favour secondary attacks of bacterial acid rot. Protected by their shelter larvae feed on up to 2–10 nearby grapes during their development (Thiéry et al. 2018). The larval escape behaviour that typically occurs on inflorescences (body wriggling backwards and falling while attached to a silk thread) may change when they cloister inside grapes in the 2nd and 3rd generations. If harassed with a sharp object through the entrance hole they aggressively stick their heads out and even try to block the intruder with the mandibles (Torres-Vila 1995). In the typical trivoltine cycle, third generation diapausing larvae pupate under the vine bark or in the cracks of stakes and wooden posts if the vineyard is trellised (Causse et al. 1984). Prior to pupation, diapausing larvae build a cocoon with a stronger and more consistent silk web than the non-diapausing larvae (R. Roehrich, per. com.) which reinforces protection against dehydration and weight loss of overwintering pupae, thus maintaining potential female fecundity (Torres-Vila et al. 1996a). Individuals overwinter as diapausing pupae from autumn until the following spring, when a new annual cycle begins. The diapause inhibition process, still not well understood, is decisively regulated by late winter and early spring mean temperatures (Gabel & Roehrich 1990).

Limited information is available on EGVM phenology in the southern hemisphere. Dagatti & Becerra (2015) highlighted that in Argentina (Mendoza region) the 1st flight occurs in October with an average of 204.05 +/- 10.73 degree days, the 2nd flight occurs in December with an average of 728.34 +/- 41.95 degree days, the 3rd flight occurs in January with an average of 1329.08 +/- 151.35 degree days, and the 4th flight in mid-February with an average of 1721.84 +/- 116.63 degree days. Overall, these values are close to those observed in other regions of the world.

2.3.3 Environmental factors

Temperature is the main climatic variable affecting EGVM population dynamics, reducing or increasing adult longevity and developmental rate of preimaginal stages (Bovey 1966; Gabel 1981; Touzeau 1981). Early observations already reported that hot springs and droughts may dry out eggs and pupae, and that abundant rains and cold springs are detrimental to moth development (González de Andrés 1935). As a result of a high developmental rate at high temperatures, larvae, pupae and adults are smaller, which constrains reproductive potential (Torres-Vila 1996; Sáenz-de-Cabezón et al. 2006). Oocyte development and female fecundity peak at around 22°C (Bergougnoux 1988). Temperatures above or below vital limits cause significant mortality of eggs and larvae (Coscollá et al. 1986; Moosavi et al. 2018) and of non-diapausing pupae under fluctuating temperature regimes (Torres-Vila et al. 1993). Diapausing pupae may withstand lower temperatures than non-diapausing pupae (Andreadis

et al. 2005). Temperature-induced dormancy has been reported in egg and larval stages (Tzanakakis et al. 1988). Dusk temperature directly affects adult flight, calling, mating, and egg-laying.

Extremes in relative humidity may kill EGVM immobile stages, such as eggs (Götz in Bovey 1966; Coscollá et al. 1986) and pupae (Torres-Vila et al. 1993), while larvae appear to be not as sensitive to humidity, perhaps due to their mobility and potential to avoid adverse conditions. High humidity favours the development of entomopathogenic fungi, especially on pupae. Excessive dehydration of overwintering pupae reduces adult reproductive potential (Torres-Vila et al. 1996a). Relative humidity affects adult activity and longevity (Marchal 1912; Bovey 1966). Pupal mortality depends on the interaction between temperature regime (constant vs. fluctuating) and relative humidity (Torres-Vila et al. 1993).

Adults need water to reach their potential reproductive output (Torres-Vila et al. 1996b; Savopoulou-Soultani et al. 1998) and water intake increases female remating rate (Torres-Vila et al. 1997b). Foliage dew may be an important water resource for adults in the summertime. EGVM is typically included among the moth species requiring water but no sugar to maximise their reproductive output (Chauvin 1956). However, Savopoulou-Soultani et al. (1998) report that sugars increase longevity and fecundity under laboratory conditions. Excessive wind and rainfall are detrimental to adult flight, mating and egg laying (by wetting host plants), and may also constrain larval performance and survival. Photoperiod triggers both diapause induction and adult diel activity at dusk. Longer photophases can increase female fecundity (Savopoulou-Soultani & Tzanakakis 1979).

Biotic factors include an array of species that interact with EGVM in the wild and potentially regulate its abundance, occupancy, and population dynamics. Predators, parasitoids and entomopathogens (viruses, bacteria, fungi, protozoa, and nematodes) are especially important (see specific section). Tortricid moths that can coexist with EGVM, especially in the larval stage, include *E. ambiguella* (the cochyliis), *Argyrotaenia ljugiana* (Thunberg) (the eulia) and *Sparganothis pilleriana* (Denis & Schiffermüller) (the vine pyral) (Bovey 1966). A vicariant species of EGVM, *Paralobesia viteana* (Clemens), is an important grape pest in eastern North America (Rufus et al. 2012). The honeydew moth *Cryptoblabes gnidiella* (Millière) (Lepidoptera: Pyralidae Phycitinae) is an opportunistic moth (Torres-Vila et al. 2002a) whose association to vine was early known (Feytaud 1924) and that recently became a primary pest in Italy (Lucchi et al. 2019).

The host plant itself may critically influence EGVM fitness in various ways, including larval survival and adult size. Host-mediated factors include host species (Thiéry & Moreau 2005; Torres-Vila & Rodríguez-Molina 2013), host-induced immune defences (Muller et al. 2015a), vine phenology (Savopoulou-Soultani et al. 1990; Torres-Vila et al. 1992; 2005; Gabel & Roehrich 1995), vine vari-

ety (Moreau et al. 2006; Sharon et al. 2009; Thiéry et al. 2014a; Muller et al. 2015b; Moreau et al. 2016), and specifically the phenology-mediated quality of vine reproductive organs (Torres-Vila et al. 1999). EGVM prefers grey-rot affected grapes (Mondy et al. 1998a; 1998b), and the fungal-derived grape nutritional change may improve larval feeding and enhance female fecundity (Savopoulou-Soultani & Tzanakakis 1988), although mutualism has been questioned (Moosavi et al. 2020). A clear link between EGVM populations and black aspergillus rot has also been demonstrated (Cozzi et al. 2006; Delbac & Thiéry 2016). Host influence on adult size strongly regulates EGVM reproductive output because female size positively correlates with fecundity, egg size and longevity, and male size with longevity and lifetime spermatophore number and size (Savopoulou-Soultani et al. 1990; Torres-Vila et al. 1995; 1999; Torres-Vila & Rodríguez-Molina 2002).

Among the rather large list of possible host plants, the numerous grape cultivars on which larvae grow represent an important source of variability. Several studies report on the female preferences between grape cultivars, and important larval or adult traits can be modified according to the grape cultivar on which larvae developed. Significant advances have been made in the last decade concerning the EGVM immune system, focussing on either the prophenoloxidase expression, the immune cells and the polypeptides (Vogelweith et al. 2011; 2016; Muller et al. 2015a). These works show relevant variation, as function of the cultivar on which larvae were fed, but also important geographical variation among different regions (Vogelweith et al. 2013a, b). Light was especially placed on the prophenoloxidase, which is key for encapsulation (Vogelweith et al. 2015). Encapsulation can be observed after parasitism by *Campoplex capitator* Aubert (Hymenoptera: Ichneumonidae) (Cerqueira de Araujo et al. 2021) and thus variation in immunity could modify larval resistance to parasitism. The host plant effect was also found on the offspring, eggs of females fed on different hosts were more or less sensitive to *Trichogramma cacaoeciae* (Marchal) (Hymenoptera: Trichogrammatidae) (Thiery & Desneux 2018). Grape cultivars were found to affect development traits, e.g., male reproductive success (Muller et al. 2015b) but also differentially the larval growth speed and the emergence phenology of both sexes with expected incidence on the sex ratio per unit of time (Thiéry et al. 2014a, b). Knowledge summarised above highlights the need for further research on these issues, for a better understanding of the EGVM population dynamics.

Natural populations of EGVM from *D. gnidium* produce on average smaller eggs than corresponding grapevine-associated populations when controlling for female size (Torres-Vila et al. 2012), which shows moth adaptation to host plant and suggests the possibility of microspeciation, even if there are no host volatile detection differences between the two populations (Pérez-Aparicio et al. 2019). This is important as larger eggs produce larger neonates, which are more

resistant to starvation and better able to settle and survive in adverse habitats, such as not compact unripe grape bunches (Torres-Vila & Rodríguez-Molina 2002). Larval host plant origin (Moreau et al. 2008), chemical composition of fruit surface (Maher & Thiéry 2004a, b), and sugar content may also influence female oviposition behaviour, and a specific fructose detector has been found on the female ovipositor (Maher et al. 2006).

2.3.4 Chemical ecology

Chemical communication using highly volatile molecules is a major route of information transfer in insects (Wyatt 2014; Harari & Sharon 2016; Nieri et al. 2022). Chemical information can be transferred intentionally (i.e., pheromones) or unintentionally (i.e., some plant volatiles).

2.3.5 Pheromones

The sex pheromone blend of EGVM shows a main component, (*E,Z*)-7,9-dodecadienyl acetate (*E7,Z9*-12:Ac) and at least four other minor compounds: (*E,Z*)-7,9-dodecadien-1-ol (*E7,Z9*-12OH), (*Z*)-9-dodecenyl acetate (*Z9*-12:Ac), (*E*)-9-dodecenyl acetate (*Z9*-12:Ac), and 11-dodecenyl acetate (11-12:Ac) (Roelofs et al. 1973; Arn et al. 1988; El-Sayed et al. 1999; Witzgall et al. 2005). Only the major component has been detected in volatile collections from calling females (0.3 ± 0.1 ng/h, Anfora et al. 2005) and it alone is sufficient to attract males, so the role of the minor compounds still needs to be verified (Sans et al. 2016) though they could help males to locate females in air impregnated with the major pheromone component under mating disruption (MD) conditions (Torres-Vila et al. 1997c). *E7,Z9*-12:Ac has only been identified in two other moths as a minor component of the blend, being the main component only in EGVM blend (El-Sayed 2022).

Females release the sex pheromone by adopting a characteristic calling posture where wings are slightly raised, legs outstretched, abdomen turned downwards, distal abdominal segments extended and the pheromone gland protruding and clearly visible at the abdominal tip (Torres-Vila et al. 2002c; Navarro-Roldán & Gemeno 2017). Calling behaviour is mild at the beginning of calling, it peaks in the middle of the calling period and decreases gradually afterwards, with high variability in duration and intensity among individuals (Navarro-Roldán & Gemeno 2017). EGVM sexual activity takes place during a 2–4 hours period right before and after sunset (dusk), as revealed by male captures in pheromone traps (Lucchi et al. 2018a). The exact period of pheromone release by females under natural conditions probably follows that of male captures, but it needs to be confirmed by observing females under natural conditions. Under laboratory conditions with no dusk, females emit pheromone only during the first 2 h of the scotophase (Navarro-Roldán & Gemeno 2017), but if a dusk period is used between day and night, females start calling at dusk (Torres-Vila et al. 1997c; Anfora et al. 2005). This highlights the importance of mimicking

natural light intensity dynamics when observing periodic behaviours in the laboratory (Vanin et al. 2012).

Male moths detect the sex pheromone with specialized olfactory receptor neurons (ORNs) housed inside sensilla trichodea located on the antennae. Pheromone receptor neurons express receptor proteins tuned to the pheromone compounds (Dekker & Karpati 2020). Candidate genes for the pheromone receptors of EGVM have been identified but their function is not known (Rojas et al. 2018). The presence of a large glomerulus at the entrance of the antennal lobe of the male brain (Masante-Roca et al. 2005) suggests a superabundance of major pheromone compound ORNs on the antennae. This has been estimated as 50% of all the ORNs on the male antenna by single sensillum electrophysiology (De Cristofaro et al. 2008). The presence of a single macroglomerulus in the antennal lobe and a 100:20 to 100:5 ratio of major to minor compounds, respectively, in the pheromone blend (Sans et al. 2016) suggests that, as in other tortricids (Pérez-Aparicio et al. 2022), ORNs tuned to the major pheromone compounds are in different sensilla trichodea than ORNs tuned to the minor compounds.

The flight response of males to the sex pheromone has the characteristic zig-zagging pattern of most insects orienting upwind to an odour source, but in comparison to related tortricid species, such as *Grapholita molesta* (Busck) and *Cydia pomonella* (L.) the flight of EGVM has more numerous and shorter zigzags, and thus it exhibits a characteristic slower flight with a narrower track (El-Sayed et al. 1999; Navarro-Roldán et al. 2019).

Chemical signals may be used to indicate the presence of eggs on a plant so that females avoid laying their eggs in already occupied plants, and in so doing, reduce offspring competition for resources. These signals have been found in *L. botrana*, and in several other moths, and this typical 'egg odour' made of saturated and unsaturated C16–C18 fatty acids provoke females to disperse oviposition (Gabel et al. 1992; Gabel & Thiéry 1996). Similar signals occur in several moth species (*C. pomonella*, *G. molesta* and the peach twig borer *Anarsia lineatella* Zeller (Lepidoptera: Gelechiidae)), and thus they are not considered as pheromones (Thiéry et al. 1995). Interestingly, one of these compounds, the oleic acid, attracted a potential EGVM egg parasitoid, *Trichogramma maidis* Pintureau & Voegel in olfactometer.

2.3.6 Plant volatiles

Volatile organic compounds (VOCs) play a role in long-range host plant recognition by EGVM (Tasin et al. 2005, Masante-Roca et al. 2007). VOCs acting as attractive allelochemicals (kairomones) emitted by different grapevine organs have been identified (Masante-Roca et al. 2005; Tasin et al. 2005, 2010). Redundancy and synergism have also been demonstrated among the kairomones for egg-laying females. This plasticity, characterising several polyphagous moths, is probably linked to the high polyphagy of EGVM and thus its ability to discriminate host plants on the

basis of the relative amount of ubiquitous plant secondary metabolites (Tasin et al. 2007). Such high polyphagy has been recently related also to the large set of odorant binding proteins and odorant receptors identified by antennal transcriptome and relative protein expression analysis, many of them putatively involved in host seeking or oviposition behaviour (Rojas et al. 2018). By means of electrophysiological and behavioural studies using volatile compounds identified in *D. gnidium* and *V. vinifera*, it has been shown that EGVM females respond to both ubiquitous and specific volatile compounds, but that the complete mixture obtained from the wild host is more attractive (Tasin et al. 2005, 2010; Pérez-Aparicio et al. 2019). Interestingly, to reproduce the attractiveness of grapevine both under laboratory and field conditions, it is sufficient to use a small subset of kairomonal compounds represented by a specific blend of the terpenoids (*E*)- β -caryophyllene, (*E*)- β -farnesene and the homoterpene (*E*)-4,8-dimethyl-1,3,7-nonatriene (Anfora et al. 2009). Its attractiveness depends on the ratio of the compounds, decreasing significantly when deviating from the ratio found in grapevine headspace collections (Tasin et al. 2011a).

Female EGVM can discriminate between smells associated with naturally occurring microorganisms that increase or decrease the food quality of the host plant for the larvae, with attractive or repellent effects. These smells could be used to develop new monitoring or control systems (Mondy et al. 1998b; Tasin et al. 2011b, 2018; Larsson Herrera et al. 2020). Furthermore, adults of EGVM are attracted to VOCs emitted by potential food sources, particularly sugars and nitrogenous substances. For example, fermenting apple juice or red wine were used as a food bait to trap EGVM adults and to predict field oviposition dynamics (Thiéry et al. 2006a; Bagnoli et al. 2013).

Short-range volatile stimuli and mechanical stimuli are used by gravid EGVM females for oviposition site selection. Indeed, grape berry extracts of *V. vinifera* and leaf and berry extract from *D. gnidium* were found to trigger dose-dependent oviposition in EGVM females (Maher & Thiéry 2004a, b; Maher & Thiéry 2006). The response varied according to the phenological stage and to the plant part considered, and tarsal contact-chemoreceptor sensilla sensitive to fructose and sucrose are involved (Maher et al. 2006). On the other hand, one may argue that EGVM is attracted by a wide number of grape cultivars, and we are still far from understanding what the minimal blend of VOCs attractive to females is. VOCs emission also varies considerably as a function of soil, rootstock, plant vigour, droughtiness and climate. This outlines that, besides VOCs, other cues are exploited by ovipositing females.

Regarding the role of non-host plants, EGVM detects the terpenes produced by tansy, *Tanacetum vulgare* L. (Asteraceae) (Gabel 1992). Furthermore, the effect of a single compound, (S)-(-)-perillaldehyde, a volatile emitted by *Perilla frutescens* (L.) (Lamiaceae), promotes oviposition by EGVM (Cattaneo et al. 2014; Markheiser et al. 2020). It has

been hypothesised that not only antennal olfactory receptors, but also gustatory sensory structures located on the ovipositor may be involved in this behaviour. In contrast, essential oil extracted from another non-host plant, *Schinus molle* L. (Anacardiaceae), deters oviposition (Silva et al. 2019).

Another modern research field deals with HIPVs (host induced plant volatiles), which are emitted by vines damaged by pests. Phenylacetonitrile, for example, is an HIPV that has been shown to be attractive to males and females of EGVM (El-Sayed et al. 2019). HIPVs could signal the presence of plants that are more susceptible to attacks by herbivorous insects than undamaged plants, thus providing an evolutionary advantage for those pests that are able to perceive them. Moreover, they could also be exploited as kairomones by various insect predators (Lucchi et al. 2017).

The employment of these allelochemicals in the vineyard can be hampered by their competition with background odours, by the difficulty in formulating right doses and mixtures, and by the production cost of these new synthetic compounds. Nevertheless, new biotechnological tools can facilitate and accelerate the use of the allelochemicals on a large scale. For example, recently stable grapevine transgenic lines, obtained via *Agrobacterium tumefaciens* technology, with altered (*E*)- β -caryophyllene and (*E*)- β -farnesene emission compared to original unmodified plants have been generated (Salvagnin et al. 2016; 2018). It has been shown that modification of the kairomone ratio within the grape bouquet is sufficient to interfere with the host-seeking behaviour of EGVM, making the transgenic plants less attractive to the female moths in wind tunnel experiments. This finding could form the basis for the development of new environmentally friendly approaches for pest control, also exploiting the new plant genome editing such as the CRISPR–Cas9 system and its subsequent developments (Anzalone et al. 2019). Relatively few studies have explored the response of larvae to chemical stimuli. Becher & Guerin (2009) demonstrated the orientation of starved larvae with a locomotor compensator to the odour of artificial diet and eight plant volatiles, like methyl salicylate which was sensed with a threshold of 1 ng load on filter paper. Calas et al. (2006) showed that larvae avoid feeding on 20-hydroxyecdysone and that they taste it with the lateral sensilla styloconica of the galea. Interestingly, adult females avoid ovipositing on surfaces treated with this compound, which is normally inside the plant tissues, and detect it with gustatory receptor neurons located on the tarsal sensilla (Calas et al. 2006).

2.3.7 Sexual behaviour

In many moth species, including tortricids, the adults emerge with sufficient nutrition to mate and lay eggs and do not need to ingest additional food sources (Wäckers et al. 2007). However, the attraction of EGVM to fermentation volatiles could indicate the search for carbohydrate sources. Although females mate and lay fertile eggs without any food intake (besides water), sugars intake has a positive impact on female

fecundity and longevity (Savopoulou-Soultani et al. 1998). In the wild, females have been observed visiting *Tanacetum vulgare* flowers, where they probably feed (Gabel 1992), but EGVM has a relatively short proboscis and is probably not a nectar-dependent species. Larval nutrition strongly impacts adult reproductive output (Torres-Vila et al. 1999; Muller et al. 2015a, b; Moreau et al. 2016).

There is evidence that sex pheromones provide information about the physical condition of the calling (pheromone releasing) female (see review by Harari & Steinitz 2013; Gonzalez-Karlsson et al. 2021). EGVM's sex pheromone is condition-dependent, with larger females producing more pheromone than smaller ones, especially more of the main pheromone component. Based on the female emitted pheromone characteristics, males prefer larger females (Harari et al. 2011), which are more fecund than smaller females (Torres-Vila et al. 1999; Harari et al. 2011). EGVM female responds to mating disruption doses of their own pheromone in the field by competitively increasing their rate of pheromone emission (Harari et al. 2015). This may affect their longevity and reproductive potential as repeated calling is costly (Harari et al. 2011). Alternatively, since females are relatively anosmic to their own sex pheromone, especially towards the minor pheromone components (Vitagliano et al. 2005; Pérez-Aparicio et al. 2019), the observed response to mating disruption concentrations of sex pheromone may not be due to a pheromone autodetection *sensu stricto* (Holdcraft et al. 2016) but to the consequence of misleading odour stimulation (Pérez-Aparicio et al. 2022). In either case, the implications of changes in female behaviour under mating disruption deserve further study (Pérez-Aparicio et al. 2022).

The mating system of EGVM is primarily monandrous, with 70–100% of females mating only once in their lifetime both in the field (Roehrich & Smitz 1992; Torres-Vila et al. 2005, 2019) and in the laboratory (Deseo et al. 1981; Torres-Vila et al. 1997b, 2002c, 2019; Dodi-Zelberzvig & Harari 2019). Female remating in EGVM has heritable variation, involving at least two autosomal recessive genes (Torres-Vila et al. 2002c). Remating is also affected by male and female physiological conditions, such as female size and the volume of the spermatophore provided by males (Torres-Vila et al. 1997b; see also Torres-Vila & Jennions 2005). Female size positively correlates with grape phenology; females originating from larvae fed in the larval stage on inflorescences are smaller than females fed on ripe grapes, whereas those fed on unripe grapes are of an intermediate size (Torres-Vila et al. 1999). Accordingly, the rate of polyandry increases with female size throughout the season (Torres-Vila et al. 2005). Spermatophore volume is positively correlated with male size (Sadeh & Harari 2015) and his remating history (Torres-Vila et al. 1995). Peculiar attention should be paid to intraspecific variation among females in their propensity to remate, as it implies a true behavioural polymorphism (Torres-Vila 2013).

Mate choice experiments, using lab-reared monandrous and polyandrous lines, revealed that males are more attracted to volatiles of calling virgin females over those of polyandrous females that have mated once (Dodi-Zelberzvig & Harari 2019). Calling in EGVM females is costly and affects female fecundity (Harari et al. 2011). Hence, the repeated calling of polyandrous females results in reduced fecundity and longevity (Dodi-Zelberzvig & Harari 2019). Males of polyandrous lines have more apyrene (i.e., non-fertilizing) sperm than males of the monandrous lines. Thus, they are better equipped for sperm competition if females remate. However, the higher number of apyrene sperm in the polyandrous lines has been associated with shorter male longevity (Dodi-Zelberzvig & Harari 2019).

In general, EGVM females prefer to mate with males providing larger spermatophores (Sadeh & Harari 2015), since small spermatophores may negatively affect female fecundity (Muller et al. 2016; but see Torres-Vila et al. 1995). When given a choice, monandrous females discriminate against experienced males having much smaller spermatophores (Muller et al. 2016). The cues involved in mate choice are not known. EGVM displays no obvious or elaborate courtship behaviour, and no courtship pheromone has been described for this species.

EGVM females are proovigenic and lay about 20–40% of their eggs on the first days after mating, then egg production progressively decreases with age (Torres-Vila et al. 1995, 1999; Thiéry et al. 2014a). Thus, as females mate once per night, increasing the time between matings may allow a limited reproductive outcome for additional males waiting to mate (Sadeh & Harari 2015). Usually, females mating with an uncompetitive male tend to delay oviposition for a chance to mate with a more competitive male in terms of fitness. To date, this attitude was not detected in EGVM females (Sadeh & Harari 2015) probably for two reasons; on the one hand, the energetic cost to attract another male mate is too high given that the production and release of pheromones requires a lot of resources from females (Harari et al. 2011; Steinitz et al. 2015), on the other hand, delayed mating negatively affects the fecundity of females, as older females are less fecund (Torres-Vila et al. 2002b).

2.4 Genomics

Despite its importance as a pest in viticulture, there is currently no annotated genome resource for EGVM and only a few genes have been sequenced and characterised to date. The draft complete mitochondrial genome with a size of 15,229 bp is available in GenBank under reference sequence NC_029193.1 and is identical to KP677508.1 from an individual sampled in France (Piper et al. 2016). The EGVM antennal transcriptome has been analysed and a set of olfactory-related genes (odorant-binding proteins and odorant receptors) were identified and further characterised (Rojas et al. 2018; Venthur et al. 2019). Recently, the transcriptome of EGVM female pheromone glands was sequenced

and 41 candidate genes that may be involved in sex pheromone production were identified (Ding et al. 2021). Nguyen et al. (2013) have shown that in line with other members of the tortricid subfamilies, Olethreutinae and Tortricinae, the EGVM sex chromosome arose by fusion between an ancestral chromosome and an autosome. It may have increased the adaptive potential of tortricid moths and contributed to their spread and subsequent speciation. This study also provided partial sequences of EGVM orthologs of the *Ace-1*, *EF-1 α* , *mago*, and *Notch* genes. For population genetics studies, a set of microsatellite markers was developed to characterise genetic diversity in populations of EGVM from Europe and the Middle East (Reineke et al. 2015). These markers allow identifying two ancestral genetic clusters underpinning the European and Asian populations, with substantial introgression between these two genetic clusters detected in a population from Germany.

A fully annotated EGVM reference genome will assist in the identification of genes involved in adaptation and speciation, as well as in chemical communication between populations. Population genomic studies will also benefit from having a reference genome of the target pest to better understand invasion biology (Pearce et al. 2017; Tay et al. 2022). As a first step, a draft genome based on short-read Illumina data has been generated that will contribute to characterisation of resistance genes, and understanding of EGVM invasion history in the South and the North Americas (i.e., Chile, Argentina, and USA) and therefore contribute to its future biosecurity preparedness (Pandey et al. 2022). EGVM populations from Chile and USA representing the pest's recent invasive range expansion were analysed using multiple mtDNA genes (partial *COI*, partial *Cyt b*) and compared with native Europe (i.e., Portugal, Spain, Italy, Germany, Switzerland, Greece) and Asia (i.e., Israel, Turkey, Syria) populations (Tay 2016). Complete mitochondrial genomes (Tay 2016; Piper et al. 2016) identified the likely presence of a minor cryptic species in the EGVM populations. Two-genes (i.e., *mtCOI*, *Cyt b*) mtDNA signatures identified three haplotypes in 17 individuals from the Chile invasive population. 17 of 18 USA EGVM individuals also were characterised by a haplotype signature (i.e., haplotype 18,11) that was present in most of the European EGVM populations. Interestingly, one Chilean EGVM individual (collected ca. 41 km north of Santiago) shared this USA EGVM haplotype, while one USA EGVM had a unique (i.e., 02,22) haplotype not found elsewhere, suggesting that both USA and Chile incursions involved multiple founders and potentially multiple independent introductions.

3 Distribution and invasiveness

Current records indicate that EGVM is widespread and abundant in much of Western Europe, Hungary, Bulgaria, and Cyprus. It is locally abundant in parts of Tunisia, and has

few records in the United Kingdom. EGVM is considered to be present in surrounding countries in these regions, but without a clear indication of its relative abundance (CABI 2022).

While broadly Western Palearctic in origin (CABI 2022), given the patterns of early EGVM detections, Maher & Thiéry (2006) posit that it may have initially originated along the Mediterranean and then subsequently spread to Central and Western Europe. Additionally, EGVM has proven to be invasive outside of this region. For example, it has been recorded in parts of East Africa, specifically Eritrea, Ethiopia, and Kenya; surely as the result of human introduction (CABI/EPPO 2012; CABI 2022). It was also reported in parts of Japan (Bae & Komai 1991), however those reports may stem from a misidentification of another species (EPPO 2022). More recently, EGVM has been introduced into grape-growing regions of the Americas. In South America, this moth species was first detected in Chile in 2008, and is now considered widespread, and it was confirmed in the Mendoza region of Argentina in 2010, after which it spread more broadly throughout the country (González 2010; Ioriatti et al. 2012; CABI 2022). In North America, EGVM was first detected in the western United States, in Napa County, California, in 2009 (Varela et al. 2010; Simmons et al. 2021a). It later spread to other areas of California, prior to being declared eradicated by 2016 (Simmons et al. 2021a). Comparisons of Chilean and U.S. populations of EGVM to those from select areas of Europe and the Middle East indicate that the genotypes from invaded areas are most closely related to populations in Spain and France, indicating a likely introduction from Western Europe (Middleton 2011).

A handful of studies have used various approaches to assess the potential invasive range of EGVM. A risk assessment that characterised effects of habitat type and crop acreage, among other variables, estimated that nearly 30% of the continental U.S. may be suitable for EGVM (Venette et al. 2003). High risk areas included major grape-growing regions in Central and Northern California, as well as grape and other fruit-growing areas of northern Oregon (Venette et al. 2003). Another study used occurrence records from native and invaded regions to develop an ecological niche model of suitability for EGVM in China (Lv et al. 2012). Based largely on temperatures in the coldest part of the year and annual mean temperature, the results predict the highest likelihood of establishment in the south-eastern portion of the Country (Lv et al. 2012). A slightly different, physiologically based, modelling framework was used to project EGVM suitability throughout the U.S., with a focus on California (Gutierrez et al. 2012). This study concluded that the most favourable environments were in interior southern California and the southern Central Valley but given different warming scenarios would likely shift to more northern and coastal areas of the state (Gutierrez et al. 2012). The most comprehensive analysis used occurrence records of both EGVM and *V. vinifera* to identify those areas globally where the

two species are likely to co-occur (Rank et al. 2020). Based primarily on strong effects of annual mean temperature and temperature variation, those areas at risk of EGVM invasion include coastal California, coastal and eastern Washington, the north-eastern U.S., central Mexico, Chile, Argentina, Uruguay, southern Brazil, South Africa, southern Australia, and south-eastern China (Rank et al. 2020).

Perhaps the best studied invasion by EGVM is the one in California, first noted in 2009 (Varela 2010; Simmons et al. 2021a). The genotypes of moths identified were most closely related to populations from Spain and France. The precise introduction pathway in this case is not known. It is although not clear whether EGVM was introduced in California directly from Western Europe or indirectly via Chile (Middleton 2011). After first being detected in Napa County in 2009 (Varela 2010), EGVM eventually spread to 9 counties in the state, up to approximately 300 km from where it was first detected (Simmons et al. 2021a). Analysis in the most heavily invaded areas documented significant spatial heterogeneity in captures, with distinct clustering in certain locations (Schartel et al. 2019). Further investigation with habitat suitability models suggested that hotspots in EGVM activity were influenced by a combination of climate (i.e., temperature, precipitation), landscape features (i.e. elevation), and potential anthropogenic effects (i.e. distance to major roads and wineries; Schartel et al. 2019). Post hoc assessments of the eradication program that was put in place, attribute its ultimate success to the well-coordinated program, with strong public and private support, coupled with informed decision making stemming from the integration of lessons learned from prior research on EGVM in its native range (Schartel et al. 2019).

3.1 Impact of climate change

Global climate change and in particular the overall increase of average temperatures will have significant impact on EGVM physiology, phenology, voltinism, and thus distribution ranges. Being a multivoltine species, it can be expected that because of higher temperatures of winter – early spring, EGVM adults will emerge earlier from overwintering pupae in spring, with the consequence of displaying an additional generation per year (Reineke & Thiéry 2016). Evidence for such an advanced phenology and increased voltinism was first reported in Spain (Martin-Vertedor et al. 2010) and more recently in Portugal (Reis et al. 2021a, b), where populations are showing a complete 4th additional flight. In line with this, modelling studies have indicated that EGVM distribution ranges will significantly shift northwards (Svobodova et al. 2014). In this regard, existing population models for EGVM have been recently reviewed by Lessio & Alma (2021) as well as by Castex et al. (2020). The latter team also developed a generic model for EGVM that can be used to assess the impact of various climate change scenarios on the future geographical distribution and the putative spread to new vulnerable areas.

Besides phenology and voltinism, rising temperatures can also affect different life history traits in insects (see also specific section above). Increasing temperatures reduce the time needed for EGVM larval development and increase survival rates as well as larval escape ability to natural enemies, but they decrease larval lipid reserves and prophenoloxidase activity (Iltis et al. 2019). Accordingly, defensive traits displayed by EGVM against infections, parasitoids or abiotic stressors will be affected by future climate change. Studies by Iltis et al. (2018) have shown that exposure to warmer conditions during larval development elicit extensive weakening of several behavioural and immune defence reactions in EGVM larvae, which in turn could increase parasitization success. Higher temperatures also improve EGVM larval tolerance to copper fungicides through temperature-driven hormesis or by shifting the hormesis-related peak of performance toward higher copper concentrations tolerated by larvae under future temperatures (Iltis et al. 2022).

Besides temperature, several other climatic factors probably will change in the future, in particular the amount and distribution of precipitation, relative humidity and atmospheric CO₂ concentration. These climatic factors will affect all trophic levels in the vineyard ecosystem, including the host plant and natural enemies (Castex et al. 2018).

4 The future: challenges for bio-ecology research

Two and a half centuries after the EGVM description, there is a long and windy road towards the full understanding of its biology and ecology, which is tightly connected with pest prevention and management. Below, we propose an agenda formulating major aims for future research in EGVM bio-ecology.

A better understanding of EGVM population dynamics would benefit from further research on the potential effects of how feeding on various grape cultivars may affect EGVM developmental traits (Thiéry et al. 2014a, b) as well as to gain insights on the EGVM immune system (Vogelweith et al. 2011, 2015, 2016; Muller et al. 2015a). Furthermore, relatively scarce knowledge is currently available about EGVM phenology in the southern hemisphere, with a focus on Argentina (Dagatti & Becerra 2015). Additional research efforts on this issue are welcome. Furthermore, understanding climate change-related effects on the trophic interactions occurring among EGVM and its natural enemies (particularly parasitoids, Castex et al. 2018) is of pivotal importance.

Regarding EGVM genomics, more detailed analyses of the gene flow directionality of the North and South America introduction histories will require a whole genome sequencing approach as demonstrated in various invasive pest studies (e.g. Elfekih et al. 2018; Tay et al. 2022).

Herbivore-induced plant volatiles (HIPVs) are considered highly detectable synomones helping natural enemies to locate the host habitat (Kaplan 2012). Research is still needed to gain knowledge on the practical use of HIPVs in the field, the suitable release rates, and related formulations, as well as the possible association of HIPVs with predator and parasitoid sex pheromones aimed at enhancing attraction of natural enemies of EGVM (Lucchi et al. 2017).

Of note, the role of secondary plant constituents and grape vigour in the larval food has received too little attention, regarding both larval and adult fitness. This knowledge would help understand population dynamics on the different grape cultivars and the sensitivity to bio-control agents (e.g., predators, parasitoids and entomopathogens). It would also provide valuable information to better understand how EGVM gets installed in production vineyards. A hypothesis could be the drastic change of grape cultivars and their biochemical quality due to the phylloxera crisis (Thiéry 2005), cultivars being more favourable to EGVM than to the other tortricid pests. The intensive use of sulphur and copper as the only fungicide products during the beginning of the 19th century could also be involved in the rapid extension of the pest. Research on the effect of sulphur and copper, for example on the immune systems of these Tortricidae, would be of interest.

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