



# The European grape berry moth, *Eupoecilia ambiguella* (Lepidoptera: Tortricidae): Current knowledge and management challenges

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## ABSTRACT

The European grape berry moth, *Eupoecilia ambiguella* (Hübner) (Lepidoptera: Tortricidae), since its first identification in 1796, was defined as a key pest for European viticulture despite its polyphagy. Although between the late 1800s and early 1900s its presence and spread in Europe was of concern, to date its populations are low and limited to cooler and wetter areas, leading to a decline in its importance. In the present work, we reviewed its global distribution as well as its morphology, biology, and ecology. Considering the monitoring and management of this pest, the present review summarised insecticidal, agronomic, and cultural control strategies. Moreover, given the need to reduce the impact of agriculture on the environment, humans, and non-target species, we focused on control strategies relying on pheromones and biological control agents (e.g. predators and parasitoids) involved in conservation biological control.

## 1. Introduction and distribution

*Eupoecilia ambiguella* (Hübner) (Lepidoptera: Tortricidae) is native to the Palaearctic region and widespread from western and southern Europe to Turkey, Iran, northern and western Russia, Kazakhstan, central Asia, southern Siberia, China, Korea and Japan (Gilligan et al., 2014) (Fig. 1). In 1986 it was reported in Brazil, but the record remained doubtful and unconfirmed in subsequent years (Ioriatti et al., 2012). To date, its presence in European wine-growing areas facing the Mediterranean seems limited. Preferring colder and wetter climatic conditions, the rise in average seasonal temperatures led its spread more confined to areas of Central Europe (Ioriatti et al., 2012).

This species is quite polyphagous, with a host range including more than 30 plant species of warm-dry environments including *Vitis*, *Prunus*, *Cornus*, *Viburnum*, and *Ligustrum* (Ioriatti et al., 2012). The mugwort, *Artemisia vulgaris* L. (Asteraceae), is considered its main wild host plant (Ioriatti et al., 2012). On vines, it has two to three complete generations, the first of which occurs on the flowers (anthophagous generation) and the second and third on the bunches (carpophagous generations).

First described by Hübner in 1796 as *Tinea ambiguella*, it was identified as the main pest affecting grape berries in Europe until the 1920s (Ioriatti et al., 2012). Considering the observations of the late 1800s, *E. ambiguella*, then known as *Cochylis ambiguella*, was predominant in

France (Vivarelli, 1924) and the central-northern Italian vineyards (Mach, 1890); by contrast, the occurrence of *Lobesia botrana* (Lepidoptera: Tortricidae), currently the main pest in Mediterranean vineyards (Benelli et al., 2023a, 2023b), was fairly sporadic (Mach, 1890; Silvestri, 1912). Things changed in the first two decades of the 1900s. Indeed, further studies in France (Feytaud 1924) and northern Italy (Catoni, 1910; Catoni and Schwangart, 1914) showed that *L. botrana* became the dominant species while *E. ambiguella* infestations declined (Voglino, 1914; Dalmasso, 1922). The causes that led to a prevalence of *E. ambiguella* over *L. botrana* in the past century and the relative economic importance in the European vineyards have been addressed and discussed in a recent publication (Ioriatti et al., 2023). The alternation observed in the past for the two moths has been ascribed to the different humidity requirements of each species (Stellwaag 1943; Bovey 1966).

Despite its importance and long history as a vineyard pest, a review of current knowledge about *E. ambiguella* is still lacking. Herein, we summarize the available information on its morphology, biology, and ecology as well as on its geographical distribution. Moreover, we report current knowledge on its monitoring and management. In the latter section, we cover insecticide-based, cultural, and biological control strategies, as well as pheromone-based mating disruption of *E. ambiguella*.

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## 2. Morphology

### 2.1. Adult

*Eupoecilia ambiguella* adults are characterized by a wing pattern that facilitates species recognition (Fig. 2A). The ochre-yellow forewings are crossed by a broad subtrapezoidal brown-black band. The hind wings are uniformly slate-gray and very finely ciliate. The wing veining is typical of Cochylini (Solinas, 1962). The male is slightly smaller than the female but basically the adults reach a length of about 6–7 mm and a wingspan of 12–15 mm. The head lacks ocelli and bears antennae of 40 articles, briefly ciliated in the male (Solinas, 1962).

The grayish abdomen shows a convex shape in the female, as in *L. botrana*, (Benelli et al., 2023a). Examination of the genital armature is conclusive for the exact determination of the species; the ovipositor is similar to that of *L. botrana* (Benelli et al., 2023a) (Table 1), although the gonapophyses are slightly different in shape and the signum of the copulatory bursa is starry. In the male, the morphological differences are more pronounced; the valves are broad at the base and narrow towards the apex, which is pointy; the sacculus is broad and well differentiated, ending in a short spine (Solinas, 1962) (Table 1).

### 2.2. Egg

*Eupoecilia ambiguella* egg is slightly larger in size (0.75 and 0.90 mm long and 0.60 and 0.65 mm wide) than the *L. botrana* egg (0.65–0.90 mm long and 0.45–0.75 mm wide) (Benelli et al., 2023a), having a straw-yellow colour at laying, the surface of the chorion reticulated with polygonal meshes, and characterized by the presence of more or less visible orange speckles due to the deposition of pigments in the polygonal vitelline cells (Fig. 2B) (Solinas, 1962) (Table 1).

### 2.3. Larva

The 1<sup>st</sup> instar larva shows a brownish-hazel head and a yellowish white body. The 5 < instar larva has a length of about 12 mm, and a grayish-yellow body (Fig. 2C) (Solinas, 1962). The cephalic capsule is reddish brown, while the prothoracic sclerite and the legs are black. The anal comb consists of 6–7 teeth (Solinas, 1962).

### 2.4. Pupa

The pupa is obtecta (chrysalis) (Fig. 2D), slender (especially in

males), with the cranial portion rounded and the caudal portion pointed and equipped with hooks. Female chrysalises are usually stockier and often even larger than male ones (Table 1).

The chrysalis measures 6–8 mm in length, varies in colour from orange to reddish-brown and is contained in a fusiform cocoon consisting of strongly appressed white silky threads (Table 1). The cremaster ends in a fan-shaped surface, fitted with 16 large hooked bristles, dorsally and ventrally arranged in a crown shape (Solinas, 1962) (Table 1). Inside the cocoon, in addition to the excrement released by the mature larva weaving the cocoon, there is always the shedding of the last larval molt anchored to the silky threads by the cremaster's hooks (Table 1). The flickering occurs when the newly formed adult, pressing against the dermaskeleton, tears it along a fracture line located dorsally to the three thoracic segments (Solinas, 1962).

## 3. Biology and ecology

In cool areas of central Europe *E. ambiguella* completes two full generations, which can become three moving towards southern areas, such as northern Italy. The highest activity of adults of this species is observed not only at dusk, as in *L. botrana* (Lucchi et al., 2018), but also in the night-early morning hours (23.00–5.00 h) (Schruff and Schmieder, 1986); mating generally occurs in the morning, while oviposition in the evening. Concerning the potential fertility, it is estimated that a female of the overwintering generation can lay up to 50–60 eggs and no more than 30 in the anthophagous generation (Sprengel, 1929).

The preferred oviposition sites of first-flight females are distinct inflorescence sites (mainly flower bracts and calyptra, but more rarely flower peduncles, inflorescence axes, tendrils and leaves), depending on the phenological stage of the vine (Thiery, 2011; Markheiser et al., 2018; Rid et al., 2018). Once the embryonic development is complete, the newly hatched larva tears the egg's chorion laterally with its mandibles and quickly shelters outside; after hatching, the first-generation larva wanders over the inflorescence briefly, then erodes a floral button, penetrates it, and feeds on the calyptra, anthers, and ovary. Females of the carpophagous generations lay their eggs almost exclusively on the berries, whose protective wax containing oleanolic acid triggers *E. ambiguella* oviposition. Eggs on the rachis can sometimes be found (Rid et al., 2018); the larva makes more than one hole in the epicarp. The affected berry may be the same one on which the egg was laid or another one of the same cluster (Frolov, 2008; Gilligan et al., 2014).

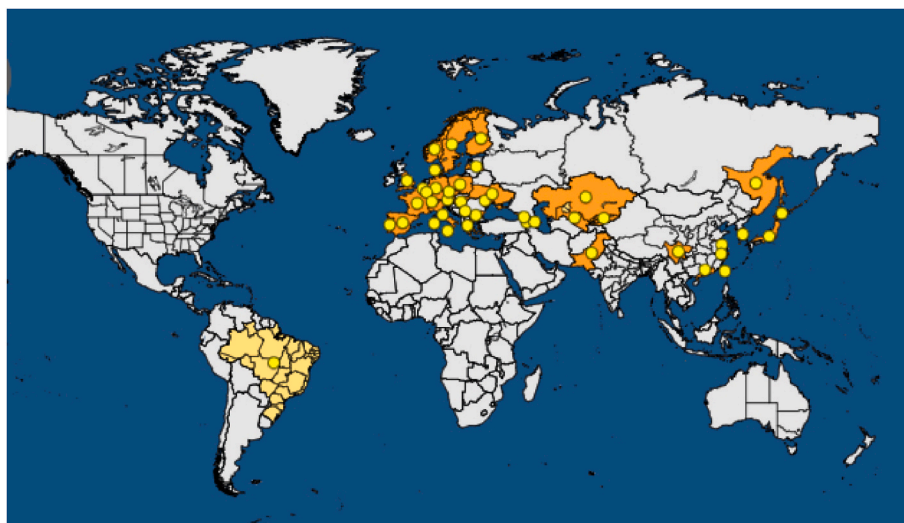


Fig. 1. *Eupoecilia ambiguella* world distribution. Orange indicates where presence is confirmed while light yellow shows that there has been a report but doubtful and not subsequently confirmed (image credit: EPPO Global Database).

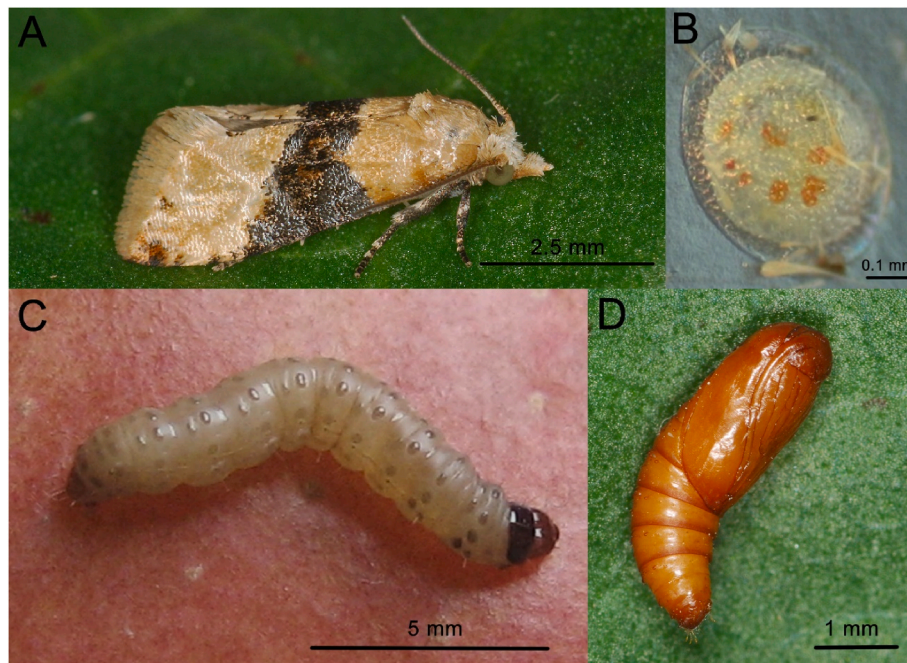


Fig. 2. *Eupoecilia ambiguella* developmental stages: A) adult, B) newly laid egg, C) fifth instar larva, D) chrysalis (photo credit: Paolo Giannotti).

#### 4. Monitoring

From the pheromone-producing glands of *E. ambiguella*, nine different acetates and alcohols have been isolated (Arn et al., 1976). Among these, only three appeared to belong to the pheromone blend, and the main component was (*Z*)-9-dodecenyl acetate (Fig. 3A). In electroantennography tests, this compound highly stimulated male antennal sensilla, proving to be essential in attracting males (Arn et al., 1976).

With the identification of the chemical structure of the sex pheromone of *E. ambiguella* (Arn et al., 1976), the monitoring of adult populations of this moth was greatly enhanced by the development of practical and effective pheromone traps designed to catch males (Arn et al., 1976) (Fig. 3B).

#### 5. Management

Given the marked morpho-physiological, biological, and behavioural similarities with *L. botrana*, the management strategies for *E. ambiguella* are quite comparable to those available for *L. botrana*, including insecticide-based, cultural, and biological control strategies, as well as pheromone-based mating disruption, as detailed in the paragraphs below.

##### 5.1. Insecticide-based control

Insecticide management of *E. ambiguella* mainly relies on synthetic (i. e., tebufenozide, emamectin and chlorantraniliprole) or insecticides of organic origin (i. e., *Bacillus thuringiensis* subsp. *kurstaki* or *aizawai*, and spinosad) (Kos, 2001; Bacci et al., 2016). Insecticide application targets eggs or larvae (1<sup>st</sup>-3<sup>rd</sup> instars), timing spray treatments after visual samplings on affected plants. In choosing the active ingredients (a.i.) to be used, those with reduced environmental impact, lower toxicity to humans, and higher selectivity against natural enemies and pollinators must be preferred (Lucchi and Benelli, 2018).

##### 5.2. Agronomic techniques

Growing less susceptible varieties can be a tool to modulate

*E. ambiguella* damage (Pavan et al., 2018), since grape variety can noticeably affects the development and fecundity of this pest (Pavan et al., 2018). Moreover, the size and shape of grape clusters, as well as the waxy bloom on grape surface, can influence the oviposition and developmental time of this moth (Pavan et al., 2018; Rid et al., 2018). Cultural practices can also be used to create a less insect-friendly environment, e.g., leaf removal in the bunch zone of the canopy (improvement of aeration and sunlight exposure of the clusters), bunch thinning (bunch clusters create a less aired habitat, reduce the penetration of active ingredients, and promote the development of fungal diseases related to larval damage), removal of the bark with metal mesh gloves to kill overwintering pupae (effective method but with high manpower costs and hence not very applicable except in few contexts) (Kiaeiian Moosavi et al., 2018).

##### 5.3. Pheromone-mediated mating disruption (MD)

Since the identification of the sex pheromone released by females of this species, new perspectives were opened to develop novel monitoring and control strategies (Arn et al., 1976). Nowadays, the gained knowledge on this pest and the effectiveness of MD developed made this strategy the main method used for its management (Kast, 2001; Thiery et al., 2023).

Currently, new technology has allowed the development of innovative active-release emitters (AE) for MD against this and several other pest (Fig. 4) (Benelli et al., 2019). Active-release emitters are equipped with electronic control units programmable according to the flight behaviour of the target pest, the vine's phenological stage and environmental conditions (Benelli et al., 2019). This strategy not only allows effective *E. ambiguella* management, but also leads to reducing insecticide requirements, thereby limiting side effects on the environment and on non-target insects, helping to preserve the populations of natural enemies occurring in the vineyard and nearby (Schindler et al., 2022).

Moreover, recent studies conducted to assess the impact of climate change on pest management have shown how future increases in atmospheric CO<sub>2</sub> concentrations will not interfere with the effectiveness of MD against *E. ambiguella* and *L. botrana* (Becker et al., 2023), proving once again the validity of this strategy.



**Table 1**  
Morphological features of *Eupoecilia ambiguella* and *Lobesia botrana* (Benelli et al., 2023a; Solinas, 1962).

Adult		Egg		Larva		Chrysalis	
<i>E. ambiguella</i>	<i>L. botrana</i>	<i>E. ambiguella</i>	<i>L. botrana</i>	<i>E. ambiguella</i>	<i>L. botrana</i>	<i>E. ambiguella</i>	<i>L. botrana</i>
Wingspan: 12–15 mm	Wingspan: 11–13 mm	Length: 0.75–0.90 mm, Width: 0.60–0.65 mm	Length: 0.65–0.78 mm, Width: 0.60–0.62 mm	Neonate larva length: 1 mm, Mature larva length: 12 mm	Neonate larvae length: 1 mm, Mature larva length: 8–10 mm	Length: 6–8 mm	Length: 4–6 mm
Ochre-yellow forewings with a broad brown-black trapezoidal band.	Front wings of highly variegated marble coloration.	Straw-yellow colour at deposition and is characterized by the presence of more or less evident orange speckles.	Pale straw yellow in colour, they turn to transparent light gray with very vivid iridescent highlights.	Ventral portion tuberculated; dorsal surface of the dermaskeleton raised into tiny convex leeks, barely protruding over the surface itself.	Dermaskeleton of the dorsal and ventral surface of the body roughened by the presence of tiny tubercles ending in a short, thin bristle, except that of the head and pronotum.	Chrysalis obteata, slender (especially in males), with the cranial portion rounded and the caudal portion pointed and equipped with hooks. Female pupae are generally stockier and often even larger than male ones. The cremaster ends in a fan-shaped surface, fitted with 16 large hooked bristles, with dorsal and ventral, crown-like arrangement.	Initially equipped with eight large hooked bristles, 4 dorsal and 4 latero-dorsal.
Convex-shaped abdomen.	Convex-shaped abdomen.	Reticulated chorion surface.	Reticulated chorion surface.	The anal comb consists of 6–7 teeth.	The anal comb consists of 6–8 teeth.	Colour varies from orange to reddish-brown.	Initially greenish then turns to dark brown.
In the female, the signum of the copulatory bag is starry.	In the female, the copulatory bursa is long, claviform, distinctly bilobed at the apex, and provided with an elongated, ridge-like raised signum.			Neonate larva: brownish-hazel head while the body is yellowish white.	Neonate larva: head blackish in colour and rest of body, including pronotum, creamy white.	The chrysalis is contained in a fusiform, nonrigid cocoon consisting of strongly appressed white silky threads.	
In the male, the valves are broad at the base and narrow towards the apex, which is pointed; the sacculus is broad and well differentiated, ending in a short spine.	In the male, the valves have a well-differentiated sacculus and a rounded apex; the uncus is bifid, and the vinculum is U-shaped and strongly sclerified.			Mature larva: the cephalic capsule is reddish brown, while the prothoracic sclerite and legs are black.	Mature larva: the prothoracic scutum has a brown coloration, generally like that of the head, the second antennomer is black and the cuticular areas around the base of the bristles are whitish		

#### 5.4. Natural enemies

##### 5.4.1. Predators and parasitoids

The range of natural enemies includes parasitoids belonging to the orders Hymenoptera (e.g., Braconidae, Chalcididae, Ichneumonidae, Elasmidae, Eulophidae, Pteromalidae, and Trichogrammatidae) and Diptera (Tachinidae) (Sentenac, 2011; Bărbuceanu and Andriescu, 2012; Thiéry et al., 2018) (Table 2) (Figs. 5 and 6). Most of the parasitoid species associated with *E. ambiguella* have also been reported for *L. botrana* (Marchesini and Dalla Montà, 1994; Lucchi et al., 2016 Scaramozzino et al., 2017, 2018, 2020; Di Giovanni et al., 2022). Indeed, as already noted by Silvestri (1912) and Catoni (1914) in pioneering works on the biology of *L. botrana* and its natural enemies in Italy, wide host-range parasitoids may attack similar species when they coexist in the same habitats. It should be noted, however, that some of the records reported may be erroneous, as results of parasitoid misidentifications or incorrect host-parasitoid associations. For example, *Dolichomitus terebrans* (Ratzeburg, 1844) (Ichneumonidae) is a parasitoid wasp that has been associated with both *E. ambiguella* and *L. botrana* (Aubert, 1969; Constantineanu and Pisica, 1970), although it is a widely distributed species in coniferous forests of Europe and North America, where it has often been obtained from bark beetles on *Pinus* (Fitton et al., 1988); likewise, the record for *Hoplocryptus confector* (Gravenhorst, 1829) (Ichneumonidae) reported by Leon (1912) in Bărbuceanu and Andriescu (2012) is somewhat dubious, this species being associated with nests of Apoidea and Vespidae (Schwarz, 2007). In

addition, confusion may emerge in species discrimination at the larval stage due to a general resemblance between *E. ambiguella* and *L. botrana* instars and, as stressed by Shaw (2023), special care must be used with parasitoids obtained by substrate rearings, as it is not always feasible to determine the host from which a parasitoid was obtained.

Concerning predators, *E. ambiguella* antagonists include insects belonging to the orders Dermaptera, Hemiptera (e.g., Miridae, Anthorcoridae, Nabidae, Reduviidae), Opliones, Neuroptera (Chrysopidae), and Coleoptera, as well as predators belonging to different families of spiders (e.g., Clubionidae, Theridiidae, Tomisidae, Linyphiidae, Salticidae), mites (Trombididae), birds, and bats (Ioriatti et al., 2012; Thiéry et al., 2018) (Table 2).

Given the difficulties in finding and breeding effective biological control agents (BCAs), it is important to sustain those already present in the agroecosystem by enhancing conservation biological control (CBC). This can be achieved through the adoption of selective and low-persistence (bio)insecticides, or using non-insecticidal techniques, but also through careful management of the vineyard agroecosystem to provide food and refugia for BCAs, increasing biodiversity and agroecosystem stability (Segoli et al., 2020). Studies conducted in Australian vineyards have shown that natural enemies of agricultural crop pests may respond to local vegetation adjacent to agricultural land (Thomson and Hoffmann, 2010). For example, egg predation of the ampelophagous lepidopteran *Epiphyas postvittana* (Walker, 1863) (Lepidoptera: Tortricidae) was relatively higher in vineyards with adjacent residual forest or planted woody vegetation (Thomson and Hoffmann, 2010).





**Fig. 3.** Example of A) chemical structure of the main component of its sex pheromone and B) a pheromone trap for monitoring *Eupoecilia ambiguella* (photo credit: A: The Pherobase; B: Renato Ricciardi).



**Fig. 4.** Example of active-release emitter used for *Eupoecilia ambiguella* mating disruption (photo credit: CBC Europe srl – Biogard).

This may incentivize individual landowners to keep the vegetation intact, even if it means incurring expenses to preserve it and reduce their farmed acreage.

#### 5.4.2. Entomopathogens

As for *L. botrana*, entomopathogenic bacteria (EPB),

**Table 2**  
Predators and parasitoids associated with *Eupoecilia ambiguella*.

Taxon	References
<b>Parasitoids</b>	
<b>Diptera Tachinidae</b>	
( <sup>a</sup> ) ( <sup>c</sup> ) <i>Bessa parallela</i> (Meigen, 1824)	Thompson (1946); Tschorsnig (2017)
( <sup>a</sup> ) <i>Eurysthaea scutellaris</i> (Robineau-Desvoidy, 1848)	Tschorsnig (2017)
( <sup>a</sup> ) <i>Nemorilla maculosa</i> (Meigen, 1824)	Tschorsnig (2017)
( <sup>a</sup> ) <i>Phytomyza nigrina</i> (Meigen, 1824) (syn. <i>P. nitidiventris</i> Rondani, 1845)	Thompson (1946); Tschorsnig (2017)
<b>Hymenoptera Aphelinidae</b>	
<i>Encarsia inaron</i> (Walker, 1839)	Noyes (2019)
<b>Hymenoptera Chalcididae</b>	
( <sup>a</sup> ) <i>Brachymeria minuta</i> (Linnaeus, 1767) (syn. <i>B. pusilla</i> (Fabricius, 1787))	Thompson (1946); Thiéry et al. (2018)
<b>Hymenoptera Eulophidae</b>	
( <sup>a</sup> ) <i>Colpoclypeus florus</i> (Walker, 1839)	Noyes (2019)
( <sup>a</sup> ) <i>Elachertus affinis</i> Masi, 1911	Noyes (2019)
( <sup>a</sup> ) <i>Elasmus flabellatus</i> (Fonscolombe, 1832)	Thompson (1946)
<b>Hymenoptera Eurytomidae</b>	
( <sup>a</sup> ) <i>Eurytoma rosae</i> Nees, 1834	Thompson (1946)
<b>Hymenoptera Pteromalidae</b>	
( <sup>a</sup> ) <i>Ablaxia parviclava</i> (Thomson, 1878)	Thompson (1946)
( <sup>a</sup> ) <i>Dibrachys affinis</i> Masi, 1907	Bărbuceanu and Andriescu (2012)
( <sup>a</sup> ) <i>Dibrachys microgastri</i> (Bouche, 1834) (syn. <i>D. cavus</i> (Walker, 1835), <i>D. boaemiae</i> (Walker, 1863))	Thompson (1946); Thiéry et al. (2018); Noyes (2019)
( <sup>a</sup> ) <i>Pteromalus chrysos</i> Walker, 1836 (syn. <i>Habrocytus acutigena</i> Thomson, 1878)	Thompson (1946)
<b>Hymenoptera Torymidae</b>	
( <sup>a</sup> ) <i>Monodontomerus aereus</i> Walker, 1834	Thompson (1946)
<b>Hymenoptera Trichogrammatidae</b>	
<i>Trichogramma agrotidis</i> Voegelé and Pintureau, 1982	Thiéry et al. (2018); Noyes (2019)
( <sup>b</sup> ) <i>Trichogramma brassicae</i> Bezdenko, 1968	Thiéry et al. (2018); Noyes (2019)
( <sup>c</sup> ) <i>Trichogramma cacaeciae</i> Marchal, 1927	Thiéry et al. (2018); Noyes (2019)
<i>Trichogramma daumalae</i> Dugast and Voegelé, 1984	Thiéry et al. (2018); Noyes (2019)
<i>Trichogramma dendrolimi</i> Matsumura, 1926	Thiéry et al. (2018); Noyes (2019)
( <sup>b</sup> ) <i>Trichogramma embryophagum</i> (Hartig, 1838)	Thiéry et al. (2018); Noyes (2019)
( <sup>a</sup> ) <i>Trichogramma evanescens</i> Westwood, 1833	Thompson (1946); Thiéry et al. (2018); Noyes (2019)
( <sup>a</sup> ) <i>Trichogramma minuta</i> Riley, 1871	Thiéry et al. (2018); Noyes (2019)
<i>Trichogramma principium</i> Sugonjaev and Sorokina, 1976	Thiéry et al. (2018); Noyes (2019)
<i>Trichogramma semblidis</i> (Aurivillius, 1898)	Thiéry et al. (2018); Noyes (2019)
<b>Hymenoptera Braconidae</b>	
( <sup>a</sup> ) <i>Aleiodes (Aleiodes) coxalis</i> (Spinola, 1808) (syn. <i>Rogas tristis</i> (Wesmael, 1838))	Thompson (1946)
( <sup>a</sup> ) <i>Ascogaster quadridentata</i> Wesmael, 1835	Thompson (1946); Yu et al. (2016)
<i>Avga opaca</i> (Hellén, 1957)	Yu et al. (2016)
<i>Charmon extensor</i> (Linnaeus, 1758)	Yu et al. (2016)
<i>Macrocentrus collaris</i> (Spinola, 1808)	Yu et al. (2016)
<i>Macrocentrus linearis</i> (Nees, 1811)	Yu et al. (2016)
<i>Meteorus pendulus</i> (Müller, 1776)	Yu et al. (2016)
<i>Meteorus rubens</i> (Nees, 1811)	Yu et al. (2016)
<i>Microplitis aduncus</i> (Ruthe, 1860)	Yu et al. (2016)
( <sup>a</sup> ) <i>Microplitis tuberculifer</i> (Wesmael, 1837)	Thompson (1946); Yu et al. (2016)
<i>Rhoptrocentrus piceus</i> Marshall, 1897	Yu et al. (2016)
<b>Hymenoptera Ichneumonidae</b>	
( <sup>a</sup> ) <i>Agrothereutes abbreviatus</i> (Fabricius, 1794)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<i>Agrypon anxium</i> (Wesmael, 1849)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
( <sup>a</sup> ) <i>Agrypon flaveolatum</i> (Gravenhorst, 1807)	Thompson (1946)
( <sup>a</sup> ) <i>Aptesis nigrocincta</i> (Gravenhorst, 1815)	Thompson (1946)
( <sup>a</sup> ) <i>Campoplex abbreviatus</i> (Brischke, 1880)	Thompson (1946)
( <sup>a</sup> ) <i>Campoplex capitator</i> (Aubert, 1960)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
( <sup>a</sup> ) ( <sup>d</sup> ) <i>Campoplex difformis</i> (Gmelin, 1790)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<i>Campoplex rufipes</i> Gravenhorst, 1829	Thompson (1946)

(continued on next page)

Table 2 (continued)

Taxon	References
<sup>(a)</sup> <i>Ceratophygadeuon varicornis</i> (Thomson, 1885)	Thompson (1946)
<sup>(c)</sup> <i>Charitopes clausus</i> (Thomson, 1888)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(a)</sup> <i>Diadegma areolare</i> (Holmgren, 1860)	Thompson (1946)
<sup>(c)</sup> <i>Diadegma armillatum</i> (Gravenhorst, 1829)	Bărbuceanu and Andriescu (2012)
<i>Diadegma consumtor</i> (Gravenhorst, 1829)	Bărbuceanu and Andriescu (2012)
<sup>(c)</sup> <i>Diadegma fenestrata</i> (Holmgren, 1860)	Thompson (1946)
<sup>(c)</sup> <i>Diadegma melanium</i> (Thomson, 1887)	Thompson (1946)
<sup>(c)</sup> <i>Diadegma tenuipes</i> (Thomson, 1887)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Dicaelotus (Dicaelotus) erythrogaster</i> (Holmgren, 1890)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Dicaelotus (Dicaelotus) pusillator</i> (Gravenhorst, 1807)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Dolichomitus terebrans</i> (Ratzeburg, 1844)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Endasys minutulus</i> (Thomson, 1883)	Thompson (1946)
<sup>(c)</sup> <i>Endromopoda detrita</i> (Holmgren, 1860)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Erytus apostatus</i> (Gravenhorst, 1829) (syn. <i>Angitia exareolata</i> (Ratzeburg, 1852))	Thompson (1946)
<sup>(c)</sup> <i>Exochus lentipes</i> Gravenhorst, 1829 (syn. <i>E. notatus</i> Holmgren, 1858)	Thompson (1946)
<sup>(c)</sup> <i>Exochus tibialis</i> Holmgren, 1858	Thompson (1946)
<sup>(c)</sup> <i>Gambrus ornatus</i> (Gravenhorst, 1829) (syn. <i>G. inferus</i> Thomson, 1896)	Thompson (1946)
<sup>(c)</sup> <i>Gelis acarorum</i> (Linnaeus, 1758) (syn. <i>G. sericeus</i> (Förster, 1850))	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Gelis areator</i> (Panzer, 1804) (syn. <i>Hemiteles pulchellus</i> Gravenhorst, 1829)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Gelis taschenbergii</i> (Schmiedeknecht, 1897)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<i>Hoplocryptus confector</i> (Gravenhorst, 1829)	Bărbuceanu and Andriescu (2012)
<sup>(c)</sup> <i>Isadelphus gallicola</i> (Bridgman, 1880) (syn. <i>Hemiteles nigriventris</i> Thomson, 1884)	Thompson (1946)
<sup>(c)</sup> <i>Ischnus alternator</i> (Gravenhorst, 1829)	Thompson (1946)
<sup>(c)</sup> <i>Ischnus migrator</i> (Fabricius, 1775)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Itopectis alternans</i> (Gravenhorst, 1829)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Itopectis maculator</i> (Fabricius, 1775)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Itopectis tunetana</i> (Schmiedeknecht, 1914)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Lathrostizus lugens</i> (Gravenhorst, 1829) (syn. <i>Angitia vestigialis</i> (Ratzeburg, 1852))	Thompson (1946)
<sup>(c)</sup> <i>Lissonota (Lissonota) carbonaria</i> Holmgren, 1860	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Linytus exhortator</i> (Fabricius, 1787) (syn. <i>Platylabus dimidiatus</i> (Gravenhorst, 1829))	Thompson (1946)
<sup>(c)</sup> <i>Mesochorus semirufus</i> Holmgren, 1860	Thompson (1946)
<sup>(c)</sup> <i>Phygadeuon dubius</i> (Gravenhorst, 1829)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Pimpla contemplator</i> (Müller, 1776)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Pimpla spuria</i> Gravenhorst, 1829 (syn. <i>P. strigipleuris</i> Thomson, 1877)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Pimpla turionellae</i> (Linnaeus, 1758) (syn. <i>P. examinator</i> (Fabricius, 1804))	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)

Table 2 (continued)

Taxon	References
<sup>(c)</sup> <i>Scambus calobatus</i> (Gravenhorst, 1829)	Thompson (1946)
<sup>(c)</sup> <i>Scambus sagax</i> (Hartig, 1838)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<i>Scambus vesicarius</i> (Ratzeburg, 1844)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Sinophorus turionum</i> (Ratzeburg, 1844) (syn. <i>Eulimneria alkae</i> (Ellinger and Sachtleben, 1928))	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Theroscopus hemipteron</i> (Riche, 1791)	Thompson (1946); Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<sup>(c)</sup> <i>Tranosemella praerogator</i> (Linnaeus, 1758)	Bărbuceanu and Andriescu (2012); Yu et al. (2016); Thiéry et al. (2018)
<b>Predators</b>	
<b>Neuroptera Chrysopidae</b>	
<i>Chrysoperla affinis</i> (Stephens, 1836)	Thiéry et al. (2018)
<i>Chrysoperla carnea</i> (Stephens, 1836)	Thiéry et al. (2018)
<i>Chrysoperla harrisii</i> (Fitch, 1855)	Thiéry et al. (2018)
<i>Chrysoperla lucasina</i> (Lacroix, 1912)	Thiéry et al. (2018)
<i>Dichochrysa flavifrons</i> (Brauer, 1851)	Thiéry et al. (2018)
<i>Dichochrysa prasina</i> (Burmeister, 1839)	Thiéry et al. (2018)
<b>Diptera Syrphidae</b>	
<i>Xanthandrus comtus</i> (Harris, 1780)	Sentenac (2011)

<sup>(a)</sup> Parasitoids also associated with *Lobesia botrana*.

<sup>(b)</sup> Species released for biological control of *L. botrana* in Italy but not reported on this host in the wild (Lucchi et al., 2016).

<sup>(c)</sup> Erroneously reported as *Bessa selecta* (Meigen, 1824) in Thompson (1946), which is however a parasitoid of Hymenoptera. See Tschorsnig (2017: 46) on the confusion between the two species.

<sup>(d)</sup> See Di Giovanni et al. (2021) on the confusion on the use of the name *Campoplex mutabilis* (Holmgren, 1860) in place of *C. difformis* (Gmelin, 1790).

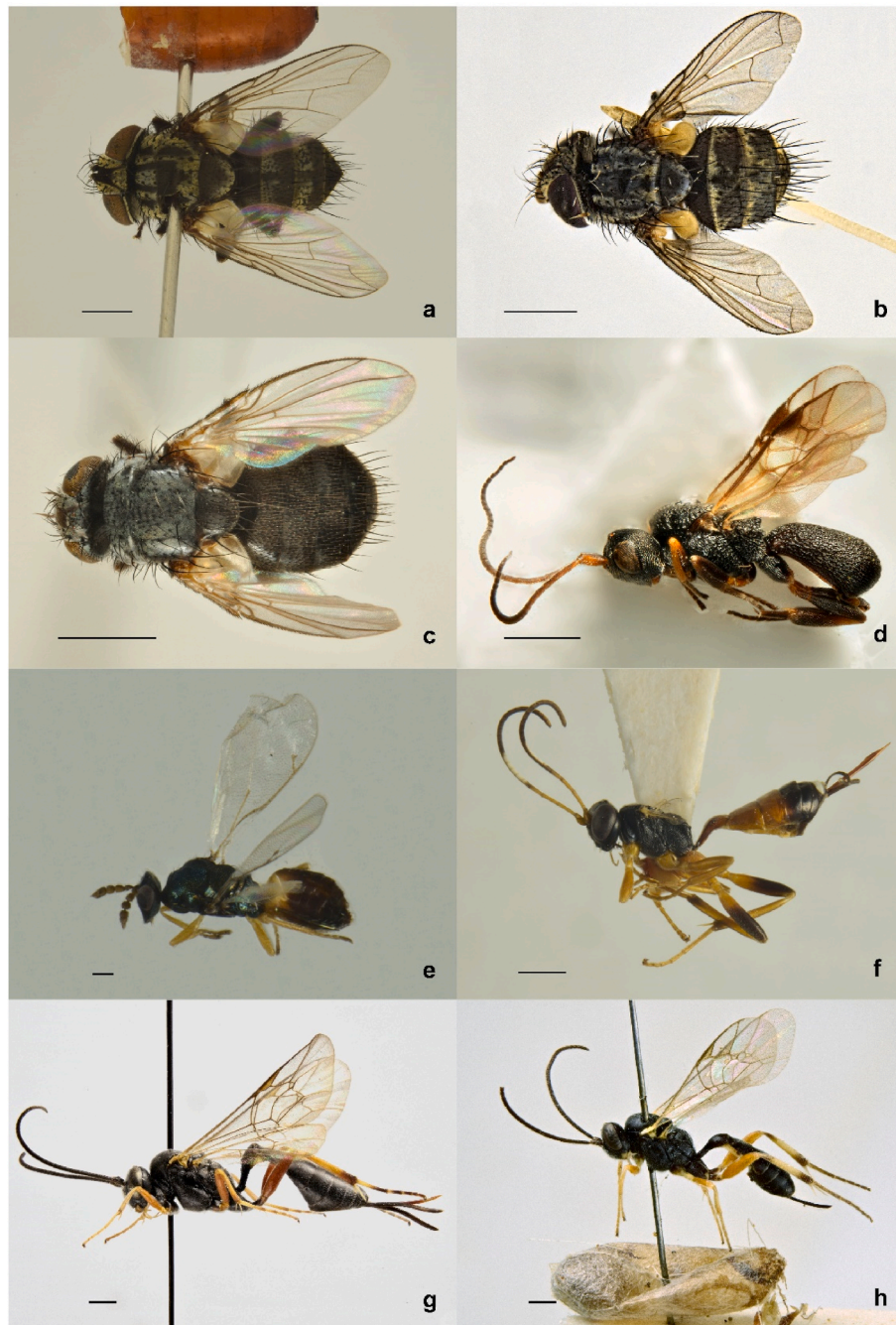
entomopathogenic fungi (EPF) and entomopathogenic nematodes (EPN) may represent alternative control tools of this species within a biological control framework (Benelli et al., 2023b; Smaghe et al., 2023). Among the most effective EPBs against *E. ambiguella* and other lepidopterans are *Bacillus thuringiensis* subsp. *kurstaki* or subsp. *aizawai* (Ioriatti et al., 2012). Regarding EPFs, to date, the most effective and widely used species is *Beauveria bassiana* (Galidevara et al., 2016). Notably, the authors showed, through *in vivo* tests on *E. ambiguella* larvae, that three specific genes (i.e., subtilisin like protease Pr1H, Exocyst component Sec15 and EC391425 transcript) of *B. bassiana* are responsible for entomopathogenicity (Galidevara et al., 2016). In the last few years, in addition to EPBs and EPFs, EPNs are emerging as effective BCAs of several plant pests of agricultural interest (Campos-Herrera, 2015; Platt et al., 2020). To give an example, Dablaka et al. (2017) showed that a post-harvest application of selected nematodes (i.e., *Steinernema carpocapsae*, *S. feltiae* and *S. kraussei*) on the soil and at the base of trunks can reduce the overwintering forms of *L. botrana* and *E. ambiguella*.

## 6. Conclusions and future perspectives

The latest studies have shown a reduction in the presence of *E. ambiguella* in the Mediterranean wine-growing regions, where it was undermined by *L. botrana* (Ioriatti et al., 2012, 2023). This trend should not lead to an underestimation of the harmfulness of *E. ambiguella*, since, in the past, changes in climatic conditions drove shifts in the prevalence of one species over the other (Ioriatti et al., 2023). For instance, in the 1950s, a drop in average temperatures and an increase in relative humidity led to a resurgence of *E. ambiguella* in places where it had been previously replaced by *L. botrana* (Zangheri, 1959).

Considering the current climate change and its impact on insects (Harvey et al., 2023; Subedi et al., 2023), we cannot exclude the possibility that *E. ambiguella* may become as harmful as it was in the past (Gutierrez and Ponti, 2022). On the other hand, climate change could





**Fig. 5.** Parasitoids associated with *Eupoecilia ambiguella*: a) *Bessa parallela* (Meigen, 1824) (Tachinidae); b) *Nemorilla maculosa* (Meigen, 1824) (Tachinidae); c) *Phytomyptera nigrina* (Meigen, 1824) (Tachinidae); d) *Ascogaster quadridentata* Wesmael, 1835 (Braconidae); e) *Colpoclypeus florus* (Walker, 1839) (Chalcididae); f) *Agrothereutes abbreviatus* (Fabricius, 1794) (Ichneumonidae); g) *Sinophorus turionum* (Ratzeburg, 1844) (Ichneumonidae); h) *Tranosemella praerogator* (Linnaeus, 1758) (Ichneumonidae). Scale bar 1 mm, except for Fig. 5e where the scale bar is 0.1 mm (photo credit: Renato Ricciardi, Filippo Di Giovanni, and Pier Luigi Scaramozzino).

lead to favourable conditions in environments where it was never present before, pushing it to colonise such areas and becoming an invasive alien species.

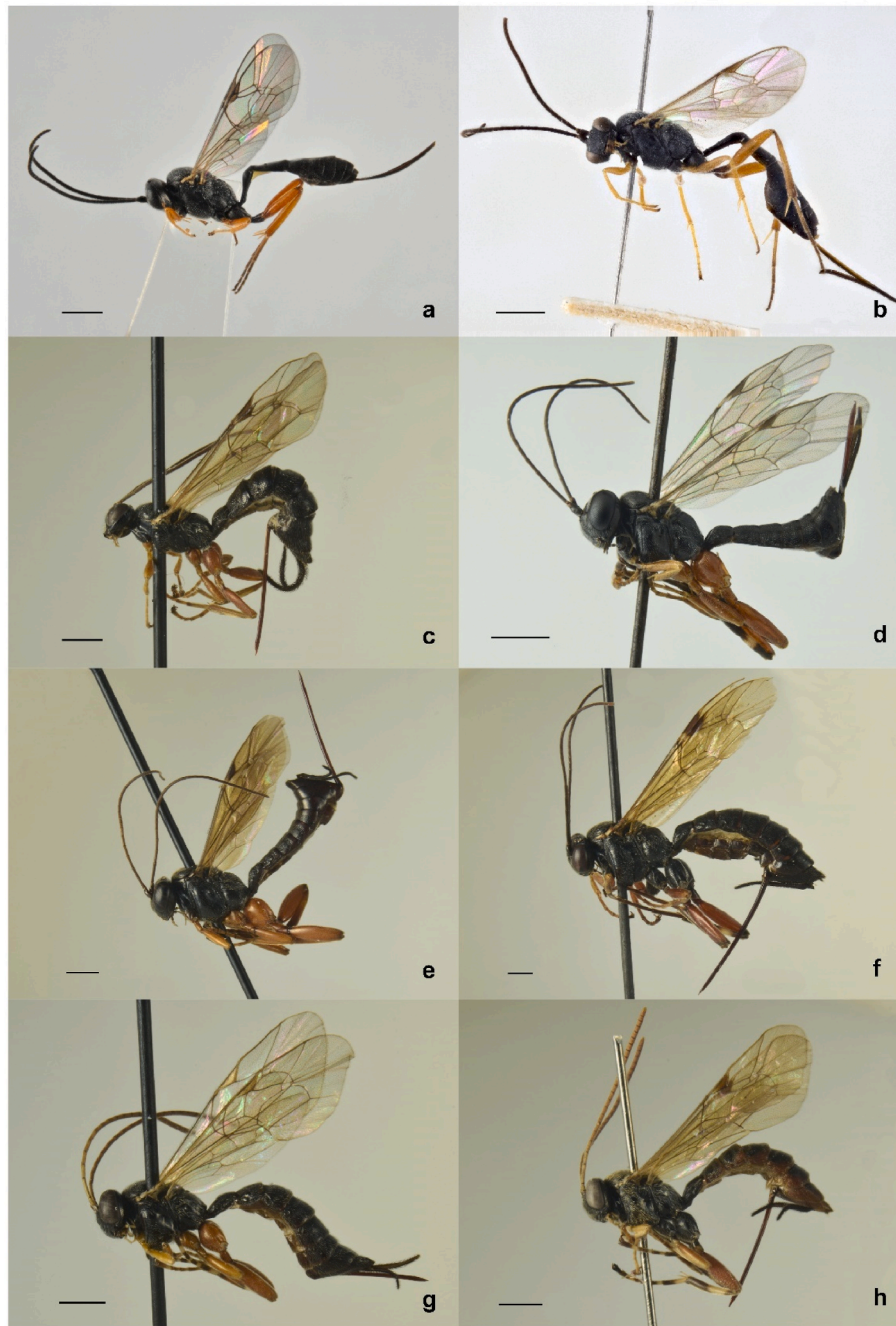
Given that predicting potential movements of invasive crop pests under climate change is essential for global food security (Ma and Ma, 2022), it will be crucial to continue monitoring *E. ambiguella* to avoid being unprepared if the environmental conditions become suitable for this pest. On these insights, multi-year studies aiming to correlate species' presence/absence with climate conditions would provide valuable insight into the ecology of both pests. At the same time, understanding how far the two species are able to coexist on the same host plant would

help shed light on the fluctuations between the two pest populations within the same habitat.

Furthermore, considering the current coexistence of *E. ambiguella* in areas where *L. botrana* is also present, Integrated Pest Management strategies against this pest may benefit from new biocontrol approaches being developed for the much more widespread and harmful *L. botrana*. The development of green pesticides and the implementation of MD strategies through active releasers, which are already developed for *L. botrana* control, may also be viable pathways in defending against *E. ambiguella* outbreaks.

Moreover, it is crucial to further investigate still little-known aspects





**Fig. 6.** Further parasitoids associated with *Eupoecilia ambiguella*: (a) *Campoplex capitator* Aubert, 1960 (Ichneumonidae); (b) *Campoplex difformis* (Gmelin, 1790) (Ichneumonidae); (c) *Endromopoda detrita* (Holmgren, 1860) (Ichneumonidae); (d) *Pimpla contemplator* (Müller, 1776) (Ichneumonidae); (e) *Pimpla spuria* Gravenhorst, 1829 (Ichneumonidae); (f) *Pimpla turionellae* (Linnaeus, 1758) (Ichneumonidae); (g) *Itopectis alternans* (Gravenhorst, 1829) (Ichneumonidae); (h) *Itopectis maculator* (Fabricius, 1775) (Ichneumonidae). Scale bar 1 mm (photo credit: Renato Ricciardi, Filippo Di Giovanni, and Pier Luigi Scaramozzino).

of the biology of this species to better understand which abiotic and biotic factors influence population trends in different years and wine-growing areas. Special attention should be paid to investigating the natural enemy complex of *E. ambiguella*. The coexistence of *E. ambiguella* with *L. botrana* means that most of the parasitoids present in the vineyard are in common between the two species; however, following precise protocols for collecting and rearing samples obtained from infested grapes would avoid doubtful host data from substrate rearing and could help in revealing the presence of parasitoids specific to this species. Although the development of a biological control strategy is often a difficult and costly path to take, assessing the parasitization rates of parasitoid species in the vineyard can be useful in planning conservation

management interventions that encourage the presence and spread of these beneficial species from surrounding semi-natural areas.

#### CRediT authorship contribution statement

**Renato Ricciardi:** Writing – original draft. **Giovanni Benelli:** Writing – review & editing, Supervision, Conceptualization. **Filippo Di Giovanni:** Writing – original draft. **Andrea Lucchi:** Writing – review & editing, Supervision.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

This is a Review.

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