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Article

Lobesia botrana as a preferred host of *Campoplex capitator*, the most occurring larval parasitoid in European vineyards

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With 2 figures

Abstract: Parasitoids are major biological agents in crop protection, and understanding their preference towards specific host species is a key aspect of successful pest control. In the present study, we have examined the host preferences of the larval parasitoid *Campoplex capitator* (Hymenoptera: Ichneumonidae), one of the major natural enemies for tortricid grapevine pest populations in European vineyards. Using a test choice between its two main and sympatric hosts, we wanted to determine whether *C. capitator* females that emerged from *Lobesia botrana* (Lepidoptera: Tortricidae) also prefer its natal host *L. botrana,* or *Eupoecilia ambiguella* (Lepidoptera: Tortricidae) as host; and consequently, if it could be a good candidate as a bio-agent for these species. Our results distinctly showed that naïve *C. capitator* females preferred *L. botrana* over *E. ambiguella* as host, as they directly sought out new *L. botrana* hosts. Overall, it reveals that *C. capitator* could be a very efficient parasitoid to control *L. botrana* populations. Our results might also suggest the importance of natal host in parasitoid host preference, which should be considered in the future when mass-rearing bio-agents.

Keywords: grapevine moth, host species preference, larval parasitoid, choice test

1 Introduction

With more than 900,000 known species, insect herbivores represent nearly a quarter of all terrestrial macroscopic biodiversity, acting as a dominant component of all terrestrial food webs on Earth (Resh & Cardé 2009, Sauvion et al. 2017). While they are well regulated by both host plant and natural enemies within their ecosystems (Kaplan et al. 2016), agroecosystems often break this balance – through agriculture intensification, monoculture development and pesticide use – and favor the emergence of pest species (Wilby & Thomas 2002). Even if only 2% of insect herbivores species are considered as pests (Dhaliwal et al. 2010), they are responsible for an estimated crop loss of up to 50% (Thacker 2002, Aggarwalim et al. 2006) and are consequently a major human concern, with implications for public health and agriculture. At a crucial time when farmers struggle to increase or at least maintain yields while reducing pesticide use for environmental and health issues, biological control and integrated pest management strategies appear to be the best current alternatives (Brewer & Goodell 2012).

Biological control is based on population regulation and specially on interactions between a host – here, insect herbivore – and its natural enemies (e.g. parasitoids, predators, pathogens) (Van Driesche et al. 2008). It includes, for example, the release of one or more natural enemies into a targeted agroecosystem to control a growing pest population. Parasitoids – specially hymenopterous parasitoids – are key biological agents, and have been the most common type of natural enemy used in crop protection (Van Driesche et al. 2008, Giunti et al. 2015). Parasitoids evolve in a complex environment and therefore rely on a variety of stimuli (e.g. visual, vibrational and olfactory cues) to locate a suitable habitat with host, food and/or mates (see Giunti et al. 2015 for reviews). Multiple factors can influence parasitoids' host foraging, including host size and density, but also importantly their learning capacity (Lin & Ives 2003, Giunti et al. 2015, Morgan et al. 2016). While there is a heritable component for habitat preference, it remains unclear as to exactly when this preference development occurs (i.e. during early life stages, after emergence, or both), despite numerous theories informing optimal parasitoid foraging (Barron 2001,

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Davis and Stamps 2004, Giunti et al. 2015). The notion of Natal Habitat Preference Induction (NHPI) has been proposed by Davis & Stamps (2004) to better understand such processes, and states that animals prefer to develop in a similar habitat to the one they experience in early life stage. The learning process associated with this notion is mostly related to chemical cues coming from the natal habitat which are memorized during ontogeny (Corbet 1985, Ruther et al. 2002). For instance, females of the parasitoid *Psyttalia concolor* (Hymenoptera: Braconidae) exhibit different oviposition preferences depending on their natal host – i.e. females did not always prefer to oviposit in their natal host (Giunti et al. 2016). Altogether, this raises one of the most important challenges in biological control: the plastic specificity between the bio-agent and targeted host.

In order to conduct an efficient and sustainable pest population control, the parasitoid should be able to successfully target its pest species (Van Driesche et al. 2008), even in an environment susceptible to host several pest species. Agroecosystems, such as vineyards, can host a large number of pests living in sympatry (Vogelweith & Thiéry 2018), and as such, investigating host preference in parasitoids is crucial for biological control. The grape berry moth *Eupoecilia ambiguella* (Hubn.) (Lepidoptera: Tortricidae) and the European grapevine moth *Lobesia botrana* (Den. & Schiff.) (Lepidoptera: Tortricidae) are two polyphagous grapevine pests (reviewed: Thiéry et al. 2018). These two species are responsible for significant damages in vineyards either directly by attacking grape bunches – a larva is able to damage between 2 and 10 berries depending on the grape cultivar – or indirectly by favoring the development of several fungi, such as *Botrytis cinerea*, *Aspergilus carbonarius*, and *Aspergilus niger* (Delbac & Thiéry 2016, Thiéry et al. 2018). *Eupoecilia ambiguella* mostly occurs in central Europe while *L. botrana* is widely distributed but mostly occurs at high density in Mediterranean climates (Thiéry 2008). However, in several European vineyards, these two species can share common distributional range where they often live in sympatry, as in Beaujolais vineyards for example (North of Lyon, France) (Vogelweith et al. 2014). The density of each species within vineyards can vary from 15:75 to an equal distribution 50:50 (unpublished data). Despite such differences, biological control of *E. ambiguella* and *L. botrana* has always been the same, mostly performed through the release of the egg parasitoid *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) (Vogelweith et al. 2014, Thiéry et al. 2018). For the past decade, the larval parasitoid *Campoplex capitator* (Hymenoptera: Ichneumonidae) has drawn more and more attention (Marchesiniand & Dalla Monta 1994, Xuéreb & Thiéry 2006). Cosmopolitan and very plastic in its ecological requirements (Moreau et al. 2010), this parasitoid is very efficient in regulating grapevine pest populations, with sometimes a level of parasitism rate up to 90% in *L. botrana* (Vogelweith et al. 2013). But, attempts to massing-rear *C. capitor* for the control of grapevine pests has always failed, chiefly because of the limited information about its biology/ecology, including the limited understanding of its ability to switch from the rearing-host (e.g. *L. botrana*) to hosts encountered in the field (e.g. *L. botrana* and *E. ambiguella*) (unpublished data). For instance, the larval-pupal parasitoid *Psyttalia concolor* (Hymenoptera: Braconidae) reared on the fruit fly *Ceratitis capitata* (Diptera: Tephritidae) (Canale & Benelli 2012) did not show any difference in oviposition behaviors and host acceptance when provided either with its rearing host *C. capitata* or the alternative host pest *Bactrocera oleae* (Diptera: Tephritidae) (Canale & Benelli 2012).

Here we seek to determine, for the first time, whether *C. capitator* females emerged from wild populations of *L. botrana* prefer *E. ambiguella* or *L. botrana* as host in a choice test, and consequently whether it could be a good candidate as bio-agent to regulate grapevine pest populations.

2 Material and methods

2.1 Model insects

Larvae of *E. ambiguella* and *L. botrana* used in this experiment came from two independent rearing facilities, maintained diapause-free at the French National Institute for Agricultural Research (INRA) (Villenave d'Ornon, France) for more than 15 years (see Vogelweith et al. 2017). These two strains were based on multiple adults reared in flying cages to which wild individuals were periodically added. Larvae of each species were provided with *ad libitum* semi-artificial diet (Vogelweith et al. 2015) and maintained in similar boxes (18 × 11.5 × 7 cm) under the same standard laboratory conditions (22 ± 1 °C, 70 ± 10% RH, and a L16:D8 photoperiod) at a density of approximately 100 individuals per 300 ml of diet. Corrugated papers were placed within each box, allowing the larvae to hide, as they did in grape berries.

Female parasitoids of *C. capitator* were obtained from wild parasitized *L. botrana* larvae collected on Grenache cultivar in a French vineyard (N 42° 44' 7.063", E 2° 52' 56.441"; Perpignan, France) in May 2013 (see Vogelweith et al. 2013). Sampled larvae were maintained in polyethylene boxes (60 × 40 × 21.4 cm) with *ad libitum* Grenache grape bunches from the vineyard, at 24 ± 1 °C, 60 ± 10% RH and under the ambient photoperiod conditions. Corrugated papers were placed in the boxes to facilitate pupae collection (larvae like to shelter in such material before pupation) and checked daily for pupation. After pupation, pupae were individually moved into glass tubes (70 × 9 mm diameter) closed with cotton plugs under the conditions stated above and checked daily until emergence from either an adult moth or a parasitoid. Different parasitoid species emerged from larvae and after identification (Thiéry 2008), only *C. capitator* females (easily visually identifiable with their ovipositor) were kept for this experiment. Parasitoid females were transferred to clean glass tubes provided with a droplet of honey and cotton plugs soaked with water, but otherwise kept at the same conditions. All *C. capitator* females used in this experiment were tested two days after their emergence, naïve (no prior oviposition) and were kept virgin because females of this species can also reproduce parthenogenetically, producing in such case only males (Morris & Fellowes 2002, Thiéry & Xuereb 2004).

2.2 Experimental design

A total of 22 *C. capitator* females were tested to determine their preference between *E. ambiguella* and *L. botrana*. Tests were carried out in an experimental arena constituted of a Petri dish (95 mm dimeter, 62 mm high) divided into two equal zones (Fig. 1): one zone dedicated to *E. ambiguella*, and the second dedicated to *L. botrana*. At the center of each zone was taped a piece of corrugated paper containing a 4th instar larva of either *E. ambiguella* or *L. botrana* (Fig. 1). Prior to the test, all larvae were checked to ensure they were at the same instar (4th instar) based on the larval head capsule size (1.2 ± 0.1 mm) (Delbac et al. 2010), and without physical damages. Then, larvae were moved to the small piece of corrugated paper using a paintbrush washed with 90% ethanol after each larva. The female parasitoid was then released in the middle of the experimental arena. Its behavior was recorded until the first attack (defined as the first oviposition attempt) or for a maximum of 30 min. During this time-period, the first species visited, the time spent by the parasitoid on each side of the arena (*E. ambiguella* versus *L. botrana* sides), the number of visits to each larva and the chosen larva (i.e. larva which suffered from an oviposition attempt) were recorded. As female *C. capitator* can perform multiple oviposition attempts in few seconds, inflicting serious injuries to the larva, a test was ended after the first attack. Each test was performed with a different female parasitoid and host larvae. The position of each species in the experimental arena was exchanged every time and a new arena was used for each repetition to avoid potential influence of cues/odor from both parasitoid and larvae. The experiment was performed for two hours (four individuals during 30 min per day), every day during six days, at the sunset – time-period where parasitoids are the most active – at 24 ± 1 °C, 60 ± 10% RH and under the ambient photoperiod conditions.

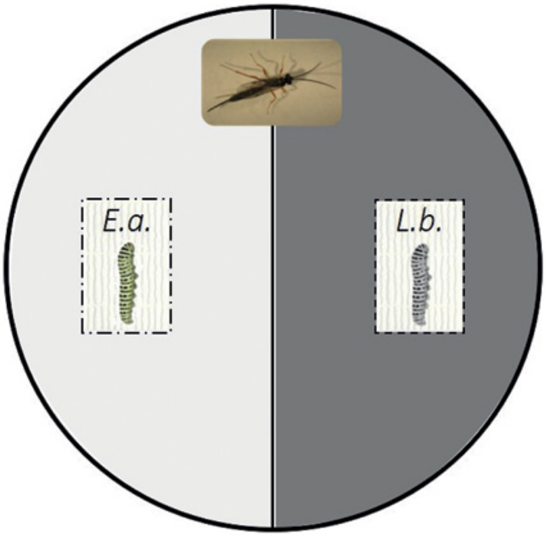

Fig. 1. Diagram of the experimental arena used to test the preference of the female *C. capitator* between the two grapevine moth species: *E. ambiguella* and *L. botrana*. The big circle represents the Petri dish. The middle line represents the border between the *E. ambiguella* zone (white) and the *L. botrana* zone (grey). The two ribbed squares represent the corrugated papers with either *E. ambiguella* (E.a.; dashed/dotted line) or *L. botrana* (L.b.; dashed line) inside.

2.3 Statistical analyses

All data analyses were conducted using the software R v3.5.1 loaded with *car* and *lme4* packages. The proportion of time spend by the female parasitoid on each side was tested using a Chi-squared test for given probabilities where the proposition of time spent on the *L. botrana* side was compared to a probability of 0.5. The number of visits per host species was tested using a generalized linear model (GLM) with poisson distribution, and the species (*L. botrana* or *E. ambiguella*) entered as explanatory categorical factors. Finally, the first species visited as well as the choice made by the female parasitoid were tested using a generalized linear model (GLM) with binomial error distribution, and the species (*L. botrana* or *E. ambiguella*) entered as explanatory categorical factors.

3 Results

The first choice (i.e. the first larva visited) by *C. capitator* females was almost always *L. botrana* (95.45% of the cases; $F_1 = 44.72$; $p < 0.0001$). Moreover, females spent significantly more time on *L. botrana* side of the experimental arena ($\chi^2_1 = 7.68$; $p = 0.006$; IC 95% = [0.59; 0.94]; Fig. 2a) and visited more often *L. botrana* larvae compared to *E. ambiguella* larvae ($F_1 = 10.11$; $p = 0.001$; Fig. 2b). Finally, *C. capitator* females almost exclusively attacked *L. botrana* larvae ($F_1 = 31.18$; $p < 0.0001$; Fig. 2c).

4 Discussion

Although host preference in parasitoids has been well studied, whether a parasitoid prefers its natal host or an alternative host in an agroecosystem hosting sympatric pest species remains unexplored. Based on a choice test experiment, our results clearly showed that *C. capitator* females emerged from wild population of *L. botrana* preferred the latter as host over *E. ambiguella*. Indeed, they went mostly directly to the *L. botrana* side, spent more time on this side and visited

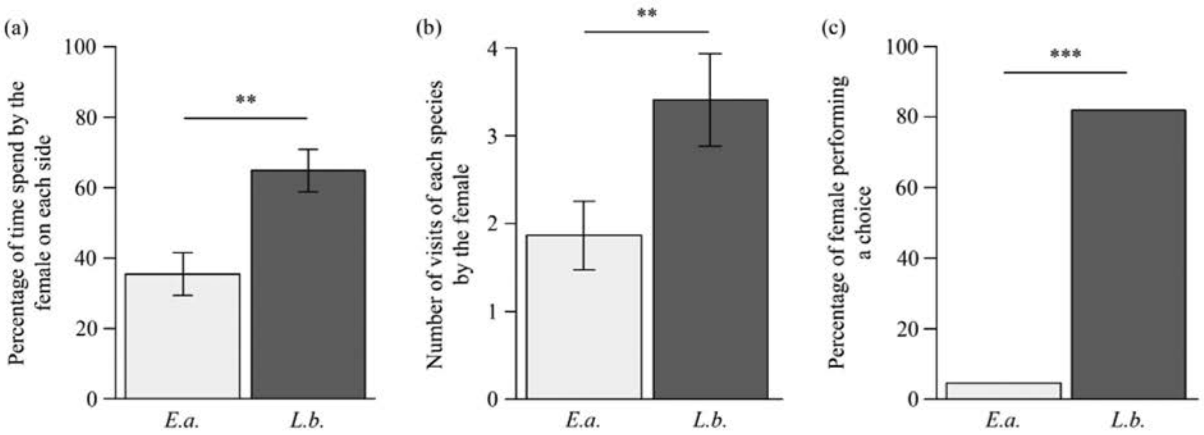

Fig. 2. **(a)** Percentage of time spend by the female *C. capitator* on *E. ambiguella* (*E. a.*) or *L. botrana* (*L.b.*) sides (± C.I. 95%); **(b)** Number of visits to each host species by *C. capitator* female (± C.I. 95%); **(c)** Percentage of *C. capitator* females performing a choice for either *E. ambiguella* or *L. botrana*. Note that 3 of the 22 female parasitoids did not perform any attack on either host. Asterisks indicate statistically significant differences ($p < 0.05$).

it more often compared to *E. ambiguella* larvae. Finally, *L. botrana* larvae were almost exclusively choose/attacked by *C. capitator* females.

At least three non-mutually exclusive hypotheses could explain such preference. The first hypothesis relies on the notion of NHPI (Davis & Stamps 2004), meaning that *C. capitator* females emerged from *L. botrana* prefer to lay their eggs in *L. botrana* larvae due to special stimuli received in early-life in their native habitat. Mounting evidence suggests the importance of the cues learned during ontogeny on parasitoid choice (Morris & Fellowes 2002, Bodino et al. 2016, Giunti et al. 2016). Such learning can take place after emergence or during pre-adult stages (when the parasitoid in still on/inside its host) and/or during adult emergence (Giunti et al. 2015), as illustrated by the endoparasitoid *P. concolor.* Females from the latter excised from their host just before emergence – and consequently did not have contact with a natal host in early adult life – were unable to show a preference for the natal host (Giunti et al. 2016). Our results are consistent with the NHPI hypothesis even though we cannot determine whether *C. capitator* females are using pre- or post-emergence learning. The same experiment should be performed with *E. ambiguella* as natal host to confirm that statement. Parasitoid learning could also occur through an associative learning where they learn to associate cues from their environment to increase their foraging efficiency (Hoedjes et al. 2011). In our study, parasitoid cocoons were removed from their environmental complex and placed under control conditions, meaning that associative learning was not tested here. As such, we do not know the consequences of host species choice upon *C. capitator* fitness. This point should be investigated in a further field survey where *C. capitator* live in an environment where *L. botrana* and *E. ambiguella* are in sympatry.

Secondly, parasitoids can also inherit natal environmental preferences related to a local adaptation that may result in a parasitoid population specializing on one host (Gutiérrez-Ibáñez et al. 2007, Zepeda-Paulo et al. 2013, Bodino et al. 2016). A previous study suggested a local adaptation of *L. botrana* larvae to existing parasitoid pressure (Vogelweith et al. 2013). Since *L. botrana* and *C. capitator* co-evolved in vineyards for many years, it is also likely that *C. capitator* have adapted to local host species. Indeed, *C. capitator* used in this experiment came from an area where *L. botrana* are predominant compared to *E. ambiguella* (Ricaud 2013).

Finally, the third hypothesis involves the defense strategies used by *E. ambiguella* and *L. botrana* larvae (Vogelweith et al. 2014). Despite many similarities in their ecological requirements and their natural enemies, these two species have been shown to invest differently in the defense mechanisms which might influence parasitoid choice (Brodeur et al. 1996, Vogelweith et al. 2014). Indeed, even though *L. botrana* larvae have been shown to express strong behavioral defenses, their cuticle and immune system are less resistant to parasitoids compared to *E. ambiguella*'s (Vogelweith et al. 2014). Therefore, the choice performed by *C. capitator* is very consistent, and could be the result of a local adaptation of *C. capitator* to *L. botrana* larvae in the field, as mentioned in the second hypothesis.

In conclusion, these results show that biological control by augmentation – relying on the release the of natural enemies (i.e. *C. capitator*) that occur in the agroecosystem – could be very efficient against *L. botrana* populations due to the high specificity of its parasitoid. However, it might be less efficient against *E. ambiguella* populations, at least if *C. capitator* has *L. botrana* as natal host. More investigations about the relationship between *C. capitator* and *E. ambiguella* should be performed in order to consider this parasitoid as a potential bio-agent. But, it is important to recall that studies and field reports indicated that *C. capitator* is parasitizing *E. ambiguella* in European vineyards (Colombera et al. 2001, Thiéry et al. 2011, 2018, Rusch et al. 2015), even if parasitism success is higher in *L. botrana* than in *E. ambiguella* when the ratio of both species in the population is close to 50:50 (Vogelweith et al. 2014). Further investigations should be done in order to determine whether it would also be a good candidate to control *E. ambiguella* populations. Altogether, this study is one of the first to reveal *C. capitator's* potential as a valuable and efficient bio-agent for the control of grapevine moths in European vineyards.

Conflict of interest

The authors declare no competing financial interests.

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References

Aggarwalim, P. K., Kalra, N., Chander, S., & Pathak, H. (2006). InfoCrop: A dynamic simulation model for the assessment of crop yields, losses due to pests, and environmental impact of agro-ecosystems in tropical environments. I. Model description. *Agricultural Systems, 89*(1), 1–25. https://doi.org/10.1016/j.agsy.2005.08.001

Barron, A. B. (2001). The life and death of Hopkins' host-selection principle. *Journal of Insect Behavior, 14*(6), 725–737. https://doi.org/10.1023/A:1013033332535

Bodino, N., Ferracini, C., & Tavella, L. (2016). Is host selection influenced by natal and adult experience in the parasitoid *Necremnus tutae* (Hymenoptera: Eulophidae)? *Animal Behaviour, 112*, 221–228. https://doi.org/10.1016/j.anbehav.2015.12.011

Brewer, M. J., & Goodell, P. B. (2012). Approaches and incentives to implement integrated pest management that addresses regional and environmental issues. *Annual Review of Entomology, 57*(1), 41–59. https://doi.org/10.1146/annurev-ento-120709-144748 PMID:21888519

Brodeur, J., Geervliet, J. B. F., & Vet, L. E. M. (1996). The role of host species, age and defensive behaviour on ovipositional decisions in a solitary specialist and gregarious generalist parasitoid (*Cotesia species*). *Entomologia Experimentalis et Applicata, 81*(2), 125–132. https://doi.org/10.1111/j.1570-7458.1996.tb02024.x

Canale, A., & Benelli, G. (2012). Impact of mass-rearing on the host seeking behaviour and parasitism by the fruit fly parasitoid *Psyttalia concolor* (Szépligeti) (Hymenoptera: Braconidae). *Journal of Pest Science, 85*(1), 65–74. https://doi.org/10.1007/s10340-011-0382-1

Colombera, S., Alma, A., & Arzone, A. (2001): Comparison between the parasitoids of *Lobesia botrana* and *Eupoecilia ambiguella* in conventional and integrated vineyards. *IOBC/WPRS Bulletin 24(7)*: 91–96.

Corbet, S. A. (1985). Insect chemosensory responses: A chemical legacy hypothesis. *Ecological Entomology, 10*(2), 143–153. https://doi.org/10.1111/j.1365-2311.1985.tb00543.x

Davis, J. M., & Stamps, J. A. (2004). The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution, 19*(8), 411–416. https://doi.org/10.1016/j.tree.2004.04.006 PMID: 16701298

Delbac, L., & Thiéry, D. (2016). Damage to grape flowers and berries by *Lobesia botrana* larvae (Denis & Schiffernüller) (Lepidoptera: Tortricidae), and relation to larval age. *Australian Journal of Grape and Wine Research, 22*(2), 256–261. https://doi.org/10.1111/ajgw.12204

Delbac, L., Lecharpentier, P., & Thiery, D. (2010). Larval instars determination for the European Grapevine Moth (Lepidoptera: Tortricidae) based on the frequency distribution of head-capsule widths. *Crop Protection (Guildford, Surrey), 29*(6), 623–630. https://doi.org/10.1016/j.cropro.2010.01.009

Dhaliwal, G. S., Jindal, I. V., & Dhawan, A. K. (2010). Insect pest problems and crop losses: Changing trends. *Indian Journal of Ecology, 37*, 1–7.

Giunti, G., Canale, A., Messing, R. H., Donati, E., Stefanini, C., Michaud, J. P., & Benelli, G. (2015). Parasitoid learning: Current knowledge and implications for biological control. *Biological Control, 90*, 208–219. https://doi.org/10.1016/j.biocontrol.2015.06.007

Giunti, G., Benelli, G., Messing, R. H., & Canale, A. (2016). Early adult learning affects host preferences in the tephritid parasitoid *Psyttalia concolor* (Hymenoptera: Braconidae). *Journal of Pest Science, 89*(2), 529–537. https://doi.org/10.1007/s10340-015-0715-6

Gutiérrez-Ibáñez, C., Villagra, C. A., & Niemeyer, H. M. (2007). Pre-pupation behaviour of the aphid parasitoid *Aphidius ervi* (Haliday) and its consequences for pre-imaginal learning. *Naturwissenschaften, 94*(7), 595–600. https://doi.org/10.1007/s00114-007-0233-3 PMID:17333099

Hoedjes, K. M., Kruidhof, H. M., Huigens, M. E., Dicke, M., Vet, L. E. M., & Smid, H. M. (2011). Natural variation in learning rate and memory dynamics in parasitoid wasps: Opportunities for converging ecology and neuroscience. *Proceedings. Biological Sciences, 278*(1707), 889–897. https://doi.org/10.1098/rspb.2010.2199 PMID:21106587

Kaplan, I., Carrillo, J., Garvey, M., & Ode, P. J. (2016). Indirect plant-parasitoid interactions mediated by changes in herbivore physiology. *Current Opinion in Insect Science, 14*, 112–119. https://doi.org/10.1016/j.cois.2016.03.004 PMID:27436656

Lin, L. A., & Ives, A. R. (2003). The effect of parasitoid host-size preference on host population growth rates: An example of *Aphidius colemani* and *Aphis glycines*. *Ecological Entomology, 28*(5), 542–550. https://doi.org/10.1046/j.1365-2311.2003.00536.x

Marchesini E, Dalla Montà L (1994). Observations on natural enemies of *Lobesia botrana* (Den. & Schiff.) (Lepidoptera: Tortricidae) in Venetian vineyards. *Bollettino di Zoologia Agraria e di Bachicoltura 26(2)*: 201–230.

Moreau, J., Villemant, C., Benrey, B., & Thiéry, D. (2010). Species diversity of larval parasitoids of the European grapevine moth (*Lobesia botrana*, Lepidoptera: Tortricidae): The influence of region and cultivar. *Biological Control, 54*(3), 300–306. https://doi.org/10.1016/j.biocontrol.2010.05.019

Morgan, W. H., Thébault, E., Seymour, C. L., & van Veen, F. J. (2016). Density dependence and environmental factors affect population stability of an agricultural pest and its specialist parasitoid. *BioControl, 62*(2), 175–184. https://doi.org/10.1007/s10526-016-9777-5

Morris, R., & Fellowes, M. (2002). Learning and natal host influence host preference, handling time and sex allocation behaviour in a pupal parasitoid. *Behavioral Ecology and Sociobiology, 51*(4), 386–393. https://doi.org/10.1007/s00265-001-0439-x

Ricaud, E. (2013). Bilan de campagne 2013 viticulture en Provence Alpes Côte d'Azur et Sud Drôme. *Bulletin de Santé du Végétal Provence Alpes Côte d'Azur Sud Drôme 22:* 1–18.

Rusch, A., Delbac, L., Muneret, L., & Thiéry, D. (2015). Organic farming and host density affect parasitism rates of tortricid moths in vineyards. *Agriculture, Ecosystems & Environment, 214*, 46–53. https://doi.org/10.1016/j.agee.2015.08.019

Ruther, J., Meiners, T., & Steidle, J. L. M. (2002). Rich in phenomena-lacking in terms. A classification of kairomones. *Chemoecology, 12*(4), 161–167. https://doi.org/10.1007/PL00012664

Sauvion, N., Calatayud, P.-A., & Thiéry, D. (2017). Insect-plant interactions in a crop protection perspective. *Advances in Botanical Research, 81*, p. 422. http://dx.doi.org/10.1016/bs.abr.2016.09.00

Thacker, J. M. R. (2002). A brief history of arthropod pest control. In Thacker, J. M. R. (Ed.), *A brief history of arthropod pest control* (pp. 1–26). Cambridge University Press.

Thiéry D (2008). Les ravageurs de la vigne. – Féret Bordeaux.

Thiéry, D., & Xuéreb, A. (2004). Vers une lutte biologique contre eudémis (*Lobesia botrana*)? *Mondiaviti* 47–52.

Thiéry, D., Delbac, L., Villemant, C., & Moreau, J. (2011). Control of grape berry moth larvae using parasitoids: should it be developed? *IOBC/WPRS Bulletin 67*: 189–196.

Thiéry, D., Louâpre, P., Muneret, L., Rusch, A., Sentenac, G., Vogelweith, F., … Moreau, J. (2018). Biological protection against grape berry moths. A review. *Agronomy for Sustainable Development, 38*(2), 15. https://doi.org/10.1007/s13593-018-0493-7

Van Driesche, R., Hoddle, M. S., & Center, T. (2008). Control of pests and weeds by natural enemies. Wiley-Blackwell.

Vogelweith, F., & Thiéry, D. (2018). An assessment of the non-targeted effects of copper on the leaf arthropod community in a vineyard. *Biological Control, 127*, 94–100. https://doi.org/10.1016/j.biocontrol.2018.08.011

Vogelweith, F., Dourneau, M., Thiéry, D., Moret, Y., & Moreau, J. (2013). Geographical variation in parasitism shapes larval immune function in a phytophagous insect. *Naturwissenschaften, 100*(12), 1149–1161. https://doi.org/10.1007/s00114-013-1119-1 PMID:24306219

Vogelweith, F., Thiéry, D., Moret, Y., Colin, E., Motreuil, S., & Moreau, J. (2014). Defense strategies used by two sympatric vineyard moth pests. *Journal of Insect Physiology, 64*, 54–61. https://doi.org/10.1016/j.jinsphys.2014.03.009 PMID:24662468

Vogelweith, F., Moreau, J., Thiéry, D., & Moret, Y. (2015). Food-mediated modulation of immunity in a phytophagous insect: An effect of nutrition rather than parasitic contamination. *Journal of Insect Physiology, 77*, 55–61. https://doi.org/10.1016/j.jinsphys.2015.04.003 PMID:25913569

Vogelweith, F., Moret, Y., Thiéry, D., Delbac, L., & Moreau, J. (2017). No evidence of an immune adjustment in response to a parasitoid threat in *Lobesia botrana* larvae. *Journal of Insect Physiology, 102*, 7–11. https://doi.org/10.1016/j.jinsphys.2017.08.010 PMID:28844653

Xuéreb, A., & Thiéry, D. (2006). Does natural larval parasitism of *Lobesia botrana* vary between years, generation, density of the host and vine cultivar? *Bulletin of Entomological Research, 96 (2)*, 105–110. https://doi.org/10.1079/BER2005393 PMID: 16556330

Wilby, A., & Thomas, M. B. (2002). Natural enemy diversity and pest control: Patterns of pest emergence with agricultural intensification. *Ecology Letters, 5*(3), 353–360. https://doi.org/10.1046/j.1461-0248.2002.00331.x

Zepeda-Paulo, F. A., Ortiz-Martínez, S. A., Figueroa, C. C., & Lavandero, B. (2013). Adaptive evolution of a generalist parasitoid: Implications for the effectiveness of biological control agents. *Evolutionary Applications, 6*(6), 983–999. https://doi.org/10.1111/eva.12081 PMID:24062806

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