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Arthropods in the spotlight - identifying predators of vineyard pest insects with infrared photography

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Abstract

Grape berry moths, particularly Lobesia botrana Denis & Schiffermüller (Lepidoptera: Tortricidae), and vinegar flies, such as Drosophila melanogaster Meigen and Drosophila suzukii Matsumura (Diptera: Drosophilidae), are important vineyard pests, causing severe quality loss of grapes. Several arthropod taxa may be involved in the natural control of these pests. However, the role of arthropod predators in the natural control of vineyard pests remains unclear. We investigated 32 vineyards in the Palatinate region, southwest Germany, under organic and conventional management, which in both cases received either full or reduced fungicide applications (2×2 design). Predation of L. botrana eggs and pupae and D. melanogaster pupae on sentinel cards exposed in the vineyards was observed with infrared cameras. In total, nine predator taxa could be identified. The most dominant predator was the European earwig, Forficula auricularia L. (Dermaptera: Forficulidae), with 90% of all predation events. We conclude that F. auricularia is likely a key predator of vineyard pests, and that special attention should be paid to maintain it at high population densities.

KEYWORDS

camera observation, Diptera, Drosophila sp., Drosophilidae, Forficula auricularia, grape berry moths, Lepidoptera, Lobesia botrana, natural pest control, Tortricidae, vinegar flies, vineyard pests

INTRODUCTION

It is a particular challenge for winegrowers to grow healthy grapes in order to produce high-guality wines, as grapevine is susceptible to several fungal diseases. Thus, depending on the pathogen pressure, vineyards are sprayed 12–15 times with fungicides per year in European temperate regions (Pertot et al., 2017; Reiff et al., 2023). Surprisingly, organically managed vineyards are sprayed as often or even more frequently than conventional ones (Reiff et al., 2021, 2023; Kaczmarek et al., 2023). Whereas organic sprayings are mainly based on copper and sulphur, conventional sprayings allow for the use of synthetic fungicides (Cabras & Conte, 2001; Provost & Pedneault, 2016; Reiff et al., 2023). Fungicides applied under both organic and conventional management may impact beneficial arthropods (Thomson & Hoffmann, 2006; Nash et al., 2010; Reiff et al., 2023). For instance, some single synthetic fungicides are documented to cause lethality on predatory mites and spiders (Pékar, 2002; Miles & Green, 2004; Fiedler & Sosnowska, 2014) and particularly sulphur, which is frequently applied in organic viticulture, is highly detrimental to natural enemies such as parasitoids and predatory mites (Thomson et al., 2000; Gent et al., 2009).

Beyond mortality, fungicides may affect metabolic processes, arthropod fecundity, and prey consumption ability (Papaefthimiou & Theophilidi, 2001; Miles & Green, 2004; Gadino et al., 2011; Beers & Schmidt, 2014). However, knowledge on sublethal effects of fungicides and their consequences on arthropod communities is still scarce (Desneux et al., 2007). In addition, combined applications of at least two fungicides (including the mixtures of active ingredients and adjuvants) as commonly sprayed in viticulture may result in synergistic interactions with even more detrimental impact (Vandame & Belzunces, 1998; Chen & Stark, 2010). Furthermore, in

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some regions 1–4 insecticide treatments are mandatory to control the vector of the quarantine disease flavescence dorée (Pertot et al., 2017; Beaumelle et al., 2023). This may also affect non-target organisms and can therefore impact natural pest control (Gurr et al., 2003; Bianchi et al., 2006; Geiger et al., 2010). Detrimental effects of insecticides on natural enemies such as spiders, ants, earwigs, and parasitoids are well documented (Pékar, 2012; Masoni et al., 2017; Orpet et al., 2019a; Schindler et al., 2022; Mansour et al., 2023). Thus, every application saved is potentially beneficial for non-target organisms. Conversely, if natural enemies of pests are protected from pesticide impacts, this might also lead to increased resilience and reduce reliance of non-mandatory insecticide applications (Cahenzli et al., 2017).

The European grapevine moth, Lobesia botrana Denis & Schiffermüller (Lepidoptera: Tortricidae), is one of the major grapevine pests in Europe and beyond (Benelli et al., 2023). Larvae feed on inflorescences and grape berries. However, the main damage arises in guality loss due to subsequent infections with bunch rot (Botrytis cinerea Pers.) and sour rot. The latter disease complex induces the development of volatile acidity causing sensorial interference in wine (Lemperle, 2007). Vinegar flies such as Drosophila melanogaster Meigen and Drosophila suzukii Matsumura (Diptera: Drosophilidae) can severely affect must guality by infecting grapes with sour rot (Entling & Hoffmann, 2020). Unlike D. melanogaster, which is able to oviposit only in overripe or damaged berries, D. suzukii can actively oviposit in healthy berries (Atallah et al., 2014). Both vinegar flies act as vector for yeasts and bacteria associated with sour rot but also trigger the development of the disease directly by larval development inside the grape berries (Barata et al., 2012; Hall et al., 2018). Several species of mites, spiders, and bush crickets as well as harvestmen, earwigs, ants, and lacewings are known to prey on L. botrana (Marchesini & Dalla Montà, 1994; Pennington et al., 2018; Papura et al., 2020; Reiff et al., 2021). Drosophila spp. and particularly D. suzukii are preyed on by earwigs, ants, bugs, harvestmen, spiders, rove beetles, and centipedes (Woltz & Lee, 2017; Wolf et al., 2018). However, the efficacy of this wide range of arthropod predators in vineyards remains poorly investigated (Thiéry et al., 2018). In contrast to molecular analysis of the gut contents of a particular predator, which reveals the diversity of ingested prey, direct observations of a target prey provides information about the diversity of predators, their predation behaviour, and their voraciousness (Luck et al., 1988; Godfrey et al., 1989; Brust, 1991; Grieshop et al., 2012). Camera observations offer a straightforward opportunity for standardized monitoring of sentinel prey, particularly with regard to the large number of nocturnal predators (Merfield et al., 2004; Grieshop et al., 2012; Nagy et al., 2020). Using camera surveyed sentinel cards, the aim of this study was to identify the most dominant predators of L. botrana and Drosophila spp. in the Palatinate region (southwest Germany), and to compare predation pressure between management systems and over time.

MATERIALS AND METHODS

Study sites

We investigated 32 vineyards in a 10-km radius around Landau in the Palatinate region, Germany (see Reiff et al., 2023, for detailed information). Of these vineyards, 18 were managed by organic standards, including an organic spraying regime (mainly copper, sulphur, and potassium bicarbonate). The other 14 vineyards were treated with conventional plant protection products (mostly synthetic fungicides). In both management types, half of the vineyards were planted with susceptible cultivars (e.g., Riesling, Pinot blanc), and the other half with fungus-resistant varieties (e.g., Cabernet blanc, Regent), which allowed a reduction of fungicide applications by 80% in organic and 50% in conventional vineyards (Reiff et al., 2023).

Camera surveillance of sentinel cards

Sentinel cards combined L. botrana eggs, L. botrana pupae, and D. melanogaster pupae. We chose D. melanogaster rather than D. suzukii because of its easier cultivation. For rearing of L. botrana we followed Markheiser et al. (2018) and for rearing of D. melanogaster Entling & Hoffmann (2020). Lobesia botrana was reared in 500-mL polyethylene cups on a semi-synthetic diet at 70% r.h. and L14 (23 °C):D8 (19 °C) photo-thermoperiod, + 1 h each of dusk and dawn. Moths originated from surrounding vineyards and were maintained in a laboratory rearing of the Julius Kühn-Institute, in Siebeldingen, Germany. To allow pupation and to ease collection of pupae, cups were lined with corrugated paper at later larval stages. Pupae were transferred to rearing containers which consisted of a paper bag closed by an acrylic glass cage (15 mm diameter, 15 mm high) to allow hatching and mating. For oviposition, the cage was either lined with a plastic bag to maintain rearing or with rings of polyethylene strips for later use in experiments. Drosophila melanogaster was reared in cages with mesh side panels (30×30×30 cm) at 23 °C, 75% r.h., and L16:D8 photoperiod. Flies were obtained from a laboratory rearing of RLP AgroScience (Neustadt an der Weinstraße, Germany). Tubes (4mm diameter, 8mm high) with drosophila cornmeal diet were placed inside the cages to allow oviposition and larval development. Egg-laden polyethylene strips were harvested after 24 h from L. botrana rearing containers. On average, 45 ± 29 eggs were present on each strip. Pupae of both insect species were harvested twice per week and stored at 4 °C until field exposure.

Each egg-laden strip was attached to an approximately 2×4 cm cutting duct tape (HEB19L10GC, Toolcraft; Conrad Electronic, Hirschau, Germany) and five pupae of *L. botrana* or *D. melanogaster* were attached to the adhesive surface, respectively. The remaining adhesive surface was covered with sand to prevent predators from sticking. Sentinel cards were stored at 4 °C until exposure. Sentinel cards

were randomly attached to selected 1-year-old branches of grape plants (1.0–1.2 m above ground) and exposed to potential predators for 24 h. The eggs and pupae were counted before and after exposure. Predation was monitored with two sentinel cards and two cameras 5 m apart, in the centre of each vineyard. To ease field work, the sampling sites were grouped in four touring blocks of eight vineyards. Half of the vineyards of each block were managed organically and half conventionally, comprising always both resistant and susceptible varieties. The chronological order of sampling of each vineyard was the same both within the blocks and between the blocks. Monitoring was repeated four times between May and August of 2018, with at least 4 weeks between two samplings within the same vineyard. This resulted in 256 days of camera observations. We used the camera system described in Pennington et al. (2018) consisting of a raspberry pi computer (3rd generation Model B; Raspberry Pi Foundation, Cambridge, UK) and a camera module with two infrared light-emitting diodes (SC15-Webcams-UK; Kuman, Glendora, CA, USA). The cameras were programmed to take a picture every 10s for 24 h. Pictures were screened manually and predators were



FIGURE 1 Identified predators of *Lobesia botrana* and *Drosophila melanogaster* on camera-surveilled sentinel cards: (A) Chrysopidae larvae, (B) *Forficula auricularia*, (C) *Vespula* sp., (D) Blattoptera nymph, (E) *Meconema meridionale* male, (F) Formicidae, (G) Opiliones, (H) *Cheiracanthium* sp., (I) *Philodromus* sp.

detected by the same observer. Predators were identified to the lowest possible taxonomic level with comparison to communities from beat-sheet samples of the same vineyards and sampling intervals (Reiff et al., 2023). We defined predation events when a predator was visibly preying on the sentinel cards (e.g., head and/or chelicera moving, or carrying pupae away) and eggs or pupae were removed or damaged after final collection and counting. It could not be excluded that single individuals visited the sentinel cards several times in the same night, or even in different months. Thus, no differentiation in terms of predation rate per individual was done.

Data analysis

All statistical analyses were executed in R v.4.3.1 (R Core Team, 2023). Due to low numbers of predation events, statistical analysis of predation by single taxa was only possible for earwigs. In this case, data were summed over all sampling dates, resulting in one observation per vineyard. Further, predation events of all observed predators were summed to analyse temporal differences. Taking zero counts into account, we used generalized linear mixedeffect models fitted with the function 'glmmTMB' in both cases (R package glmmTMB; Brooks et al., 2017). For predation by earwigs, models contained 'site' as a random factor and 'grape variety' plus 'management' as the explanatory variables, including their interaction. For temporal variance, models contained 'site' as a random factor and 'date' as the explanatory variable. Model distribution was checked graphically using the function 'simulateResiduals' (R package DHARMa; Hartig & Lohse, 2022) and family distribution was chosen accordingly. Post-hoc tests were conducted with the function 'emmeans' (R package emmeans) using Tukey adjustment and a confidence level of 0.95.

RESULTS

We could identify predators on 100 of 257 observation days with 52 positive observation days for egg predation, 59 for L. botrana pupae predation, and 80 for D. melanogaster pupae predation. We observed nine taxa preying on the sentinel cards (Figure 1, Table 1). The European earwig, Forficula auricularia L. (Dermaptera: Forficulidae), accounted for 93% of L. botrana egg predation, for 90% of L. botrana pupae predation, and for 89% of *D. melanogaster* pupae predation.

Predation rates did not differ significantly between organic vs. conventional management, nor between resistant vs. susceptible grape varieties. However, we found a trend that L. botrana eggs were preyed more frequently in resistant grapes under conventional compared to organic management. In addition, L. botrana pupae tended to be more frequently preyed in susceptible grapes under organic than under conventional management (Figure 2, Table 2).

TABLE 1

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	L. botrana	eggs			L. botrana þ	pupae			D. melanog	<i>aster</i> pupae		
	Organic		Convention	lal	Organic		Convention	al	Organic		Convention	al
	Resistant	Susceptible	Resistant	Susceptible	Resistant	Susceptible	Resistant	Susceptible	Resistant	Susceptible	Resistant	Susceptible
Forficula auricularia	242	346	717	439	54	61	41	16	75	94	84	60
Formicidae	33	I		33	-	ı		-	12		9	ε
Chrysopidae larvae	,		4				-					ı
Vespula sp.	ı	I	ı	I	,	ı	-	ı	ı	2	ı	I
Meconema meridionale	ı	ı	ī	ı	ε		ı		ī	ı		
Blattoptera									2			
Opiliones	,		,		5	5	-	-	5	2	2	1
Cheiracantium sp.	,	40	ı	ı		I	2	ı	,	ı	,	I
Philodromus sp.	·	13	ı		ı							2
Exposed	3051	3144	2705	2640	360	359	279	280	360	360	280	280

Overall predation rates of *L. botrana* eggs were highest in May and August (23.9% and 19.7%, respectively), whereas those of *D. melanogaster* pupae were highest in May and June (40.6% and 43.8%, respectively; Figure 3, Tables 3 and S1). Highest predator diversity on sentinel cards was found in May and July with six predatory taxa observed (Table S1).

DISCUSSION

Earwigs were by far the most dominant predators in all studied vineyards and the sole taxon that was observed in all vineyards and on all sampling dates. Likewise, Frank et al. (2007) detected highest predation activities of earwigs in the canopies of New Zealand vineyards. The dominance of earwigs as predators is scarcely documented and studies are mainly restricted to orchards of cherry (Bourne et al., 2019), cherry, blackberry, and raspberry (Wolf et al., 2018), citrus (Romeu-Dalmau et al., 2012), and apple (Orpet et al., 2019b). Although sometimes considered a pest in viticulture (Huth et al., 2011; Kehrli et al., 2012), earwigs may also contribute to pest control in vineyards (Pennington et al., 2018; Englert & Herz, 2019; Reiff et al., 2021). However, earwig abundance strongly varies between viticultural regions and pest control potential by earwigs may vary accordingly (Reiff et al., in preparation). For instance, high proportions of harvestmen were tested positive for grape berry moth DNA in southwestern France (Papura et al., 2020). In the same vineyards, harvestmen were considerably more abundant than earwigs (Muneret et al., 2019a). Sario et al. (2021) highlight the importance of spiders, ants, and lacewings for natural control of D. suzukii in Portuguese orchards. Thus, the prevalence of different enemies can vary between study regions. Increased proportions of high biomass generalist predators (like harvestmen and earwigs) may on the other hand promote intra-guild predation (Ostandie et al., 2021). Shifts in predator communities towards single dominant generalist predators may weaken resilience for biological control (Tscharntke et al., 2008).

Eight other taxa were identified to be involved in predation incidents. To our knowledge, predation by Blattoptera and *Vespula* sp. on *L. botrana* and *Drosophila* sp. in vineyards has not been recorded before. We assume that the range of natural enemies of important vineyard pests may be even broader than currently assumed. For example, bush crickets are important predators of *L. botrana* in Austrian vineyards (Reiff et al., 2021). By contrast, our observations in the Palatinate region revealed just one predation event by the bush cricket *Meconema meridionale* (Costa). However, with climate change bush crickets may become more prominent predators in Palatinate vineyards (Buse & Griebeler, 2011).

Overall, 17% of *L. botrana* eggs, 15% of *L. botrana* pupae, and 27% of *D. melanogaster* pupae were preyed on in only 24h. For comparison, predation rates of *L. botrana* eggs were 2- to 5-fold higher than in our study when sentinel

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FIGURE 2 Observed predation rates (%) of *Forficula auricularia* on (A) *Lobesia botrana* eggs, (B) *L. botrana* pupae, and (C) *Drosophila melanogaster* pupae in 32 vineyards under conventional vs. organic management, planted with resistant vs. susceptible varieties. In the boxplots, the top and bottom box indicate the first and third quartile of the data, the thick line in between is the median, the whiskers indicate 1.5× the interquartile range, the black dots are outliers, and the white dot indicates the mean.

cards were exposed for 72 h in the same study region (Pennington et al., 2018; Reiff et al., 2023). Given that the natural development time of vineyard pests is considerably longer (6 weeks for *L. botrana*; Thiéry & Moreau, 2005; 10–30 days for *D. suzukii*; Winkler et al., 2020), the possibility for natural predation is higher, accordingly. We thus assume that under natural conditions pest control could be higher than estimated with short-time exposed sentinel cards.

TABLE 2 Model parameters and output for the three fitted models of predation by earwigs. Model formula included response variable ~ management*variety + (1 | site).

	Parameters		Output: $p(\chi^2)$		
Response variable	Distribution	df residuals	Management	Variety	Management*variety
Lobesia botrana egg predation	Tweedie	25	0.12 (2.3871)	0.95 (0.0047)	0.083 (3.0071)
L. botrana pupae predation	Gaussian	26	0.12 (2.4351)	0.36 (0.8304)	0.080 (3.0618)
Drosophila melanogaster pupae predation	Gaussian	26	0.63 (0.2298)	0.87 (0.0283)	0.14 (2.1922)

The degree to which artificial predation experiments reflect true intensities of pest control is uncertain. For example, prey may be more visible and clustered than under natural conditions and pest females may be able to avoid sites with high predation risk, e.g., by detecting chemical cues of predators (Dicke & Grostal, 2001). For instance, the eggs of L. botrana are usually laid solitarily and the pupae, covered by a silky cocoon, are hidden in grape bunches and leaves, on the ground, or between the bark (Benelli et al., 2023). Further, the artificial immobilisation of prey may favour attacks by arthropods which are naturally not able to overpower this type of prey, possibly leading to overestimation of natural pest control potential (Zou et al., 2017; Gardarin et al., 2023). Nevertheless, Pennington et al. (2018) demonstrated that, under reduced fungicide applications, the proportion of damaged berries after infestation with L. botrana eggs decreased to the same extent as egg predation on sentinel cards and predator abundance increased. Thus, we expect that the sentinel cards used in our experiments provide a useful proxy to indicate differences in the actual natural pest control on L. botrana eggs between vineyards.

Sentinel cards are a useful method to assess the potential for natural pest control in comparative studies (Pennington et al., 2018; Muneret et al., 2019b; Gardarin et al., 2023). However, this method is also limited by the choice of prey, and the community of natural enemies and their control potential can be better estimated by the selection of several prey types (Nagy et al., 2020; Gardarin et al., 2023). By using both eggs and pupae of *L. botrana* and pupae of D. melanogaster, we were able to address a broad spectrum of predators in the vineyard canopy. However, the use of several prey types on one sentinel card may also create bias. For instance, predators could have been more attracted by the diverse buffet which may have led to an overestimation of predation rates. Camera observations are considerably more time consuming and expensive than only exposing sentinel cards (Grieshop et al., 2012; Nagy et al., 2020). Yet, they may add valuable information on predator-prey interactions and identify hitherto unrecognized predators (Merfield et al., 2004; Nagy et al., 2020). Therefore, we chose to expose multiple prey per card in order to maximize predator observations.

Beyond the observed predation events, other taxa in different strata may be of importance for the control of

vineyard pests. For example, *D. suzukii* larvae were reported to be preyed on already inside infested fruits and *D. suzukii* pupae were predominantly found in the soil (Woltz & Lee, 2017), where also other taxa may be involved in predation, such as staphylinid and carabid beetles. Adult stages of *L. botrana* and *Drosophila* sp. which were not observed in this study may be rather regulated by, e.g., web-building spiders than by earwigs (Englert & Herz, 2019; Michalko et al., 2019). In conclusion, the number of predators and their pest control potential in vine-yards is expected to be even higher than observed by our sentinel card snapshots.

Expected effects of organic management or reduced fungicide applications in resistant grapes were not significant in this study. Nevertheless, the highest predation rates in conventional vineyards with resistant grape varieties coincided with the highest abundance of earwigs and total carnivores in the same vineyards in southwestern Germany (Reiff et al., 2023). Earwigs are sensitive to several insecticides but appear to be unaffected by fungicides (Shaw & Wallis, 2010; Logan et al., 2011; Malagnoux et al., 2015). The use of insecticides was mainly avoided in this study, which may be one reason for high predation rates by earwigs. Other factors, such as soil management and the implementation of cover crops, could be significant bottlenecks for earwig abundance and predation. For instance, frequent tillage operations may affect earwig reproduction by disrupting belowground nesting (Gobin et al., 2008; Orpet et al., 2019a). Hitherto unaware of the dominance of earwigs in vineyards, we did not systematically take into account these factors. The low predation rates in July and partly August may be explained by the high temperatures and low precipitation during these months in 2018. The activity of many arthropods is known to be reduced under hot and dry conditions which consequently affects foraging activity and predation pressure (Kessler & Guerin, 2008; Benoit, 2010; Romero et al., 2021). However, this may have little direct relevance for Drosophila pest management, as also pest species such as D. suzukii suffer from hot and dry conditions during summer (Tochen et al., 2014; Asplen et al., 2015; Gutierrez et al., 2016).

Our study highlights the added value of camera observations in sentinel prey experiments. We identified earwigs, which had hitherto been underestimated as predators in vineyards, as the key predators in the Palatinate viticultural



FIGURE 3 Temporal variation of overall predation rates (%) on (A) *Lobesia botrana* eggs, (B) *L. botrana* pupae, and (C) *Drosophila melanogaster* pupae in 32 vineyards. In the boxplots, the top and bottom box indicate the first and third quartile of the data, the thick line in between is the median, the whiskers indicate 1.5× the interquartile range, the black dots are outliers, and the white dot indicates the mean. Boxes within a panel capped with different letters indicate significant differences between means (emmeans with Tukey adjustment: P < 0.05).

region. Vineyards provide suitable habitats for earwig populations (perennial crop, fissured bark providing shelter) if insecticide use and frequent tillage operations are avoided. Other identified predators showed less control potential. However, with regard to agroecosystem resilience, the maintenance of a diverse predator community should be pursued. We recommend camera observations to identify key predators also in different predator–prey interactions, study systems, and regions. **TABLE 3** Model parameters and output for the three fitted models for temporal variance. Model formula included response variable ~ month + (1 | site).

	Parameters	Output: p (χ^2)	
Response variable	Distribution	d.f. residuals	Month
<i>Lobesia botrana</i> egg predation	Nbinom2	122	0.0038 (13.403)
<i>L. botrana</i> pupae predation	Tweedie	121	0.22 (4.459)
Drosophila melanogaster pupae predation	Tweedie	121	0.0086 (11.674)

AUTHOR CONTRIBUTIONS

Jo Marie Reiff: Conceptualization (equal); formal analysis (lead); methodology (equal); visualization (lead); writing – original draft (lead). Konrad Theiss: Investigation (lead); writing – review and editing (supporting). Christoph Hoffmann: Conceptualization (equal); funding acquisition (equal); project administration (equal); supervision (equal); writing – review and editing (supporting). Martin H. Entling: Conceptualization (equal); funding acquisition (equal); project administration (equal); funding acquisition (equal); project administration (equal); supervision (lead); writing – review and editing (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary material.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article. **Table S1.** Exposed and consumed eggs and pupae of *L. botrana* and *D. melanogaster* per vineyard and sampling date listed by predator.

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