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Predation of grape berry moths by harvestmen depends on landscape composition

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ABSTRACT

Landscape complexity can benefit natural enemy communities and the biological pest control services they provide in agricultural landscapes. Harvestmen are generalist predators consuming a large range of prey in terrestrial ecosystems including agroecosystems. However, their ecology and their role in controlling pest populations in such ecosystems remain poorly studied. In this study, we examined predator–prey interactions between the European harvestmen (*Phalangium opilio* L.) and several potential prey species found in a vineyard agroecosystem. We sampled 20 populations of harvestmen in vineyards selected along a gradient of proportion of semi-natural habitats and used gut-content molecular analyses to quantify interaction strength between harvestmen and the grape berry moth, the main insect pest of grape, and two alternative prey species, springtails and the grape phylloxera. We found a high proportion of harvestmen positive to each type of prey with, on average, half of the individuals collected that had consumed grape berry moths. Increasing the proportion of semi-natural habitats in the landscape enhanced the proportion of harvestmen preying upon grape berry moths. Despite a significant number of harvestmen preying on springtails and grape phylloxera, the strength of the feeding interaction between harvestmen and these alternative prey species never significantly explained predation rates of the grape berry moth. Our results indicate that conserving semi-natural habitats increases biological pest control services delivered by harvestmen in vineyard landscapes and highlight the potentially important role of harvestmen in those agricultural systems.

1. Introduction

Agricultural intensification is a main driver of biodiversity loss in human-modified landscapes (Stoate et al., 2001; Tscharntke et al., 2005). Future agricultural landscapes will need to better balance productivity with minimising negative impacts on the environment (Doré et al., 2011). One promising way to achieve this balance is to design farming systems that replace external inputs, such as agrochemicals, by ecosystem functions and services, such as biological control, generated by biodiversity (Bommarco et al., 2013). To design farming systems that efficiently rely on services provided by beneficial species, we need to considerably improve our understanding of their ecology, particularly on two key aspects: (i) the role of species and functional groups key to functions and services; (ii) the consequences of environmental changes at several spatio-temporal scales on populations and community dynamics (Bommarco et al., 2013; Schellhorn et al., 2015).

Trophic interactions in agroecosystems are affected by several variables acting at different spatio-temporal scales, such as crop management at the field scale or landscape context (Rusch et al., 2010; Tscharntkea et al., 2007). Two comprehensive reviews demonstrated that the proportion of semi-natural habitats in the landscape (i.e., landscape complexity) enhances the abundance and the diversity of natural enemies (Bianchi et al., 2006; Tscharntkea et al., 2007). Moreover, there is some evidence that this positive effect of landscape complexity on natural enemies led to increased predation or parasitism rates of insect pests in agroecosystems (Rusch et al., 2016; Dainese et al., 2019). This positive effect of landscape complexity is due to semi-natural habitats providing several key resources for natural enemies such as alternative host and prey species, nectar, overwintering sites or favourable microclimatic conditions (Rusch et al., 2010; Sarthou et al., 2014). However, very few studies have examined the indirect effects of landscape context on lower trophic levels (i.e., herbivores and plants) mediated by trophic cascades. Moreover, a large majority of studies considers spiders, ground beetles or parasitoids, yet the effects of landscape complexity remain largely unexplored for several other groups of arthropods, such as staphylinids, earwigs or harvestmen.

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Recent works have shown that the taxonomic richness of service-providing organisms contribute to supporting biological pest control service in agriculture (Dainese et al., 2019). Species-rich communities tend to increase the level of predation owing to niche complementarity between natural enemies, sampling effect or even facilitation (Cardinale et al., 2003; Letourneau et al., 2009; Greenop et al., 2018). However, negative or neutral relationships between more diverse natural enemy communities and the level of pest control emerge in a non-negligible number of cases (approximately 30% in the meta-analysis of Letourneau et al., 2009). These relationships may arise from negative interactions between species (e.g., intraguild predation, behavioral interference) or sampling effect (Letourneau et al., 2009). Much of the unexplained variation in studies investigating how the structure of natural enemy communities affect pest control services comes from the lack of basic knowledge about the ecology, behavior and diet of a large number of species groups. Producing such knowledge about the role of key predator species in real-world agroecosystems and their impact on pest populations and crop damage is of major importance if we are to develop farming systems integrating natural pest control services (Welch et al., 2014; Schellhorn et al., 2015).

Arthropod predation is generally difficult to observe and estimate, especially in real-world ecosystems. One way to study trophic interactions is to analyze gut contents of field-collected predators (Kuusk et al., 2008; Sheppard and Harwood, 2005; Birkhofer et al., 2017). Several studies have demonstrated the added value of using molecular tools to detect prey-specific DNA sequences within the gut contents of predators and to reveal feeding links in complex food webs (Davey et al., 2013; Kuusk et al., 2008). However, these approaches are not widely used in agroecosystems and a very limited number of studies have used them to study how trophic interactions respond to environmental changes, such as changes in landscape context or predator diversity (but see Roubinet et al., 2015). Moreover, Harwood and Obrycki (2005) revealed that in over 100 studies that have used some sort of gut content analysis, more than 70 of them studied carabid beetles. This clearly highlights the need for more studies on other taxa.

Harvestmen (Opiliones), the third largest order of the class Arachnida that encompasses more than 6000 species are considered as important predators in many terrestrial ecosystems (Curtis and Machado, 2007; Pinto-da-Rocha et al., 2007 and references therein). Several studies have shown that harvestmen consume a large range of prey including collembolans, aphids, lepidopteran larvae, dipterans, ants, spiders, mites, earthworms or gastropods in arable land (Wolff et al., 2014; Leathwick and Winterbourn, 1984; Dixon and McKinlay, 1989; Clark et al., 1994; Halaj and Cady, 2000; Acosta and Machado, 2007). However, even if they are usually found in arable land at high abundance, their ecology and their role in controlling pest populations in such habitats remains poorly studied (Acosta and Machado, 2007).

In this study, we examined predator-prey interactions between the European harvestmen (*Phalangium opilio* L.) and several potential prey species found in a vineyard agroecosystem. We decided to study the European harvestmen in vineyards because they are found at high level of abundance and that no basic ecological understanding of their role in this agroecosystem exists to our knowledge (Muneret et al., 2019). Moreover, developing conservation biological control of pests is a major applied issue in vineyards because vineyards are submitted to very high level of pesticide use (Muneret et al., 2018). In this study, our aims were (i) to quantify the strength of trophic links between the European harvestmen and potential prey species, including grape berry moth, using molecular gut content analysis, (ii) to examine how population density of harvestmen and potential alternative prey species (grape phylloxera and springtails) affect interaction strengths between harvestmen and grape berry moth populations, (iii) and how the proportion of semi-natural habitats in the landscape context modify these trophic interactions. We particularly hypothesized that the proportion of semi-natural habitats in the landscape would have a direct positive effect on the level of predation of grape berry moth by harvestmen and an indirect negative effect on the level of pest infestation. Moreover, we hypothesized a negative effect of the interaction strengths between harvestmen and their alternative prey species on the level of predation of grape berry moths.

2. Material and methods

2.1. Study design

We established a study design in the Bordeaux area in south-west France. This area is about 138,000 ha of vineyards, approximately 20% of the French wine-growing area. Vineyards in this region receive between 13 and 16 treatments of pesticides a year per unit area (Agreste, 2019). Our study design consisted of 20 independent (minimum distance of 2 km between fields) conventional vineyards selected along a gradient of proportion of semi-natural habitats ranging from 0% to 68% in a 1-km radius (Fig. S2). As conventional fields, farmers used a variety of herbicides, fungicides and insecticides. This study design makes it possible to test for the effects of landscape complexity (defined as the proportion of semi-natural habitats in the landscape) on abundance of harvestmen, grape berry moth and their alternative prey species. Semi-natural habitats mainly consisted of woodlands, grasslands, hedgerows and shrubs. All the surveyed vineyards used Merlot as the cultivar and the same vine stock density (about 5000 vine stocks ha^{-1}). Landscape complexity was calculated using ArcGIS software (Version 10, ESRI, Redlands, CA, USA) as the proportion of semi-natural habitats in a 1-km radius around each vineyard. All types of semi-natural habitats were grouped together and analyzed as on explanatory variables.

2.2. Harvestmen and grape berry moth sampling

Harvestmen density was estimated in June 2013 in each vineyard by beating. Beating was done on 30 vine stocks located at least 5 vine stocks away from each other along a transect in the middle of the field at two dates. In June 2013, we independently collected *Phalangium opilio* by visual inspection and hand-collection to screen their gut contents using molecular approaches (see below). The sampling effort was standardized to a maximum of 2 h inspection for one person. All individuals were separately stored in 2-ml Eppendorf sterilized tubes with 96% ethanol and maintained at −80 °C until DNA extraction. We collected 135 individuals from beating and 818 individuals (ranging between 8 and 54 *P. opilio* by site) for gut content analyses.

Density of grape moth larvae (*Lobesia botrana*) was estimated at the same time as harvestmen sampling (early June was the first generation of the grape berry moth). Because larvae build nests with silk, we monitored nest occurrence along transects of 100 independent grape clusters per field to assess grape moth density. All larval nests were collected and returned to the laboratory. They were maintained in small individual boxes with fresh parts of bunches (collected on the same sampling plot) to provide additional larval food until the end of their larval development. Larval populations were checked until pupation, upon which pupae were removed from the flower buds and the individuals were placed into separate glass tubes and stored at 22 °C, 60% relative humidity and at a 16/8-h light/dark cycle. Adult moths were identified after emergence (201 *Lobesia botrana* were identified corresponding to 81% of the larval nests sampled).

2.3. Harvestmen gut content analyses

2.3.1. Specific primers for prey-digested DNA amplification

We considered three prey species in our gut content analyses: the grape berry moth, *Lobesia botrana,* which is a main insect pest of grape, and two potential alternative prey species, the grape phylloxera (*Daktulosphaira vitifoliae*) and springtails because these are suspected to be potential prey of harvestmen (Pinto-Da-Rocha et al., 2007).

A set of seven Simple Sequence Repeat (SSR) markers, developed for

Table 1
Target and non-target species used to assess the specificity of the different primer pairs for the gut content analysis.

Class, Order	Family	Species
Hemiptera	Phylloxeridae	*Daktulosphaira vitifoliae*
	Cicadellidae	*Empoasca vitis*
		Scaphoideus titanus
Lepidoptera	Tortricidae	*Lobesia botrana*
		Sparganothis pilleriana
		Eupoecilia ambiguella
		Cydia pomonella
Hymenoptera	Ichneumonidae	*Campoplex capitator*
Diptera	Tachinidae	*Phytomyptera nigrina*
Dermaptera	Forficullidae	*Forficula auricularia*
Coleoptera	Carabidae	*Nebria brevicollis*
		Harpalus honestus
		Harpalus tardus
		Pseudoophonus rufipes
		Calathus fuscipes
	Collembola	
	Coccinellidae	*Adalia bipunctata*
Hemiptera	Anthocoridae	*Orius laevigatus*
Diptera	Syrphidae	*Xanthandrus comtus*
Araneae	Salticidae	*Salticus scenicus*
Neuroptera	Chrysopida	*Chrysoperla carnea*
Opiliones		*Phalangium opilio*

Lobesia botrana, was tested to amplify short fragments of digested *L. botrana* DNA from the gut content of *P. opilio* following the approach describe in Amsellem et al. (2003). The ability of these primer pairs to specifically amplify *L. botrana* DNA was first evaluated by using target *L. botrana* and non-target DNA extracts, focusing on the arthropod groups of taxa commonly present in the grapevine agrosystem (Table 1). Most of these arthropods were collected from the Bordeaux vineyard of a previously study (Muneret et al., 2018). Only the DNA of three Tortricid species (*Lobesia botrana, Sparganothis pilleriana and Eupoecilia ambiguella*) was extracted from the insect reared collection of Bordeaux INRAE laboratory and the DNA of *Cydia pomonella* was obtained from Avignon INRAE. We selected the SSR markers that were able to specifically amplify *L. botrana* DNA for the following gut content analyses.

Preliminary tests were also performed for the 10 *D. vitifolia* primer pairs of the standardized microsatellite reference alleles database PHYLLI (Forneck et al., 2017) to amplify short DNA digested fragments of grape phylloxera from the *P. opilio* gut content. These tests were done using the Pcf7 phylloxera clone from Bordeaux INRAE laboratory collection. Only the primer pairs able to specifically amplify *D. vitifolia* DNA and no other non-target arthropod (Table 1) were chosen for the *P. opilio* gut content analysis.

Finally, 18S rDNA primers designed by Kuusk and Agusti (2008) for springtail (Collembola) fragment detection within the predator gut content, have been tested on target springtail DNA (extracted from 20 adults collected in June 2016 from INRAE Bordeaux vineyards and taxonomically identified as Collembola family) and non-target arthropod species (Table 1). All PCR products were then sized in 2% agarose gel electrophoresis.

2.3.2. Feeding tests to calibrate the PCR diagnostic approach

To assess the post-ingestion detection limit of the specific primers, feeding tests were performed using 36 additional *P. opilio* that were fed with mealworms for 4 days and then starved for 5 days before the feeding tests. Three starved *P. opilio* were directly stored at −80 °C and served as negative controls. Eighteen *P. opilio* were fed for 30 min with four third-instar *L. botrana.* Batches of three *P. opilio* were freezed (−80 °C) after 1 h, 4 h, 6 h, 24 h, 48 h and 6 days of feeding time. Another 15 starved *P. opilio* were fed each with 50 grape phylloxera (radicicoles) and batches of three *P. opilio* were frizzed (−80 °C) after 1 h, 4 h, 24 h, 48 h and 4 days of feeding time. All individuals were stored in separate 2-ml Eppendorf sterilized tubes.

No new feeding tests were done for the springtail specific primers in this study as there were previously tested on 17 springtail target species from agricultural habitats (Kuusk and Agusti, 2008) and were successfully used for the multiplex diagnostic PCR assays that unraveled food web interactions in cereal crops (Staudacher et al., 2015).

2.3.3. Sampling preparation and DNA extraction

The amount of *P. opilio* tissue for DNA extraction was reduced only by removal of the legs because the broadly joined abdomen and cephalothorax could not be separated. Prey-target insects (grape berry moths, grape phylloxera and springtails) were individually extracted using all body material. However, only leg muscle tissues were used for the non-target arthropod DNA extraction, including the negative control *P. opilio*, to prevent the co-extraction of arthropod DNA from the gut content contaminants. A DNeasy 96 Blood & Tissue Kit (Qiagen, Inc, Chatsworth, CA) was used for DNA extraction, following the manufacturer's instructions. DNA quantification was done by fluorescence assays using a DS-11 FX Spectrophotometer/Fluorometer (DoNovix) and DNA concentrations across samples were normalized to 20 ng/µl.

To verify that PCR amplification products from field-collected *P. opilio* can be identified as being a prey target species (grape berry moths, grape phylloxera and springtails), 12 field-collected samples and eight samples from each feeding test scored as positive were purified and sequenced. Sanger sequencing of purified PCR products was conducted by GENEWIZ Germany in both forward and reverse directions. Generated SSRs (including their flanking regions) and 18S rDNA sequences were aligned using MEGA version 6 (Tamura et al., 2013) and were blasted against the GenBank and BOLD sequence libraries.

2.4. Statistical analyses

We examined how the proportion of semi-natural habitats affects the abundance of harvestmen and grape berry moths as well as the trophic links between harvestmen, grape berry moths and two alternative prey species (grape phylloxera and springtails) using a structural equation modelling (SEM) approach. We developed a conceptual model to test direct and indirect effects of the proportion of semi-natural habitats on these components (Fig. 1). This model allows us to test for direct effects of the proportion of semi-natural habitats on harvestmen density, grape berry moth density, and the interaction strengths between harvestmen, grape berry moth and the two alternative prey species. We used the proportion of harvestmen detected as positive to a given prey as a proxy for the relative importance of this prey for the diet of harvestmen. We used separate generalized linear models with appropriate error distributions as a preliminary step to inform our SEMs approach. In this preliminary step, we also examined how the sample size of harvestmen used for molecular screening affected the proportion of harvestmen that were positive to the different prey tested using generalized linear models and found no effect of sample size on the proportion of harvestmen positive to the different prey (P-values associated to GLM testing the effect of harvestmen sample size on the proportion of individuals detected positive for collembolans, grape berry moth and phylloxera are respectively: 0.10, 0.76 and 0.25). We then used piecewise SEMs that allow using a wide range of response distributions to evaluate the hypothesized pathways (Lefcheck, 2016). We used the d-separation test to evaluate whether the non-hypothesized independent paths were significant and whether the models could be improved with the inclusion of any of the missing paths.

3. Results

3.1. Molecular markers to assess trophic links between P. opilio and its prey species

From the seven *L. botrana* SSR primer pairs tested in this study

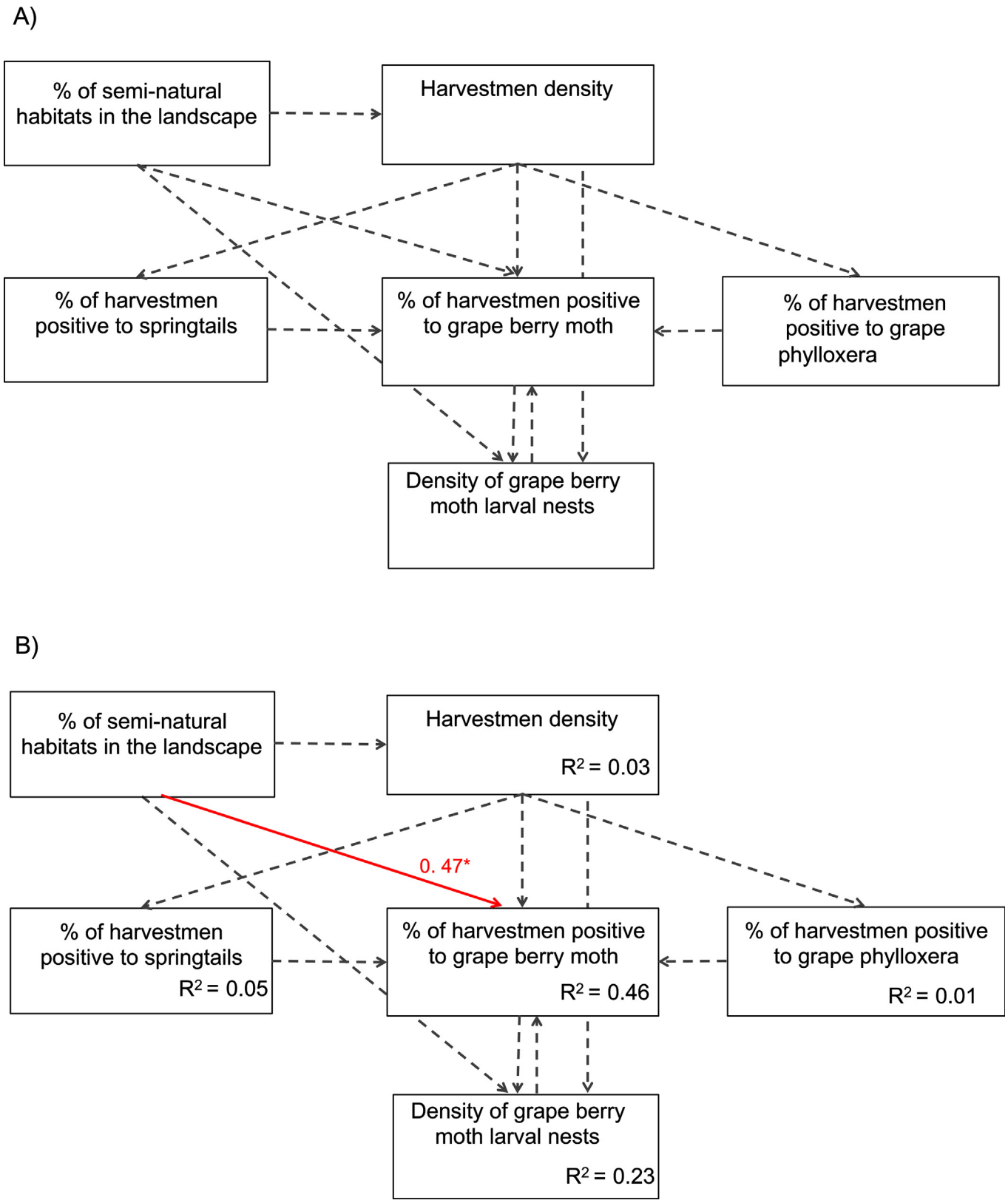

Fig. 1. A) conceptual model of our structural equation modelling approach examining how the proportion of semi-natural habitats in the landscape affects harvestmen and grape berry moth density as well as the trophic interactions between harvestmen, grape berry moths and two alternative prey species, grape phylloxera and springtails. Dashed lines represent hypothetical relationships tested in the model. B) Outputs of the structural equation model. Significant variables with standardized estimates are shown by the red solid line, non-significant relationships are represented by the grey dashed lines * $P < 0.05$. Each R^2 is indicated in the boxes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Lobot 3, Lobot 6, Lobot 9, Lobot 10, Lobot 11, Lobot 14 and Lobot 15), six amplified specifically *L. botrana* DNA and only one primer pair, Lobot 6, amplified short digested *L. botrana* DNA fragments (340 bp) from the *P. opilio* gut content. Analysis of the range digestion time using Lobot 6 showed that digested DNA traces of *L. botrana* could be specifically detected until 6 days post-ingestion from the *P. opilio* gut content. Short digested DNA fragments of *D. vitifolia* (186 bp) could also be amplified from *P. opilio* gut content until 4 days post-ingestion using the SSR primer pair Cv4. This marker was found to be specific for the target species *D. vitifolia* and none of the other non-target species tested gave any amplification product. Finally, the detection of springtail (Collembola) DNA as an alternative food source of *P. opilio*, was possible using the 18S rDNA primer pair Col4F/Col5R. A short fragment of 177 bp was specifically amplified from the target springtail DNA and no cross-amplifications with the non-target DNA were observed when this primer pair was tested against the 22 arthropod species commonly present in vineyards (Table 1)

3.2. Predation of grape berry moth and the two alterative prey species by P. opilio

On average, a large majority of harvestmen collected for molecular gut content analyses were adults (93.5%) distributed between males (66.4%) and females (27.1%), whereas only 6.5% were juveniles. Digested DNA fragments of grape berry moth and grape phylloxera were detected in all 20 *P. opilio* populations, but we did not detect any springtail DNA fragments in only one population of harvestmen out of 20 (Fig. 2). The proportion of harvestmen that were positive to the grape berry moth ranged from 12% to 98% with a mean of 55.4% (SD = 26.1). The proportion of harvestmen that were positive to grape phylloxera ranged from 24% to 66% with a mean of 45% (SD = 11.8) (Fig. 2). The proportion of harvestmen that were positive to springtails ranged from 0% to 94.5% with a mean of 70.4% (SD = 27.4) (Fig. 2).

3.3. Effects of semi-natural habitats and alternative prey species on predation levels of grape berry moths

Our SEM model that explored direct and indirect effects of semi-natural habitats and alternative prey species on the predation levels of grape berry moth by harvestmen fitted the data well (Fisher's C = 12.6,

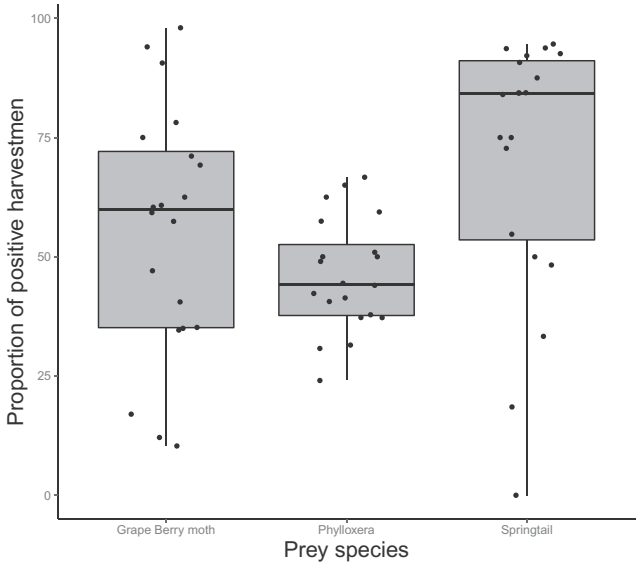

Fig. 2. Box plot showing the proportion of harvestmen positive to the different prey species: grape berry moth, grape phylloxera and springtails, in each of the 20 populations.

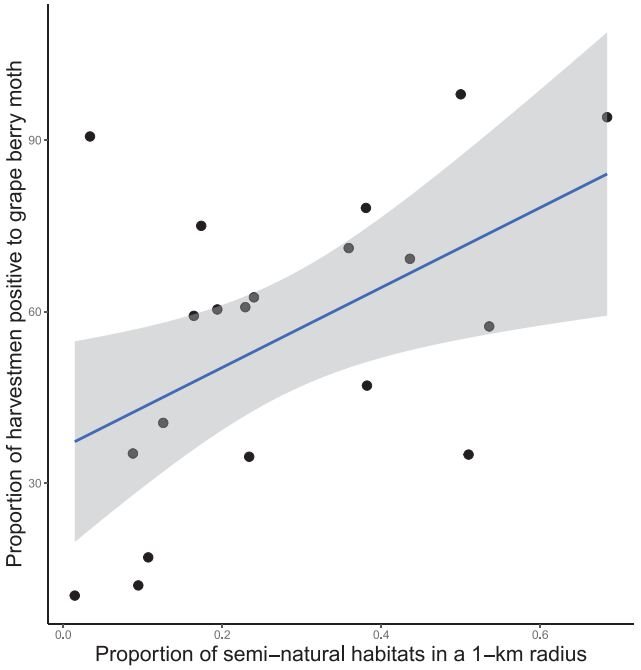

Fig. 3. Effects of the proportion of semi-natural habitats on the proportion of harvestmen detected positive to the grape berry moth. Each point represents a harvestmen population in a given vineyard.

df = 10, P = 0.24). No significant links were missing in the model. We found a significant positive effect of the proportion of semi-natural habitats in the landscape on the proportion of harvestmen positive to the grape berry moth (standardized estimate = 0.47, P = 0.03) (Figs. 1 and 3). We found no significant relationships between harvestmen density, grape berry moth density or the proportion of harvestmen positive to the two alternative prey species considered on predation rates of grape berry moth by harvestmen (Fig. 1, Table S1). Interestingly, the proportion of harvestmen positive to the grape berry moth tended to negatively affect the density of grape moth larvae (standardized estimate = −0.43, P = 0.06).

4. Discussion

Our study provides new insights into the diet of harvestmen in viticultural landscapes. Although not quantitative, our semi-quantitative approach revealed a relatively high proportion of adults positive to the grape berry moth as, on average, half of the individuals collected were found to consume this pest species. Our results also revealed that increasing the proportion of semi-natural habitats in the landscape led to higher proportion of harvestmen preying upon grape berry moths, suggesting that conserving semi-natural habitats increases biological pest control services delivered by harvestmen in vineyard landscapes.

Good predation ability of harvestman males was previously reported on several lepidopteran pests as *Spodoptera frugiperda* in cornfields (Clark et al., 1994), *Helicoverpa zea* in soybean fields (Newton and Yeargan, 2001; Pfannenstiel and Yeargan, 2002), *Pieris rapae* in cabbageworm fields (Schmaedick and Shelton, 2000) and *Cydia pomonella* and *Grapholita molesta* in apple orchards (Boreau de Roincé et al., 2012). However, no information was yet available concerning *P. opilio* diet composition and their capacity to consume grape pests. Most harvestman prey species are small and soft-skinned invertebrates that can easily be seized by pedipalps and/or chelicerae. But it has been reported that most phalangiid species are able to kill large lepidopteran larvae by subduing the prey with chelicerae and pedipalps, until it no longer offers resistance (Pinto-Da-Rocha et al., 2007). We therefore expected that *P. opilio* adults living on the grape canopy would be

efficient predators of the first-generation grape berry moth larvae, which are still exposed to predation before perforating and entering berries. Our results, showing the positive range of half of the *P. opilio* natural population for *L. botrana* DNA, therefore support this hypothesis.

Our data also indicate that prey species such as springtails or grape phylloxera are significantly consumed by harvestmen and are therefore important alternative resources in this system. However, our analysis revealed that the feeding rate between harvestmen and grape berry moth increases with the proportion of semi-natural habitats in the landscape but was not affected by harvestmen densities or amount of alternative preys. This suggests that the interaction strength between harvestmen and grape berry moth might not be driven by intra-specific competition, density dependence or alternative resource availability in the vineyards, but directly by the amount of semi-natural habitats in the landscape. The positive effect of semi-natural habitats in the landscape on the spillover of natural enemies and biological pest control are usually attributed to several non-exclusive mechanisms, such as the habitats serving as overwintering sites, providing alternative food or hosts or providing refuge from disturbance due to more mild microclimatic conditions (Landis et al., 2000). Our results suggest that the beneficial effect of semi-natural habitats on biological pest control by harvestmen is not driven by higher population density of harvestmen but may result from better body conditions and a higher feeding rate in complex landscapes compared with simple landscapes. Indeed, we did not find any effect of the proportion of semi-natural habitats on harvestmen density. Several studies have demonstrated that landscape complexity positively affects body conditions, measured by fecundity and body size, of arthropod predators due to the key role of semi-natural habitats in providing overwintering sites, alternative resources and prey (Bommarco, 1998; Östman et al., 2001). These studies, in line with our results, suggest higher feeding rates of predators in more complex landscapes compared to simple landscape with low amount of semi-natural habitats. Finally, our analyses indicate that the density of grape berry moth larval nests tend to be negatively affected (even if marginally significant) to the proportion of harvestmen positive to grape berry moth suggesting a functional role of harvestmen on the biological control of the grape berry moth. However, this effect might be also affected by the well-known positive effect of semi-natural habitats on other predator species such as spiders (Kolb et al., 2020). The functional role of harvestmen on the biological control of the grape berry moth remains to be explored.

The long digestion time observed during the laboratory predation tests on grape berry moths and in grape phylloxera (the target DNA was amplified after 6 and 4 days, respectively, after ingestion) confirm previous reports on several species of harvestmen: the adults are able to resist long periods of starvation and, when food is available again, they consume large amounts at one time, producing a noticeable abdominal expansion and a dramatic increase of body weight (Pabst, 1953, Immel, 1954, 1955). Thus, this ability to consume a great quantity of food at one time, the highly efficient food-storage organ and the low metabolic rate may together enable harvestman to survive long periods of food deprivation (Pinto-Da-Rocha et al., 2007).

5. Conclusion

Our study, using molecular gut-content analyses on harvestmen sampled along a landscape complexity gradient, highlights the strong positive effect of semi-natural habitats on feeding rates of harvestmen on the grape berry moth, a major insect pest of grape. Our results suggest that this positive effect is mediated by better body conditions of harvestmen because we did not find any effect of the amount of semi-natural habitats on harvestmen density, interaction strength with alternative prey or grape berry moth density. Further research is needed to test this hypothesis and to analyse the effect of different semi-natural habitat types as well as a larger range of potential prey species on harvestmen populations. However, our study suggests that *P. opilio* is a predator of the grape berry moth that could contribute to natural pest control services delivered by generalist predators in vineyard landscapes even if the effect of harvestmen on crop damage resulting from grape berry moth attacks remains to be quantified.

CRediT authorship contribution statement

Daciana Papura: Conceptualization. **Pascale Roux:** Investigation, Resources. **Benjamin Joubard:** . **Laureen Razafimbola:** Investigation, Data curation. **Olivier Fabreguettes:** Investigation, Resources. **Lionel Delbac:** Resources. **Adrien Rusch:** Supervision, Conceptualization.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2020.104358.

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