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RESEARCH PAPER

Assessing ground predation by invertebrates in crops: Camera observations clarify the relevance of aphid cards and coleopteran sentinel prey

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ABSTRACT

Redesigning cropping systems to promote natural pest control requires a sound understanding of the regulation potential of natural enemies. Sentinel preys are useful to quantify biological control, but the use of aphid cards (aphids glued to a sandpaper card) is controversial for their lack of realism. The objectives here were: (1) to compare aphid cards to non-fixed beetle larvae resembling coleopteran pests, with respect to the consumers attracted; and (2) to ascertain whether predation on coleopteran prey larvae responds to different invertebrates communities.

We used cameras to identify the consumers of two types of sentinel prey on the ground, and compared aphid cards to an original sentinel prey, bruchid beetle larvae. Aphids glued to predation cards attracted opportunistic consumers and scavengers with very long handling times, and even scavengers, including harvestmen (33% of consumption events), spiders and slugs, and a very few carabid beetles. Unattached bruchid beetle larvae were consumed largely by carabids (64%), and secondarily by rove beetles, ants and chilopods. As the sentinel prey were not consumed by the same organisms, these findings demonstrate the importance of the choice of organisms exposed to estimate pest predation.

Knowing the identity of the bruchid larvae consumers from the images, we investigated whether the assemblages of epigeic arthropods could explain their predation rates under contrasting field conditions. Accounting for all the expected consumers, sentinel prey disappearance rates could be explained statistically with a satisfactory goodness-of-fit. Slugs and ants contributed more strongly to the disappearance of sentinel prey than carnivorous carabids and chilopods. Finally, alternative prey (especially Collembola) reduced consumption by diverting consumers from their usual prey. Camera observations were valuable to assess the relevance of two different sentinel preys and of the consumers involved. With this knowledge, it is possible to estimate the pest control potential from the ground-dwelling communities present.

Introduction

Agricultural pest control using synthetic chemicals is facing multiple challenges such as resistance of herbivores to pesticides Robert et al. (2016), biodiversity losses (Schulz et al., 2021) and adverse effects on human health (Viel et al., 2015). Agroecological crop protection has been proposed as a means of managing the communities of all living organisms within an agroecosystem, with the aim of preventing or reducing the risks of outbreaks and infestations of pests (Deguine, 2017). It involves redesigning cropping systems to enhance biotic interactions and the functions they support, especially pest regulation by natural enemies present in the agroecosystem (Begg et al., 2017). Natural pest control has been shown to reduce pest population outbreaks and crop damage (Tschumi et al., 2015).

Within agroecosystems, communities of ground-dwelling arthropods, including key predators such as carabid beetles and spiders, regulate phytophagous insect populations Kromp. (1999); Marc et al. (1999). The impact of these organisms depends on the density, species richness, and functional composition of their communities Jonsson et al. (2017); Rusch et al (2015). It is classically assessed with sentinel preys, which provide a direct and quantitative measurement of predation under field conditions (Lövei & Ferrante, 2017). However, the

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assessment of predation rates from sentinel preys is subject to several methodological limitations. First, artificial preys such as plasticine caterpillars are useful for estimating attack rates, but the measure of predation efficiency is biased since the handling time is reduced with a non-living prey (no necessity to subdue the prey). The use of artificially immobilised live preys (glued or pinned to cards), or preys frozen before exposure, may affect the behaviour of their consumers due to the emission of chemical compounds by the glue or the injured prey (Birkhofer et al., 2017; Greenop et al., 2019). This issue raises questions about the suitability of sentinel prey for quantifying pest predation functions in agroecosystems.

Second, the small range of the sentinel preys used (Lövei et al., 2017) is hardly representative of the taxonomic diversity and size heterogeneity of crop pests. For instance, aphids have been widely used to assess predation rates on the soil surface in arable crops (Boetzl et al (2020); Ricci et al., 2019). Measuring predation on only one type of prey, which is not always representative of the pests present in the crop, may not be adequate to estimate the predation service in agroecosystems. Coleopteran herbivores such as *Brassicogethes aeneus* (Fabricius, 1775), *Ceutorhynchus pallidactylus* (Panzer, 1795), *Psylliodes chrysocephala* (Linnaeus, 1758), *Leptinotarsa decemlineata* (Say, 1824) and *Oulema* spp. (Des Gozis, 1886) are also regular pests on oilseed rape, potatoes, and cereals. They are the main targets of insecticides used on oilseed rape and potatoes in Western Europe (Alyokhin et al., 2008; Kheirodin et al., 2019; Nilsson et al., 2015; Ortega-Ramos et al., 2022). The larvae of these pests are highly vulnerable to predation, especially when they fall on the soil surface before pupating underground (Alvarez et al., 2013; Büchs & Alford, 2003; Gagnon, 2017; Zaller et al., 2009), but to our knowledge their predation has not been assessed (Büchi, 2002). Inferring their predation with aphids or plasticine artificial prey would not be useful since these larvae are very different from glued aphids or plasticine caterpillars in terms of size, appearance, and behaviour. The predation rates of coleopteran larvae may differ from that assessed with these sentinel prey, which may be consumed by different predator assemblages (Greenop et al., 2019). Given these limitations, methodological progress is required to make studies more realistic in terms of the types of prey considered and the ways in which they are exposed at the soil surface.

Predatory arthropods are generally considered to be the main consumers of prey on the soil surface in European agroecosystems (Furlong & Zalucki, 2010). The characteristics of their communities, such as total activity-density, and taxonomic and functional diversity, are often used as a proxy for natural pest control. However, this relationship has rarely been confirmed in field conditions. Boetzl et al. (2020) found a positive relationship between the abundance of arthropod predator taxa and prey removal, but conflicting results were obtained in other studies (Rusch et al., 2015; Zou et al., 2017). The direct observation of the predators by photography or camera recordings revealed that the presumed predators (generally carabids, staphylinids and arachnids) were not always involved in predation (Frank et al., 2007). The combination of camera recordings with the use of sentinel preys provides an opportunity to identify the consumers of sentinel preys and to investigate their behaviour when faced with different kinds of sentinel preys (Grieshop et al., 2012).

Given the controversy around the use of aphid cards to quantify an overall pest predation potential, our objectives were: (1) to compare them to a non-fixed prey closely related to coleopteran pests, with respect to the consumers attracted, and (2) to establish whether coleopteran prey predation responds effectively to different communities of epigeic invertebrates. We addressed the following two key questions:

(1) Which animals consume fixed aphid and unfixed bruchid beetle larva sentinel preys, when observed with a camera trap?
(2) Across fields with contrasting management, can the predation rates of bruchid larvae be explained by the consumers identified with the camera?

Materials and methods

Experiment 1: camera recordings of the consumers of two types of sentinel preys

Biological material

In this first experiment, we used camera recordings to identify the consumers of two types of sentinel preys. Live aphids, *Acyrthosiphon pisum* Harris (Hemiptera: Aphidiidae), were bought from KatzBiotech (Germany) and reared on *Pisum sativum* L. plants growing at room temperature in the laboratory. Immediately before the experiment, the largest aphids available (3 to 4 mm in length) were glued, by their tarsa, to 5 × 5 cm sandpaper cards (reference LEMAN 4,320,312, grain 120) with an odourless solvent-free glue (Cléopâtre Aero'Colle). Ten aphids were glued onto each card and the card was then fixed to the ground with a nail.

Larvae of *Callosobruchus maculatus* F., 1775 (Coleoptera: Chrysomelidae), hereafter referred to as "bruchids", were chosen as an alternative sentinel prey. In terms of shape and size, they more closely resemble the larvae of several Coleopteran pests exposed to the risk of predation on the soil surface when they leave their host plant to pupate. This species was chosen because it is easy to use and has a sedentary nature, although the larvae can wriggle a little. Bruchids were reared in transparent plastic boxes (57 × 39 × 28 cm) from a starting strain (GFM La Cigale, France). They were fed once weekly with two handfuls of *Vigna unguiculata* subsp. *unguiculata* (L.) Walp. seeds. The seeds were then carefully dissected to recover 3 to 4 mm-long last-instar larvae. The larvae were stored for up to seven days before use in a refrigerator at 4 °C. Ten bruchid larvae were placed on the surface of an open Petri dish (8 cm diameter) filled with black compost for contrast. The dish was buried such that the surface of the compost was flush with the soil surface. As the area of the Petri dishes was twice as large as the predation cards, the bruchids were distributed over a larger area than the aphids. Nevertheless, it is not clear how this might have influenced their predation. Although more widely spaced prey are more difficult to detect one after the other, this spacing limits the probability of negative interactions between consumers.

Description of the image-acquisition device

We designed a device for image acquisition (Fig. 1) composed of a Raspberry Pi 3 minicomputer (Raspberry Pi Fdn, Caldecote), a Raspberry Pi NoIR camera (2592 × 1944 pixel images) for night vision, and a microSD card. This equipment was powered with a 5 V powerbank lithium-ion battery (VOLTCRAFT PB-19 Powerbank). The arena was illuminated with an infrared LED light emitting at 940 nm (Kingbright BL0106–15–28) and powered by a dedicated lead acid battery. The images were taken in colour. However, the colours could not be distinguished at night since the only light source was the infrared lamp. The camera was placed vertically with the lens pointing directly at the sentinel preys on the ground. Its focal length was adjusted to record at a distance of 20 cm. The camera had a range of about 400 cm^2. The entire recording apparatus was placed in a sealed box equipped with four adjustable legs. The Raspberry Pi was powered by the Linux Ubuntu Mate system. Images were taken every 2 s between 17:00 CET and 08:00 CET the following day since ground-dwelling predators are mainly nocturnal (Petersen & Woltz, 2015; Thiele, 1977).

Study site and design

The experiment was conducted on the AgroParisTech experimental farm at Grignon, France (N 48.84807, E 1.93987), from 2016 to 2019, between April and July each year. The sentinel preys were exposed to various ground-dwelling macro-invertebrate communities by positioning them at sites with contrasting vegetation (winter wheat, oilseed rape, faba bean crops and perennial flower strips) managed under contrasting cropping systems (conventional, organic, and no-tillage) (see Appendix A: Table S1). The aim here was to compare not crops or

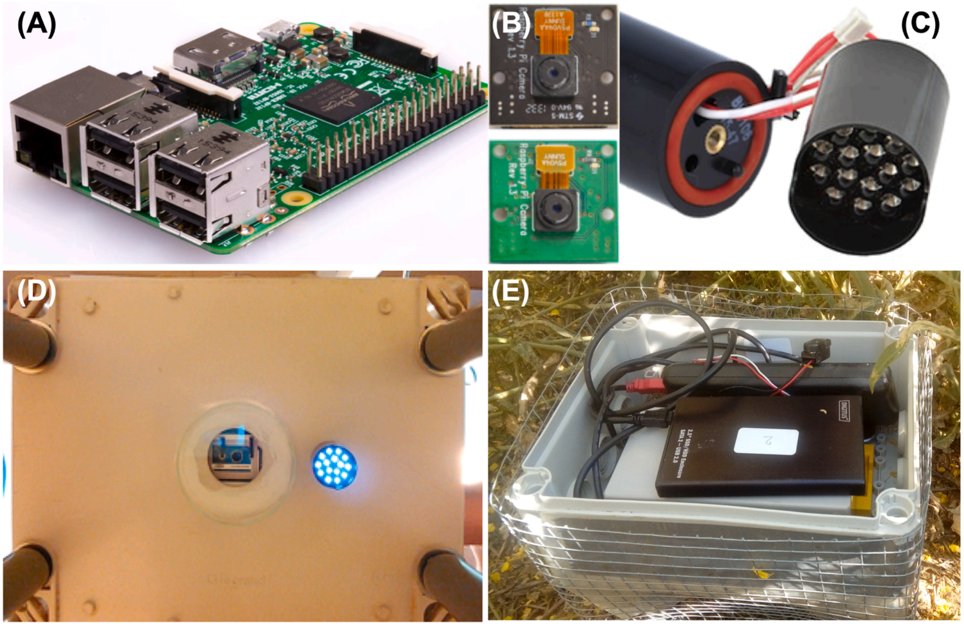

Fig. 1. The image acquisition device consists of a Raspberry Pi minicomputer (A), a Raspberry Pi NoIR camera for night vision (B) and an infrared LED light (C, D). These elements, with their batteries, were assembled in a sealed box (E) equipped with four adjustable supports.

cropping systems, but the consumers of aphids on predation cards with those of unfixed bruchid larvae. Sentinel preys were placed on the ground between 17:00 and 18:00 CET and were left in place for 14 h. Data were obtained with two image acquisition devices (simultaneously or sequentially) for a total of 70 nights (1036 h; 42 nights with bruchids, 28 with aphids).

Image analysis

The images were screened by a single observer. The organisms were identified to the lowest possible taxonomic level, generally to order, but sometimes to family level for some Coleoptera, and even species or genus level for Carabidae. As images were taken every 2 s, it was possible to distinguish five mutually exclusive types of event: “passing”, in which the organism crosses the observation arena (Petri dish or predation card) rapidly without any active search pattern, often following a straight path; “exploration”, in which the organism actively searches the arena; “handling without predation”, in which the organism comes into contact with a prey without eating it, sometimes displacing the prey within the arena; “removal”, in which the prey is removed from the camera’s field of vision; and, finally, “consumption”, in which the organism consumes all or part of the prey in the camera’s field of vision. Here, the organisms eating prey were all named “consumers”, and not “predators”, since consumption on immobile prey could be opportunistic, by organisms known as scavengers. We recorded the times at which each of these events started and ended. For each type of sentinel prey, we report summary statistics for the observed events and their duration, by interacting organisms.

Experiment 2: effect of ground-dwelling invertebrates on the predation of bruchid sentinel preys

Sentinel prey exposure

In this second experiment, we investigated whether the assemblages of consumers identified on the camera images could quantitatively explain the rates of bruchid predation across contrasting field conditions. We used bruchid larvae reared as in experiment 1. In preliminary trials, we found that in most situations all the larvae disappeared during the night, indicating a maximal predation rate. We therefore tried to increase the sensitivity of measurement such that predation rates varied between fields, by decreasing the accessibility of the sentinel preys by placing the ten bruchid larvae on a 10 × 10 cm patch of artificial grass (ALICANTE reference 1938/0, Saint Maclou, France). This patch of grass was buried a few millimetres underground and was anchored in place by two diagonally positioned nails (Fig. 2). As sentinel prey were hidden in the patch of grass, no camera could be used in this experiment.

The sentinel preys were exposed between 17:00 CET and 9:00 CET on three occasions (17/4/2018, 15/5/2018, and 13/6/2018). They were protected from vertebrate predation by a wire cage 15 cm in diameter × 15 cm high, with a mesh size of 11 mm × 11 mm. At retrieval, we recorded the number of intact preys. We then searched the immediate vicinity, within a radius of about 20 cm around the predation card or the Petri dish, for prey that had been moved without being consumed. If the faeces of small mammals were observed (shrews could easily penetrate the cages), the data were removed from subsequent analyses.

Monitoring of arthropod abundance

On the day when sentinel prey were set in place, pitfall traps were placed 1 m away to sample ground-dwelling macro-invertebrates. The pitfall traps consisted of transparent plastic containers (9.5 cm diameter, 7 cm high), filled with water, salt (50 $g{\cdot}L^{-1}$) and unscented detergent to break the surface tension (20 $ml{\cdot}L^{-1}$). They were protected from the rain by inverted opaque plastic flower-pot saucers (14 cm in diameter) supported about 2 cm above the soil surface with two nails. The traps were left in place for seven days and seven nights to obtain a sufficiently representative assessment of the invertebrate communities present. Invertebrates were sorted and identified to the lowest possible taxonomic level (from order to species), for assignment to a trophic group. Carabids were identified to species level (Roger et al, 2012), except for *Amara spp*. (Bonelli, 1810), which were identified only to genus level due to uncertainties concerning species identification. Adult spiders were identified to genus level (Roberts, 1993, 2014).

Study sites and design

We exposed the sentinel preys to diverse ground-dwelling invertebrate communities in 13 fields or sites representing a gradient of agricultural intensification and soil cover (see Appendix A: Table S2), on the AgroParisTech experimental farm at Grignon, France. The sites were arable field crops (mostly wheat or oilseed rape) or perennial flower

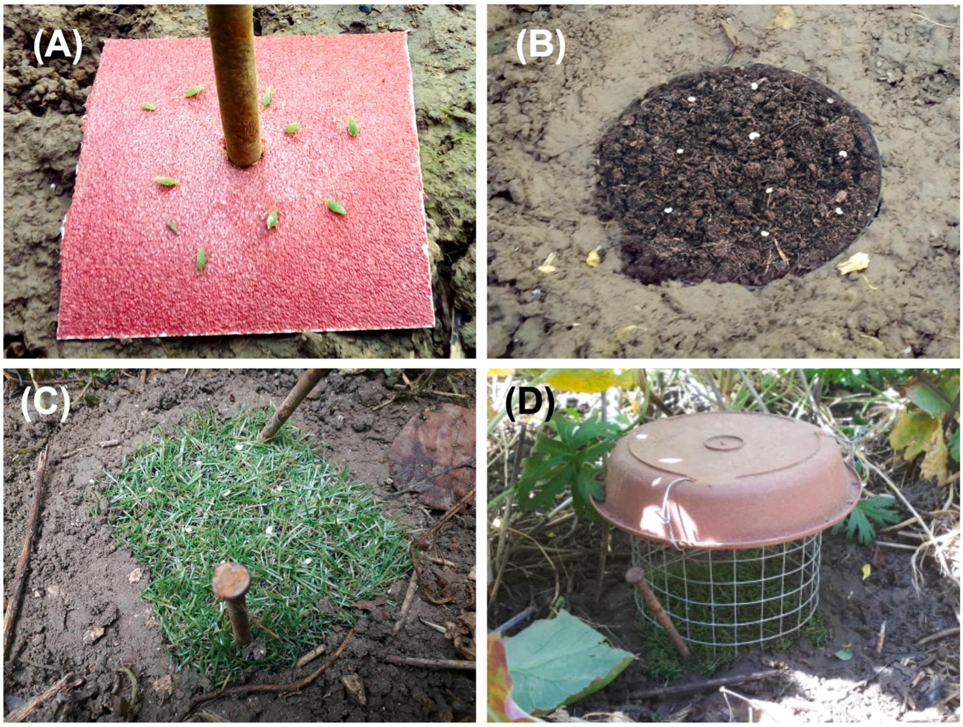

Fig. 2. In experiment 1, we observed the consumers of sentinel preys under the camera, by depositing 10 aphids (A) glued onto predation cards or 10 bruchid larvae (B) on a layer of compost at the soil surface. In experiment 2, we deposited 10 bruchid larvae on a patch of artificial grass (C), which we then protected from rodents with a wire cage (D).

strips. In crops, sentinel prey were placed at 30 m from the field edge, while in flower strips, they were placed at the centre of the 6-m-wide strips. These crops were managed with various cropping systems (conventional, no-tillage and organic). At each site and on each date, we placed one set of sentinel preys and a pitfall trap at three stations located 20 m apart. This resulted in a total of 117 sets of sentinel preys and pitfall traps.

Statistical analyses

We investigated the relationship between the rate of bruchid predation and the composition and diversity of the epigeic macroinvertebrate communities found in the pitfall traps. We included the activity-density of the known consumers, their diversity, and the activity-density of potential alternative prey taxa in the model as explanatory variables (see Appendix A: Table S3).

We tested, as explanatory variables, the consumers observed in experiment 1: Limacidae, Chilopoda, Araneae (we distinguished between the two dominant families, Lycosidae, Linyphiidae, and other families), Opiliones, Carabidae, Staphylinidae, Formicidae and Dermaptera. Carabid beetles were identified to species level. For Carabidae, we summed the activity-density (AD_s) of each species s weighted by its dietary affinity for consuming living animal prey ($Diet_s$, varying from 0 to 1 over a gradient running from herbivory to zoophagy), extracted from the BETSI database (https://portail.betsi.cnrs.fr/). This new variable was named “carnivorous Carabidae”:

$$Carnivorous\ Carabidae = \sum_s AD_s \cdot Diet_s$$

All the variables related to activity-densities were log-transformed (ln(x)+1) to account for their dispersion.

We investigated the effect of the taxonomic diversity of consumers, using the Shannon diversity index computed as follows: (1) for all species within the family Carabidae, (2) for families within the order Araneae, and (3) for the abovementioned consumers grouped at order or class level (Limacidae, Opiliones, Araneae, Chilopoda, Coleoptera, Hymenoptera and Dermaptera). We also considered the activity-density of alternative prey required to divert the consumers from eating the sentinel prey, as an explanatory variable. Aphidiidae (mean number of individuals collected per trap over 7 days ± SD = 0.07±0.35), Curculionidae larvae (12.29±77.58), Diptera larvae (0.02±0.20) and Lepidoptera larvae (0.01±0.10) were present at low densities at most sites. We therefore grouped them with Collembola (54.53±42.53) by summing their numbers. All explanatory variables were centred and scaled (divided by the standard-deviation) to enable the comparison of their effects.

Statistical analyses were performed with R software version 3.6.3 (R Development Core Team, 2020). We used generalised linear mixed models in the *lme* package (Bates et al. 2015) with a binomial error distribution. The models included the *date* as a fixed-effect covariable and a *station-nested-within-site* random effect. Using a multi-model inference procedure with the *MuMin* package (Bartoń 2016), we tested models including all possible combinations of the fixed-effect predictors (see Appendix A: Table S3), ranked according to the Akaike information criterion (AIC), with fitting by maximum likelihood methods. Only models containing a maximum of seven explanatory variables were evaluated, to avoid over-parametrisation (Harrell 2010). The significance of the effects of explanatory variables was tested with Wald chi-square tests. Models with a $\Delta AIC<2$ with respect to the best model were selected, and we present the statistical results for the full averaged model (Bartoń 2016). Partial R^2 values were calculated to assess the relative importance of each predictor.

Results

Experiment 1: camera recordings of the consumers of two types of sentinel prey

With glued aphids, we observed 864 events of all categories, using the camera during the 28 nights of observation. We were able to identify the organism involved in 702 events. The insufficient image quality precluded the identification of millimetre-sized organisms in the remaining 162 events, which were probably Acari in most instances, based on our visual observations in the field. The interactions in which these organisms were involved could not be distinguished either. Opiliones were the main identified consumers, accounting for 33% of all predation events *sensu lato* (consumption and prey removal). Limacidae, Araneae and Carabidae (especially *Anchomenus dorsalis* Pontoppidan, 1763) were also heavy aphid consumers (Fig. 3), but many other organisms, including birds (*Sylvia communis* Latham, 1787) and Cantharidae larvae likewise fed on them. Numerous Dipterans (always adults) were observed from the time at which the prey was placed in position until nightfall. Some appeared to be feeding on the aphids and the following day the aphids concerned were flaccid. Prey consumption by Diptera, Isopoda and small carabid beetles (probably Trechinae) was rarely observed, accounting for less than 1.5% when compared to the number of passages without interaction with the prey.

With bruchid larvae, we observed 2431 events with the camera during the 42 nights. We could identify the organism involved in 1987 events. As above, the unidentified predators were too small to be assigned with certainty to a taxonomic group. In contrast to what was observed for aphids, most organisms passed through the camera field without interacting with sentinel preys (Fig. 3). As the bruchids were not fixed, they were either consumed in view of the camera or were removed out of the camera's field of vision, possibly for consumption in a shelter. A large number of organisms were found to feed on bruchid larvae (Fig. 3). Carabid beetles were, by far, the main consumers, accounting for 64% of the prey consumption and removal events. These beetles included *A. dorsalis, Pterostichus melanarius* (Illiger 1798), *Poecilus cupreus* (Linnaeus, 1758) and *Amara sp*. Members of the Staphylinidae, Limacidae and Diptera (as for aphids) also consumed bruchid prey, but in much smaller amounts, accounting for a smaller proportion of events. Araneae and Opiliones consumed far fewer bruchid larvae than aphids.

The removal of bruchid larvae took a few seconds (see Appendix A: Fig. S1). For prey consumption, the time spent by each organism on the observed event varied considerably. It was shortest for *P. cupreus, P. melanarius* and ants, whereas prey consumption by Araneae and Diplopoda took more than one hour in some cases (see Appendix A: Table S1).

Experiment 2: effect of ground-dwelling invertebrates on the predation of bruchid sentinel prey

We captured 27 019 invertebrates over the three sampling dates at the 13 sites. We discarded data for sentinel preys in 17 instances, due to animal damage or signs of predation by small mammals, resulting in a dataset of 100 observations. On average, 64% of the sentinel prey disappeared during the 24-hour exposure period. Predation rates increased significantly with the number of Limacidae, Formicidae, carnivorous Carabidae and Chilopoda found in the pitfall traps (Fig. 4A-D). The first two groups of consumers had a greater impact on predation (steeper slopes, higher weighting and higher partial R^2) compared with the last two (Table 1). The other taxa, including members of the Lycosidae, Opiliones and Staphylinidae, were not significant in the averaged model. The predation rates decreased with the number of alternative preys (Table 1, Fig. 4E). These explanatory fixed-effect variables explained 38% of the variation in predation rates.

None of the three diversity metrics (Shannon diversity indices calculated at class/order level, at family level within Araneae and at species level within Carabidae) were related to predation rates. The Shannon diversity of all possible consumers had a negative effect only in the full initial model, including all variables before inference (see Appendix A: Table S4). These explanatory variables were either not retained in any of the best-fitting models, or were not significant (Table 1).

Discussion

Our primary goal was to identify the assemblages of organisms involved in the consumption of two types of sentinel prey, and to assess the validity of sentinel preys to quantify predation on the ground. The comparison of the two types of prey showed that their consumers were very different. Aphids were consumed mainly by Opiliones (33%), Limacidae, Araneae and Carabidae, in decreasing order of importance, while bruchid larvae were consumed primarily by Carabidae (64%), followed by Staphylinidae and Limacidae. Predation rates across different fields were found to increase significantly with the number of carnivorous Carabidae, Limacidae, Formicidae and Chilopoda, while alternative prey had a negative effect on predation rates.

For the evaluation of pest predation, these findings highlight the

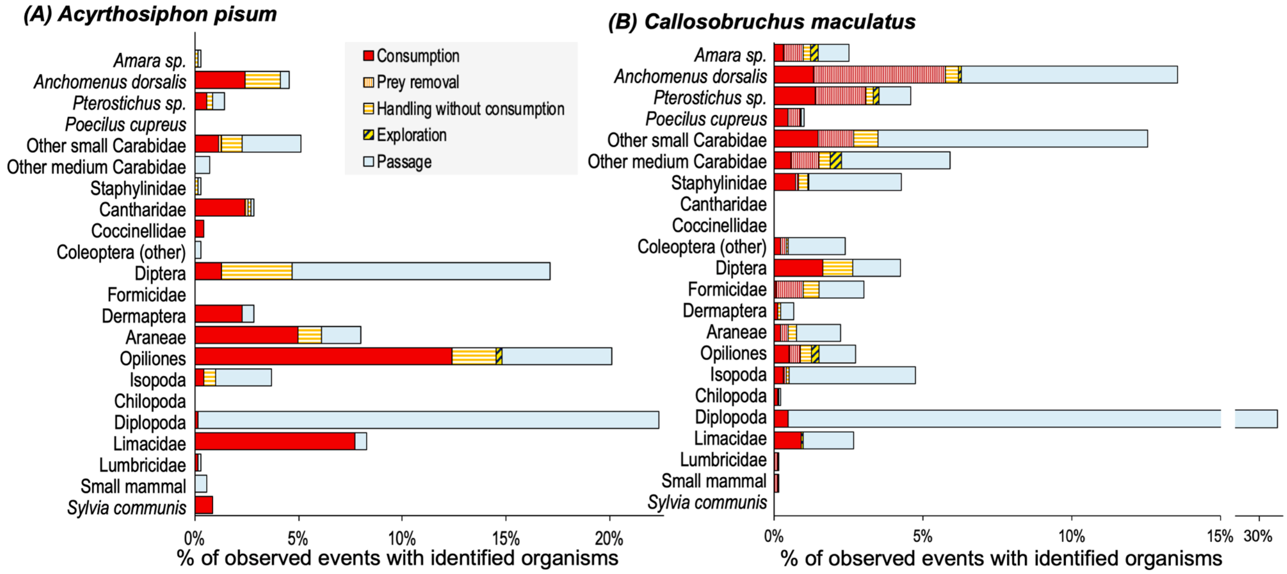

Fig. 3. Percentages of events observed with the camera for each taxon involved in an interaction (or not) with aphids (A, *Acyrthosiphon pisum,* 702 events in total) and bruchids (B, *Callosobruchus maculatus*, 1987 events in total) exposed as sentinel preys. Events are ordered, from left to right, in descending order of intensity, i.e. from predation (red) to lack of interaction (blue).

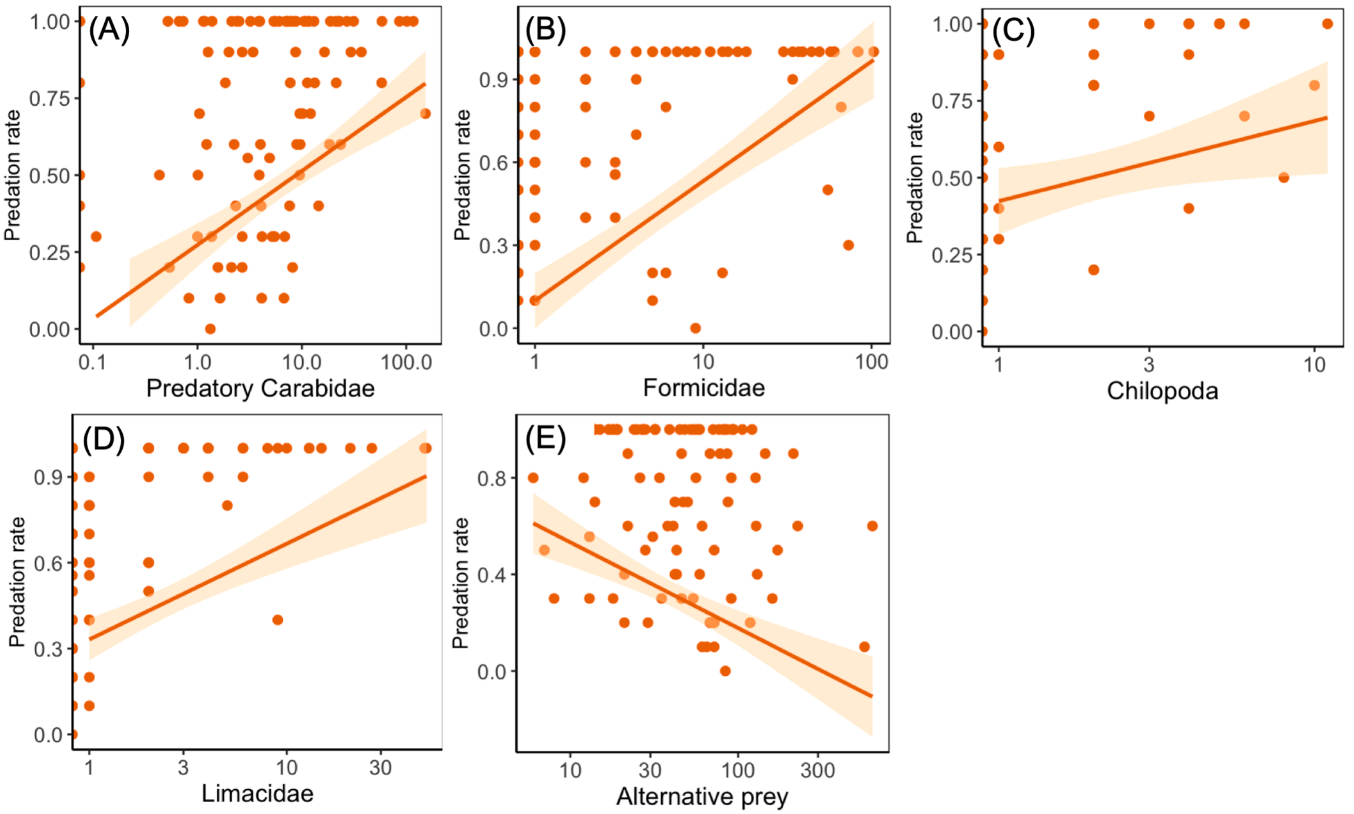

Fig. 4. Relationships between the observed predation rate of sentinel preys and carnivorous Carabidae (A), Formicidae (B), Chilopoda (C), Limacidae (D), potential alternative prey (E), from the averaged regression model in Table 1. The shaded areas represent the 95% confidence intervals.

Table 1
Effect of the composition of arthropod communities on the predation of bruchid sentinel prey. Results of the full averaged model (final model) after multi-model inference. Generalised linear mixed-effect models were used, assuming a binomial error distribution. All explanatory variables were centred and scaled. The variables included in the initial model (see Appendix A: Table S3), which do not appear here, were not selected. The Akaike weight indicates the relative importance of explanatory variables.

Explanatory fixed variables	Effect ± SEM	z-value	*P* (>|z|)	Weight	Partial r^2
Intercept	1.477 ± 0.267	5.424	$< 10^{-4}$		
Limacidae	1.182 ± 0.178	6.572	$< 10^{-4}$	1	0.247
Formicidae	0.937 ± 0.177	5.325	$< 10^{-4}$	1	0.139
Carnivorous Carabidae	0.623 ± 0.189	3.262	$1.11 \cdot 10^{-3}$	1	0.090
Chilopoda	0.467 ± 0.128	2.117	$3.22 \cdot 10^{-4}$	1	0.029
Alternative prey	−0.533 ± 0.115	4.595	$< 10^{-4}$	1	0.045
Staphylinidae	0.175 ± 0.159	1.097	0.27	0.65	0.010
Opiliones	0.091 ± 0.145	0.629	0.53	0.35	0.009
Class/order Shannon diversity	−0.332 ± 0.226	1.466	0.14	0.79	0.031
Marginal R^2 = 0.38					
Conditional R^2 = 0.49					

importance of the choice of organisms exposed as sentinel prey, and of their fixation, as these factors have a determinant effect on the organisms consuming the prey. Samplings were however not always conducted at the same time, which could partly explain the difference observed. Zou et al. (2017) have already observed that dead-immobilised, living-immobilised and living-unattached prey are consumed by different organisms. They found that mobile prey were removed by taxa already known to be predators, whereas the agents removing dead-immobilised prey included omnivores (Tettigoniidae), scavengers (Diptera), known predators (Lycosidae, Carabidae), and even herbivores (Acrididae). In the present study, some of the expected predators of aphids (small, fixed prey), such as carabid beetles, made a very small contribution to predation, whereas slow consumers such as spiders and harvestmen, and opportunistic consumers such as slugs, made a greater contribution. These observations may explain why the densities of carnivorous and omnivorous carabid beetles had no effect on aphid predation in the study by Badenhausser et al. (2020), whereas spiders had a positive effect on predation.

By contrast, bruchids, which were not immobilised, were overwhelmingly consumed or removed by numerous carabid species known to play an important role in the predation of coleopteran pests, such as *Pterostichus melanarius* (Symondson, Glen, Ives, Langdon, & Wiltshire, 2002), *Anchomenus dorsalis* (Frank & Bramböck 2016), *Poecilus cupreus* (Frank & Bramböck, 2016), *Amara* spp. (Schlein & Büchs 2006), and small species belonging probably to Trechinae (Warner et al. 2003). Although the difference was small, the slightly larger size of bruchid larvae (3–4 mm vs 2.5–4 mm for *A. pisum*) might also have contributed to the higher attack rates by carabids (Ball, Woodcock, Potts, & Heard, 2015). Bruchids were also consumed by ants and slugs. This is highly consistent with the consumers of pollen beetles observed at the soil surface in oilseed rape crops (Gagnon 2017) and confirms that the predation of bruchids has similarities with that of beetle pests. However, despite their morphological proximity with pest species, these bruchid larvae are not pest species in studied crops, contrary to aphids. Unlike Gagnon (2017), we also observed predation by rove beetles. This discrepancy may reflect differences in community composition, because this family contains species with highly heterogeneous trophic habits

(Potapov et al. 2022).

The use of cameras made it possible to identify the diversity of animals consuming aphids and bruchid larvae, thus providing important new insight into trophic interactions. Even if interactions mainly involved expected predators, this technique also allowed for original observations and revealed unsuspected interactions. The consumption of prey by dipterans was unexpected, but the quantitative contribution of this group to predation remained small. The contribution of slugs to aphid predation was relatively large in this study. Aphids were glued to the predation card, which enabled slugs to predate on them, but also highlighted a technical limitation related to the immobilisation of these preys. In real-life conditions, we do not know if slugs would be able to catch aphids, especially as they are not often off the ground, and therefore probably make a smaller contribution to aphid control. Even a few earthworms were observed removing aphids. In previous studies, cameras likewise often the role disregarded predators, especially vertebrates, in seed predation (Tschumi et al. 2018) and in banana weevil predation (Tresson et al. 2022), in cereal fields and banana crops, respectively. These observations suggest that there is a need to reconsider the role of arthropods in the consumption of aphids fixed on predation cards, especially in conditions in which slugs are very numerous and climatic conditions are favourable for molluscs. The design of experiment 1 was not balanced (predation was not at the same time in the same fields for both types of prey) due to technical constraints related to the functioning of the camera. This might bias the observations in favour of the predators most present in one type of field, although it is not clear which ones would have been advantaged here. Furthermore, behavioural observations, concerning handling time for example, revealed differences between organisms in the efficiency of prey removal or consumption. We were therefore able to identify efficient consumers, as organisms with high predation rates and low handling times, possibly linked to internal digestion (for glued prey) or the size and strength of the mandibles (Wheater & Evans 1989), facilitating the rapid removal of prey. This rapid removal enabled the consumption of the prey to start almost immediately after the consumer had detected it. The efficient consumers identified here included carabids and harvestmen. Other organisms, such as dipterans and spiders, were much less efficient at consuming prey. Their contribution to the regulation of ground-dwelling insect pests is less obvious. Any generalisation should be made with caution as the observations made are contingent on the conditions and the invertebrate communities to which the sentinel prey were exposed.

After observing that the predation of bruchid prey provided different information from that observed on aphids, we performed a second experiment to evaluate the effect of ground-dwelling invertebrate communities sampled in pitfall traps on the disappearance of bruchid sentinel preys. Taking into account the consumers observed in experiment 1 and their alternative preys, our model effectively accounted for prey disappearance rates. Although slugs were poorly involved in bruchid predation in video observations, slugs and ants made the largest statistical contribution (partial R^2) to the disappearance of sentinel preys in these data.

An increase in sentinel prey predation with carabid activity density has already been reported (Boetzl et al. 2020; Rusch et al. 2016), but this relationship has not been observed in all studies (Badenhauser et al. 2020). The originality here was to reveal the joint and positive effects of carabid beetles, slugs, ants and chilopods on predation. By contrast, we found no significant link with rove beetles and harvestmen, which played only a minor role in prey consumption in experiment 1. These results demonstrate the importance of taking into account all invertebrates in the community contributing to predation, as previously suggested by Zou et al. (2017) for the rice pest *Nilaparvata lugens* (Stål, 1854). Without the input of camera images, we would not have taken slugs into account (as they are generally not expected to be predators), and the statistical model would have been of lower quality to explain predation. However, like Badenhausser et al. (2020), we found no effect of taxonomic diversity on prey loss. Often, at a given site, predation can be driven by a single highly efficient taxon (Frank et al. 2007) and might explain the result observed here.

Cameras provide the considerable advantage of making it possible to identify consumers with certainty, and this is a major step forward in the elucidation of trophic interactions (Birkhofer et al. 2017). However, the level of identification of consumers remains coarse (often only to family or genus level), especially for small organisms. The trapping of organisms remains a useful approach for characterising the local species pool. In our case, the insufficient resolution of the camera precluded the identification of millimetre-sized organisms. This limitation could easily be overcome by using more recent equipment with a higher resolution. Trophic interactions can also be characterised through DNA sequencing of the predator's gut content, with a high taxonomic resolution (Paula et al. 2016), but this method is predator-centred. It is moreover not quantitative and does not allow the estimation of predation rates (Birkhofer et al. 2017).

In previous literature studies, the sentinel preys were often wounded during attachment, which may have decreased or increased their attractiveness to consumers (Zou et al. 2017). This bias was limited here by the use of bruchid larvae, which were able to wriggle a little but not to move out of the camera's field of view. The use of live uninjured bruchid larvae to infer predation of coleopteran pests, to which they are morphologically very close, potentially better enable to select organisms capable of predation rather than scavengers or other consumers using odour cues. However, fixed sentinel prey may cause us to overestimate the diversity of potential consumers by increasing the access of opportunistic consumers to the preys presented, which cannot defend themselves or escape (Birkhofer et al. 2017; Greenop et al. 2019). Live observations or video surveillance of predation on naturally occurring prey would be more realistic but this requires a significant observation time (in the field or for viewing video) to detect a sufficient number of observations.

Conclusion

Sentinel preys are a very useful tool to assess natural pest control, but it is important to check their relevance by identifying the predators in the field. It is not sufficient to work only with putative roles or trophic groups that are too broad. We observed that aphids glued to predation cards attracted inefficient consumers, and even scavengers, and only a few carabid beetles. Unattached bruchid larvae were consumed largely by carabid beetles, and secondarily by rove beetles, ants and chilopods.

These observations improve the choice of taxa to be taken into consideration when trying to predict the outcome of natural pest control. We found that the activity-density of ants, slugs, carabid beetles and chilopods was positively associated with the disappearance of bruchid larvae as the sentinel prey, with a negative effect of alternative prey. With these advances, the pest control service available in different cropping systems could be estimated based on knowledge of the communities present and the functional traits of the organisms concerned.

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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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.07.002.

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