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RESEARCH ARTICLE

Variation in parasitoid attraction to herbivore-infested plants and alternative host plant cover mediate tritrophic interactions at the landscape scale

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Abstract

Context Tritrophic interactions may be affected by local factors and the broader landscape context. At small spatial scales, carnivorous enemies of herbivorous insects use herbivore-induced plant volatiles (HIPVs) to find herbivores, but it is unknown whether variation in plant attractiveness due to differential HIPV emission can enhance recruitment of carnivores from the wider landscape.

Objectives We studied whether parasitism of caterpillars of the butterfly *Pieris brassicae* on white cabbage was influenced by landscape composition and cover with brassicaceous species that provide hosts for parasitoids of *P. brassicae* in 19 landscapes in the Netherlands. We also investigated whether differential attraction of parasitoids to herbivore-infested plants affected parasitism of *P. brassicae* caterpillars by using different accessions as proxies for HIPV emission.

Results The cabbage accession that is highly attractive to parasitic wasps recruited more wasps than a less attractive accession, but only when parasitism rates were high. Parasitism rate as proxy of wasp recruitment correlated positively with the cover of brassicaceous plants and area of arable land, suggesting that these habitats support hosts for the wasps and their population growth. In contrast, forest area was negatively associated with parasitism rates.

Conclusions Our study shows that the degree of attractiveness of plants to parasitoids, which is probably mediated by HIPVs, can be a useful predictor of parasitism, but needs to be considered within the landscape context. To understand the strength of tritrophic interactions it is crucial to consider local-scale processes driven by plant-trait variation in combination with landscape-scale processes that determine carnivore abundance.

Keywords Parasitoid · Parasitism · HIPV · Spatial ecology · Animal behaviour · Insect–plant interactions · Plant odours · Host location · Landscape ecology · Spatial scales

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Introduction

Species abundance and trophic interactions can be influenced by processes that extend beyond the local scale of a single patch or habitat (Thies et al. 2003; Tscharntke and Brandl 2004). For example, host-parasitic wasp dynamics can be influenced by characteristics of the landscape in which these interactions take place (Cronin and Reeve 2005). Parasitic wasps (parasitoids) are important natural enemies of pest insects in agriculture, but rely on resources, such as floral resources, alternative hosts or overwintering sites, that may be scattered across the landscape (Schellhorn et al. 2014). There is a mature body of studies that focus on host-parasitoid dynamics in agricultural landscapes (Cronin and Reeve 2005; Chaplin-Kramer et al. 2011; Karp et al. 2018; Dainese et al. 2019). These studies indicate that parasitoid abundance and biological control of pest populations in agro-ecosystems are influenced by a wide range of landscape features, such as crop/non-crop area (Chaplin-Kramer et al. 2011), configuration (Martin et al. 2019) and landscape management (Holland et al. 2016).

In studies at the landscape scale, land cover in different land use classes is often used to explain variation in parasitoid abundance and diversity. For example, parasitism rates can be positively associated with non-crop area such as forests and non-woody semi-natural habitats (Thies et al. 2003; Costamagna et al. 2004; Bianchi et al. 2008), and arable land area can be negatively associated with parasitism rates in agricultural fields (Chaplin-Kramer et al. 2011; Poveda et al. 2012). However, land use classes may not be a meaningful predictor of parasitoid abundance when they do not capture the function of the habitats, for instance in terms of resource distribution for parasitoids and their hosts (Tscharntke et al. 2016; Karp et al. 2018). In these cases a functional land cover approach may be advantageous and contribute to a more mechanistic classification of the habitats in terms of the life-support functions they provide (Fahrig et al. 2010; Bianchi et al. 2012). For example, a metric capturing the abundance of wild plants that support host plants for the hosts of parasitoids might be a better predictor for parasitoid abundance than a general land use class such as "non-crop habitat" that may comprise a wide range of habitats with varying suitability for the parasitoid species (Crist et al. 2006; Isaacs et al. 2008). Especially for specialist parasitoids with a low dispersal capacity, the presence of plant patches with hosts may be important for the colonization of new habitat patches (Elzinga et al. 2007) to secure population viability and to determine the strength of trophic interactions.

There has been limited attention to the ways in which local-scale ecological processes interact with processes at the landscape scale to explain arthropod movement and their redistribution (Kremen 2005; Schellhorn et al. 2014). Population redistribution processes can be understood in terms of patch leaving, interpatch movement and patch finding behaviour. These processes can be influenced by many factors, including habitat characteristics, motion and navigation capacity, perceptual range and environmental conditions (Schellhorn et al. 2014). Parasitoids use herbivore-induced plant volatiles (HIPVs) as cues to find their hosts (Vet and Dicke 1992; Hare 2011). Herbivore-induced plant volatiles are emitted upon damage by herbivores and spread through space, where—together with volatiles from other plants—they may form a spatially heterogeneous volatile mosaic that parasitoids use to locate hosts (Aartsma et al. 2017). However, little is known about the spatial range at which HIPVs influence parasitoid foraging behaviour, especially at larger scales such as the landscape scale (Aartsma et al. 2017). Furthermore, there can be considerable variation in HIPV emission among plants, which may affect the distance from which they can be perceived (Rasmann et al. 2005; Poelman et al. 2009; Mumm and Dicke 2010; Aartsma et al. 2019). The effect of the attractiveness of herbivore-infested plants on parasitoid recruitment and parasitism of herbivorous insects has, to the best of our knowledge, not been studied at the landscape scale. This leaves the question unanswered how plant varieties with different attractiveness to parasitoids that are associated with differences in HIPV emission pattern moderate parasitism in different landscape settings.

In this study we quantified parasitism rates of *Pieris brassicae* caterpillars on two white cabbage accessions that differ in attractiveness to the parasitoid *Cotesia glomerata* as a result of differences in HIPV blends (Poelman et al. 2009; Aartsma et al. 2019). The assessment was conducted in 19 landscapes that varied in the abundance of brassicaceous species (both wild plants and crops) that might act as a source of parasitoids. We hypothesized that Brassicaceae cover is a meaningful predictor of parasitism rates of *P. brassicae* because Brassicaceae are likely to support parasitoid populations by providing herbivore hosts. We also expected that a plant accession, which is more attractive to parasitoids has higher parasitism rates than a less attractive accession, independent of landscape composition. Finally, we hypothesized that the area of arable land and intensively managed pastures is negatively associated with parasitism rates on the premise that these do not fulfil resource requirements of *C. glomerata*, and that the area of forest and non-woody semi-natural area are positively associated with parasitism rates, on the premise that wild Brassicaceae are important sources of *C. glomerata* and would occur more in such non-crop habitats.

Materials and methods

Plants and insects

Seeds of white cabbage *(Brassica oleracea* var *alba*) accessions Badger Shipper and Christmas Drumhead were obtained from the Centre for Genetic Resources (CGN-Wageningen, the Netherlands). In previous work, the accession Christmas Drumhead was found to be more attractive to the parasitoid *C. glomerata* than Badger Shipper, both under laboratory and field conditions (Poelman et al. 2009; Aartsma et al. 2019). Plants were grown in peat soil in a greenhouse at Unifarm, Wageningen (L16:D8, 18–26 °C and 40–70% RH). Potted plants of six weeks old were used in the experiment.

Pieris brassicae caterpillars were reared in a greenhouse compartment (20–22 °C and 50–70% RH) on Brussels sprouts plants and first (L1) and second instar (L2) caterpillars were used in the experiment.

Landscape selection

We selected 19 landscapes in the vicinity of Wageningen, the Netherlands (Fig. 1). Landscapes were selected on the basis of the expected cover of brassicaceous plants in the area. The landscapes included a variety of land use types to reflect variation in landscape composition that is typical of the area (arable land, pastures, forest, and non-woody semi-natural areas). In the case of arable land, we selected organically managed fields to minimize interference from pesticides. The minimum distance between the centres of two landscapes was at least 2 km (Fig. 1).

Field experiment

To examine parasitism rates of *P. brassicae* caterpillars on cabbage plants of the accessions Badger Shipper and Christmas Drumhead, we performed a series of field experiments from May–August 2016. Badger Shipper and Christmas Drumhead were used as proxies for weak and strong attractions as mediated by HIPV emission, respectively. In each of the 19 locations, we placed potted cabbage plants near the centre of the landscape. The plants were placed in two small patches of four potted plants, one patch with the accession Badger Shipper and the other with the accession Christmas Drumhead. Both patches were positioned 25 m from the centre of the landscape and there was 50 m between the two patches (Fig. 2a). The four plants were arranged in a square, with leaves touching. The two patches in each landscape were placed in a similar grassy background vegetation. The plants were each inoculated with ten *P. brassicae* caterpillars per plant (40 in total in the patch) and were surrounded by a metal wire fence to prevent damage by vertebrate herbivores. The study was conducted without release of parasitoids, so that parasitoids had to be recruited from the surrounding landscape.

Four days after placing the plants in the landscape, the plants (and the remaining caterpillars) were recollected. The plants were placed individually in labelled plastic bags and stored at 4 °C. The caterpillars were dissected to assess parasitism, and the parasitoid species were identified by the shape and number of eggs using a binocular microscope. In five cases, no caterpillars were recollected from a patch due to excessive slug damage.

The experiment was replicated five times over the season, in weeks 20, 22, 27, 29 and 34 of 2016. Between replicates the location of the two accessions in each landscape was swapped to minimize local vegetation background effects, but locations of the patches remained the same over the season. Placement of the plants and recollection four days later was conducted in two days (nine or ten locations per day).

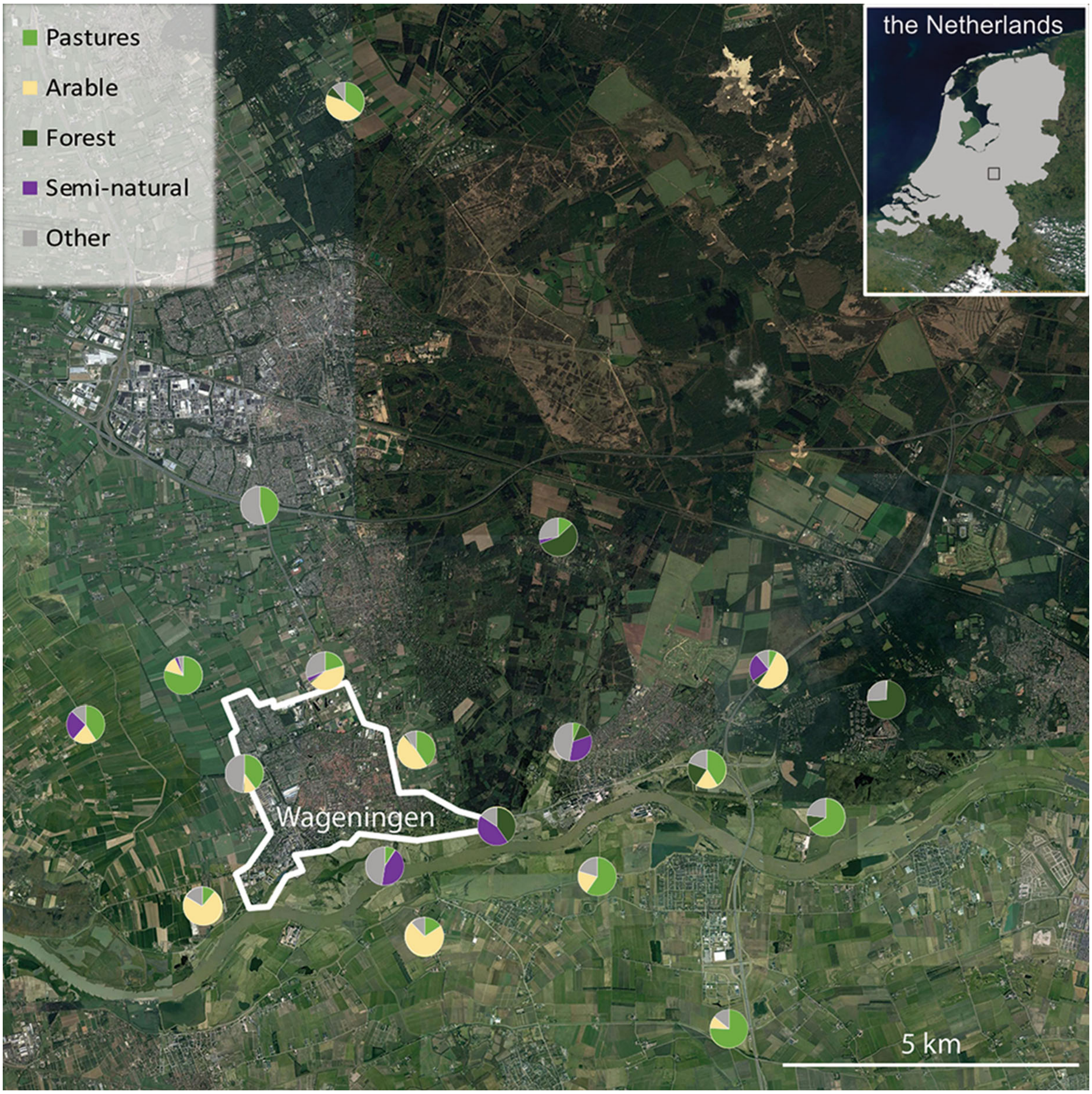

Fig. 1 Locations of the 19 landscapes around Wageningen, the Netherlands (white outline). Pies show the composition of the landscape at 300 m radius around the centre of each landscape. The satellite image was obtained from Google Earth Pro

Quantification of landscape variables

Land use data were extracted from the TOP10NL database (PDOK 2016). The vector-based TOP10NL database was used in ArcMap 10.4.1 ©ESRI to assess the area of arable land, pasture, forest and non-woody semi-natural habitat within circles of 100, 200, 300 and 1000 m radius around the centre of each landscape. The map information from TOP10NL was checked by ground-truthing and adjusted when needed in June 2016.

Brassicaceous plant cover was used as a functional cover type associated with the abundance of hosts of parasitoids and hence for parasitoid reproductive potential. Brassicaceous plant cover was assessed in a radius of 300 m around the centre of each landscape between week 24 and 27 of 2016, which coincides with the flowering time of many brassicaceous

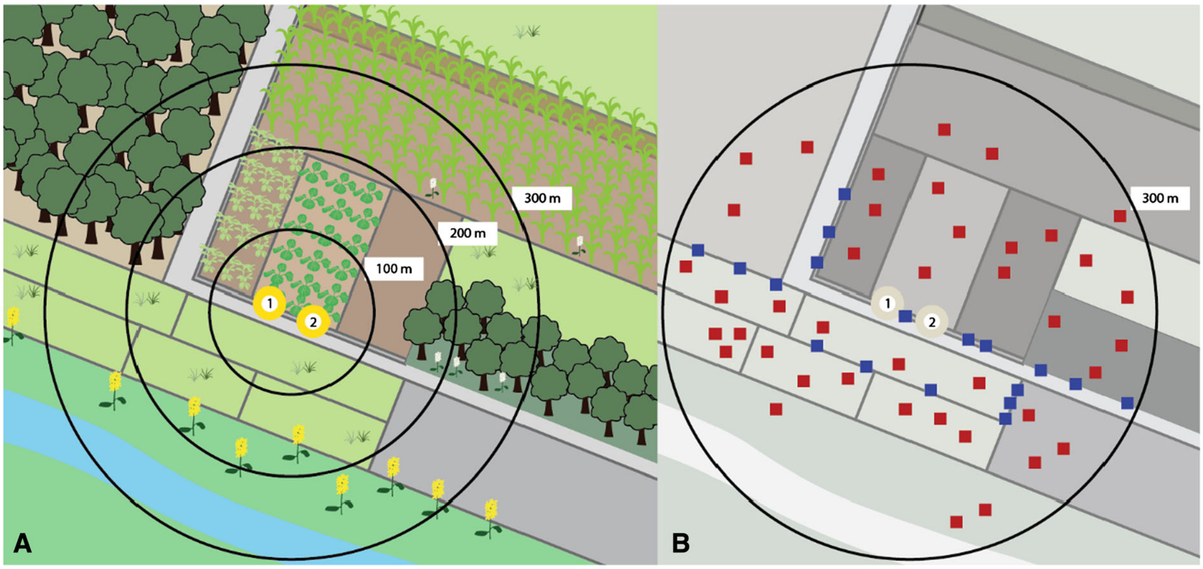

Fig. 2 **a** Hypothetical landscape with the location of the experimental cabbage patches (white circles with yellow border, location 1 and 2 for two cabbage accessions differing in HIPV profile) and the 100 m, 200 m and 300 m radius circles surrounding the patches (1000 m circle not shown). **b** The landscape was subdivided into different elements and brassicaceous plant cover was assessed in each element by three quadrant observations in the interior (red squares) and three in the border (blue squares)

species. The brassicaceous plant cover, including brassicaceous crops and wild plants, was assessed in each landscape element (e.g. arable field, pasture, forest patch) by randomly selecting three locations in the interior and three at the border of the element (directly at the interface of the adjoining element), and estimating the percentage cover of brassicaceous plants in a 1 m^2 quadrat (Fig. 2). Edges and interiors were sampled separately because these tended to hold a different brassicaceous plant cover (Table 1).

Recorded Brassicaceae cover data from quadrats were converted to Brassicaceae cover in m^2 for each landscape element by multiplying the mean brassicaceous plant cover per element section (border or interior) with the area (m^2) of each element section. For borders we multiplied the length of the border with a width of the quadrant (1 m) to obtain the area of the border. Brassicaceae covers for all elements were summed to obtain Brassicaceae cover estimates in 100, 200 and 300 m radius landscape sectors. For the analysis, data were converted to proportions of the respective landscape sector area.

Data analysis

To investigate whether cabbage accession and landscape variables affect parasitism rates in patches across landscapes, data on parasitism rates were analysed using a generalized linear mixed model with logit link. Parasitism rates were calculated by dividing the number of parasitized caterpillars by the total number of recollected caterpillars from the four plants in each patch. Parasitism rates were analysed as a binomially distributed response variable and we did not discriminate between different parasitoid species in the analysis.

We first constructed models using only structural landscape variables, i.e. proportion of arable land (including cabbage fields), pasture, forest, and non-woody semi-natural habitat, and accession (Christmas Drumhead vs. Badger Shipper) as fixed factors. Landscape, the location of the patch within a landscape (on which the accessions were switched between trials), and the five replications in time were included as random factors, whereby patch location and the temporal replicates were nested within the landscape. We used the Akaike Information Criterion, corrected for the number of data (AICc), to determine the model structure for the random effects (Zuur et al. 2009). We

Table 1 Overview of descriptive statistics of brassicaceous plant cover in landscape elements in 300 m landscape circles in 19 landscapes

Land use type	Area (ha)	N	N Brassicaceae	Cover interior (proportion)	Cover border (proportion)	Cover combined (proportion)
Pastures	212.9	138	3	$4.8 \times 10^{-5} \pm 4.8 \times 10^{-5}$	$4.0 \times 10^{-4} \pm 6.0 \times 10^{-5}$	$6.3 \times 10^{-5} \pm 6.0 \times 10^{-5}$
Arable land						
Total	120.6	73	21	0.071 ± 0.023	0.067 ± 0.022	0.071 ± 0.023
Maize	43.9	20	1	0.012 ± 0.012	0.007 ± 0.007	0.012 ± 0.012
Wheat	37.1	16	1	0	0.003 ± 0.003	$5.3 \times 10^{-6} \pm 5.3 \times 10^{-6}$
Brassicaceae	11.5	10	10	0.44 ± 0.119	0.412 ± 0.126	0.438 ± 0.12
Mixed crops*	8.4	7	5	0.055 ± 0.018	0.055 ± 0.018	0.055 ± 0.018
Carrots	7.3	1	0	0	0	0
Fallow	5.0	8	1	0.013 ± 0.013	0.013 ± 0.013	0.013 ± 0.013
Potatoes	3.4	6	1	0	0.003 ± 0.003	$8.6 \times 10^{-5} \pm 8.6 \times 10^{-5}$
Onions	1.6	1	0	0	0	0
Lettuce	1.5	1	0	0	0	0
Flower strip	1.0	2	2	0.205 ± 0.195	0.205 ± 0.195	0.205 ± 0.195
Forest	66.4	57	7	$5.8 \times 10^{-5} \pm 5.8 \times 10^{-5}$	0.007 ± 0.003	2.2 × 10–4 $\pm 1.19 \times 10^{-4}$
Non-woody semi-natural	9.5	7	2	0.007 ± 0.007	0.057 ± 0.056	0.007 ± 0.007
Other	70.5	53	11	0.02 ± 0.007	0.023 ± 0.009	0.02 ± 0.007

Columns represent total area (ha), number of examined elements (N), number of elements with brassicaceous plant species (N Brassicaceae), average proportion Brassicaceae cover ± SEM (dimensionless) in element interiors (Cover interior), average proportion Brassicaceae cover ± SEM (dimensionless) in element borders (Cover border) and the overall area-weighted proportion of interior and border combined (Cover combined)

The land use type 'Other' includes road verges, urban areas and some miscellaneous elements occurring only once in the 19 landscapes

*Mixed crops consisted of vegetable gardens or small-scale strip cropping

determined which fixed factors were most important for the model by using the 'dredge' model selection procedure, which calculates all possible factor combinations and sorts the models according to the value of AICc. For the selected models with the lowest AICc values, we also calculated the more conservative Bayesian Information Criterion (BIC). The marginal R^2 was calculated to evaluate the explained variance of the fixed effects (Nakagawa and Schielzeth 2012). This analysis was conducted separately for spatial scales of 100 m, 200 m, 300 m and 1000 m radius.

In a second analysis, we used a functional landscape variable, i.e. the proportion brassicaceous plant cover (including cabbage fields and wild brassicaceous plants), which captures information on the alternative host plant cover in the landscape, and accession (treatment) as fixed factors. Proportion Brassicaceae cover was double square-root transformed to meet normality criteria. The same structure for random effects was used as in the analysis using land use classes. We checked for spatial autocorrelation in model fit using Moran's I statistics to test for the presence of a spatial pattern in model residuals and no significant spatial autocorrelation was observed.

All analyses were performed in R and the packages lme4, MuMIn, sp and ape (Bates et al. 2015; Pebesma 2018; Paradis and Schliep 2018; Barton 2019). Plots were made in ggplot2 and model output tables with the package stargazer (Wickham 2009; Hlavac 2018). The spatial autocorrelation analysis was conducted using the R packages sp and ape.

Results

The most common brassicaceous species in the landscapes were cultivated *Brassica oleracea*, and the wild plants *Brassica nigra*, *Brassica rapa*, *Alliaria petiolata*, *Raphanus* spp., *Capsella bursa-pastoris* and *Sinapis* spp. Across the five replicates of the experiment, we recovered 3302 out of 7400 caterpillars (44% ± 21.9% per patch; mean ± SD) that were placed on plant patches in the 19 landscapes. The overall average parasitism rate of the recovered caterpillars was 20 ± 35% (mean ± SD), varying from 6.6% to 34% between replicates. Overall parasitism rates in weeks 20, 22, 27, 29 and 34 were 6.6, 17.4, 32.6, 13.5 and 34.2%, respectively. *Cotesia glomerata* was responsible for 98% of the parasitism events, while *Cotesia rubecula* and tachinid flies were responsible for the remaining 2%. The tachinid fly larvae were always found in caterpillars that were also parasitized by *C. glomerata*.

The first analysis, considering structural land-use variables, indicated that parasitism rates were significantly negatively associated with forest at scales of 100 m, 200 m and 300 m, but not at 1000 m (Fig. 3a, Table 2). Parasitism rates were also negatively related to non-woody semi-natural habitat, but this was only significant at 200 m. There was a significant interaction between arable land area and cabbage accession at all scales, indicating that parasitism rates were higher on Christmas Drumhead than on Badger Shipper when the area of arable land was high, whereas there was no significant difference between the accessions when the area of arable land was small (Fig. 3b, Table 2). While the interaction between accession and area of arable land was also significant at a scale of 1 km, parasitism rates were not strongly influenced by the area of arable land and the largest differences between parasitism rates on the two cultivars were found in landscapes with a relatively low proportion of arable land (Fig. S1, Table 2).

In the second analysis with the functional variable brassicaceous plant cover, parasitism rates were significantly influenced by brassicaceous plant cover, cabbage accession and their interaction (Table 3). In landscapes where cover by Brassicaceae was low, parasitism rates were low on both accessions. Parasitism rates increased with higher brassicaceous plant cover, and parasitism rates were higher on the attractive accession Christmas Drumhead than on the less attractive Badger Shipper (Table 3, Fig. 4).

There was a strong positive correlation between area of arable land and Brassicaceae cover ($r = 0.79$, $p < 0.001$). When comparing the first analysis with the second, the analysis with land use variables had a lower AICc than the model with the functional variable Brassicaceae cover at the 100 m scale, but at 200 m and 300 m AICc's were similar (Fig. S2). Using the more conservative Bayesian Information Criterion, the analysis with land use variables had a lower BIC than the model with the functional variable Brassicaceae cover at the 100 m scale, but higher BIC values at 200 m and 300 m, indicating that the model with the functional variable Brassicaceae cover received more support from the data than the model with land use variables at 200 m and 300 m (Fig. S2). Marginal R^2 for the land-use and Brassicaceae-cover models were similar for 100 m and 200 m, while the land use models contain more variables, but was higher for the model with the functional Brassicaceae cover model than the model with land use variables for 300 m (Fig. S2).

Discussion

Our data show that parasitism rates of *P. brassicae* caterpillars are associated with local and landscape scale factors. We report three key findings. First, parasitism rates of caterpillars feeding on the more attractive accession, Christmas Drumhead, were higher than on the less attractive accession, Badger Shipper, but this was only the case in landscapes with relatively high parasitism rates. Second, parasitism rates were positively associated with the cover of brassicaceous plants and the area of arable land, and negatively associated with forest and non-woody semi-natural habitat. Third, the functional landscape variable brassicaceous-plant cover was strongly and positively correlated with the structural landscape variable proportion of arable land.

Parasitism rates were influenced by the relative attractiveness of the cabbage accession, but only when parasitism rates were relatively high (> 15%; Figs. 3 and 4). This confirms findings of Poelman et al. (2009) who showed that the accession Christmas Drumhead is more attractive than Badger Shipper in laboratory and small-scale field experiments. Here we show that the

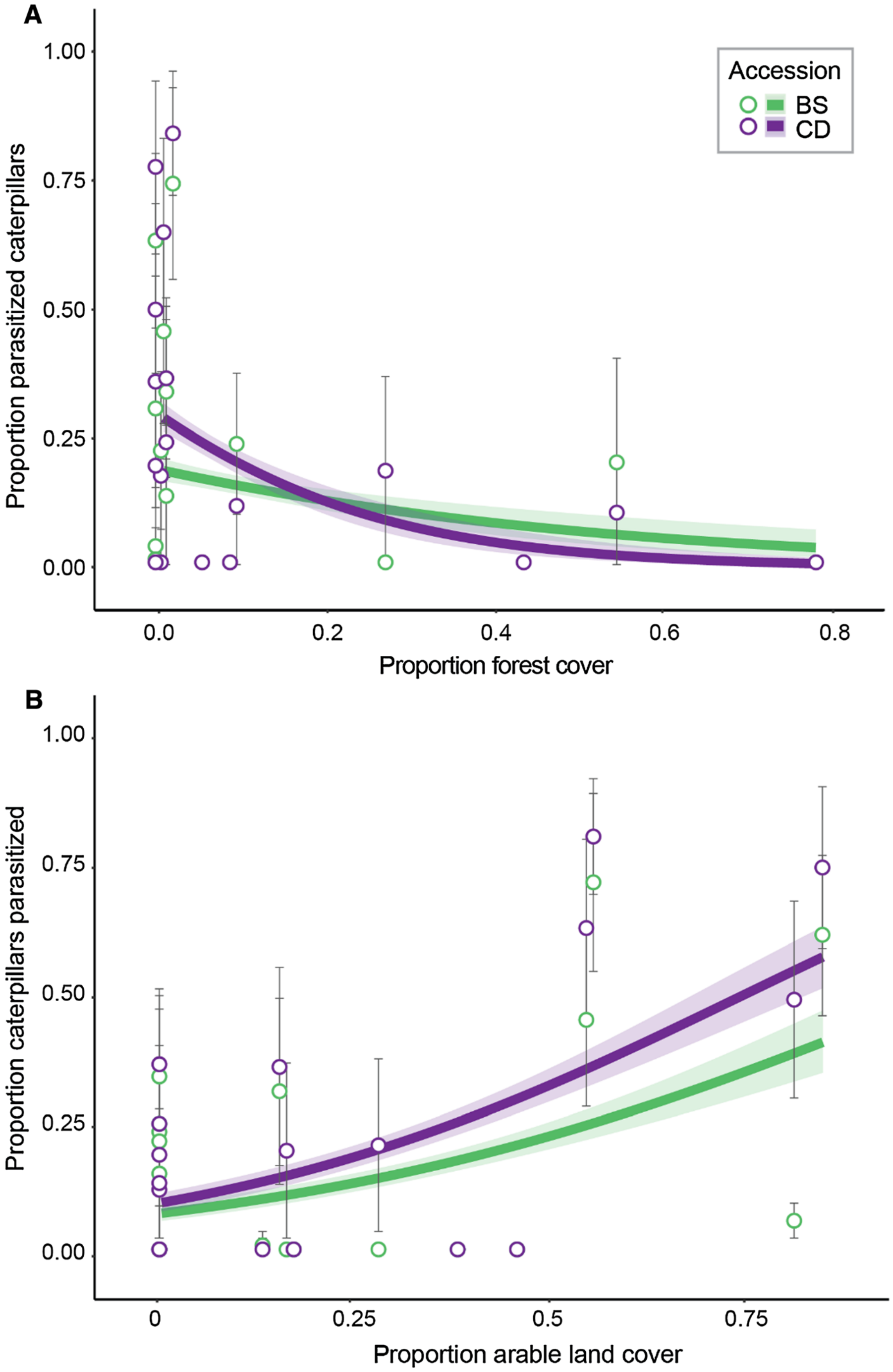

Fig. 3 Parasitism rates on the white cabbage accessions Badger Shipper (BS; green) and Christmas Drumhead (CD; purple) in landscapes varying in proportion of forest (**a**) and proportion of arable land (**b**) in a 200 m radius surrounding the patches. Open circle markers show averages across five temporal replicates and error bars reflect SEM

attractiveness of accessions interacts with landscape variables to mediate parasitism rates at the landscape scale. Since parasitism rates were positively associated with Brassicaceae cover and proportion of arable land, this suggests that landscapes with a high Brassicaceae cover and proportion of arable land

Table 2 Overview of explanatory variables and estimated coefficients of the selected most parsimonious models for parasitism rate (number of parasitized caterpillars/total number of caterpillars recovered from patch) at four different spatial scales, when using structural land use variables (proportion) and accession of the focal plants (more or less attractive via HIPV emission) as explanatory variables

Fixed effect ↓	Circle radius →	Response variable: parasitized caterpillars/total recollected caterpillars			
		100 m	200 m	300 m	1000 m
Accession	Badger shipper	–	–	–	–
	Christmas drumhead	0.359 (0.324)	0.236 (0.335)	− 0.030 (0.376)	− 0.693 (0.536)
Arable		− 3.122 (4.399)	− 3.490 (4.609)	1.516 (4.523)	-14.905 (10.775)
Forest		**− 17.537*** (7.446)	**− 27.640**** (10.027)	**− 15.722*** (7.814)	-10.152 (6.915)
Pastures		− 11.351 (7.611)	− 14.969 (8.067)	/	/
Semi-natural		− 14.920 (7.805)	**− 22.643*** (10.085)	-9.054 (7.132)	-24.500 (17.822)
Accession × Arable		**2.976***** (0.618)	**3.532***** (0.705)	**4.505***** (0.901)	**18.090***** (4.031)
Constant		1.713 (5.242)	3.275 (5.184)	**− 5.780*** (1.693)**	**− 4.610* (2.075)**
AICc		604.4	604.4	608.6	612.4
BIC		671.6	671.7	673.2	677.0

A slash symbol (/) indicates that this variable was not selected at this spatial scale. The reference treatment for accession was Badger Shipper. Bold numbers indicate significant differences

*p < 0.05; **p < 0.01; ***p < 0.001

Table 3 Overview of explanatory variables and estimated coefficients of the selected most parsimonious models for parasitism rate (number of parasitized caterpillars/total number of caterpillars recovered from patch) at four different spatial scales when using brassicaceous plant cover (proportion) and accession of the focal plants (Christmas Drumhead and Badger Shipper being more and less attractive for parasitoids, respectively) as explanatory variables

Fixed effect ↓	Circle radius →	Response variable: parasitized caterpillars/total recollected caterpillars		
		100 m	200 m	300 m
Accession	Badger Shipper	–	**–**	**–**
	Christmas Drumhead	− 0.787 (0.674)	**− 1.226* (0.599)**	**− 1.201* (0.604)**
Transformed Brassicaceae cover		**15.858** (5.605)**	**17.982** (6.251)**	**20.133** (6.968)**
Brassicaceae cover × Christmas Drumhead		**5.618*** (1.596)**	**7.266*** (1.548)**	**7.910*** (1.721)**
Constant		**− 10.129*** (1.472)**	**− 10.225*** (1.518)**	**− 10.144*** (1.494)**
AICc		614.2	605.3	605.2
BIC		673.4	663.6	664.5

*p < 0.05; **p < 0.01; ***p < 0.001

supported higher parasitoid densities than landscapes with low Brassicaceae cover and proportion of arable land. There was no difference between the cabbage accessions when parasitism rates were low. This could be a consequence of the low numbers per se, which generally tends to make it difficult to find significant effects.

Higher cover of food plants for caterpillar hosts has earlier been linked to higher parasitoid densities, usually indirectly via host abundance (Costamagna et al. 2004; Petermann et al. 2010). Our results suggest that the difference in parasitism rates on Christmas Drumhead and Badger Shipper is probably not only due to choice behaviour associated with a preference for more attractive plants (i.e. preference for one accession when perceiving the odours of two accessions), but also to the parasitoid's ability to locate the plant via HIPVs from longer distances. Previously, we

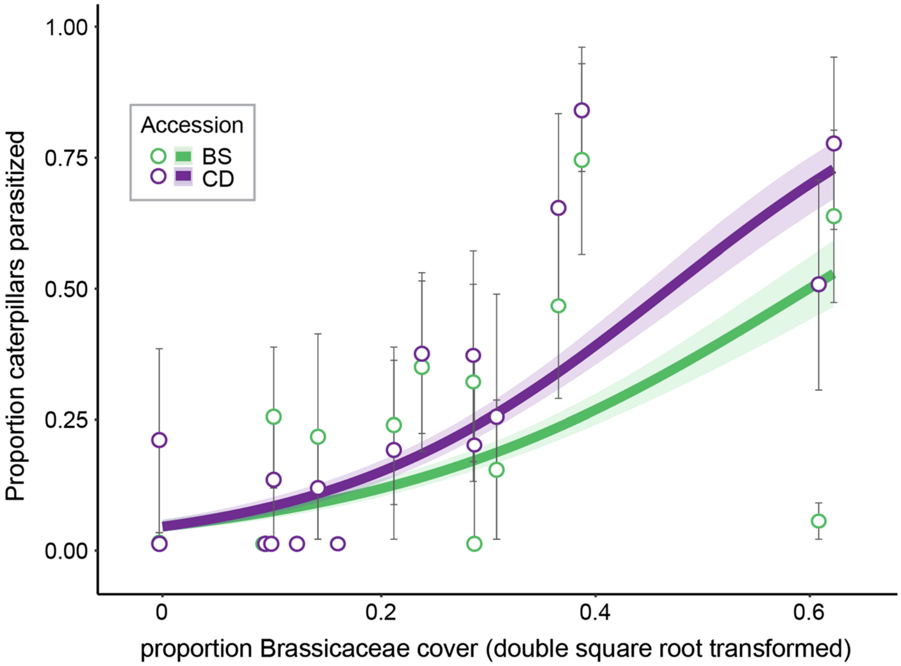

Fig. 4 Relationship between parasitism rates on the white cabbage accessions Badger Shipper (BS; green) and Christmas Drumhead (CD; purple) and brassicaceous plant cover within a radius of 200 m from the experimental patches. Open circle markers show averages across five temporal replicates and error bars reflect SEM. The proportion Brassicaceae cover was calculated by multiplying the proportion cover with the area of the element for all elements in the landscape and summing the areas of Brassicaceae cover, and dividing these by total area of the 200 m landscape circle. Brassicaceous plant cover was transformed as $y = \sqrt[4]{x}$ where x is the proportion cover in the landscape sector. Double square root transformed proportion Brassicaceae cover of 0, 0.2, 0.4 and 0.6 correspond with 0, 0.0016, 0.026 and 0.13 on a linear scale

found that the attractive accession Christmas Drumhead attracted parasitoids from a distance of 20 m in the field whereas the less attractive accession Badger Shipper showed such attraction at 10 m distance, but not at 20 m (Aartsma et al. 2019). Larger distance of attraction would result in a larger ‘parasitoid catchment area’ and may therefore explain higher parasitism rates on the attractive accession. We are not aware of other landscape scale studies on parasitism that accounted for a possible role of attractiveness of host plants associated with the release of HIPVs (Schellhorn et al. 2014; Aartsma et al. 2017). The current results are therefore unique, suggesting that plant traits associated with the attraction of parasitoids have consequences for natural biological control in a landscape context.

Parasitism rates in *P. brassicae* caterpillars were positively associated with the proportion arable land, which was most likely driven by cabbage crops. Positive associations between natural enemy abundance and arable land have earlier been reported for parasitoids of cereal aphids (Vollhardt et al. 2008), and ladybeetles, which were positively associated with maize (Zhou et al. 2014). However, there are also reports of negative associations between natural enemy abundance and arable land (Bianchi et al. 2008; Poveda et al. 2012; Rusch et al. 2016). Furthermore, the negative association between parasitism rates and forest and non-woody semi-natural habitats in our study contrasts with previous work that reported positive associations (Bianchi et al. 2008; González et al. 2017). These contrasting findings indicate that species responses to landscape composition are species specific (see also Menalled et al. 2003; Karp et al. 2018), which may be driven by complex interactions between the ecological requirements and dispersal capacity of the species, and the life-support function provided by the landscape.

In our study system of *P. brassicae* and their dominant parasitoid species, *C. glomerata*, the life history of the parasitoid species might help explain variation in parasitism in different landscape settings. Brassicaceae cover in forests was rather low in our study area and consisted mostly of the species *Allaria petiolata*. While the main hosts of *C. glomerata*, *P. brassicae* and *P. rapae*, can oviposit on and feed from this plant species (Heinen et al. 2016), it may not be their preferred host plant in natural conditions because of their occurrence in shaded habitats (Heinen and Harvey 2019). In contrast, *Pieris* spp. and *C. glomerata* prefer open landscapes with low tree cover where wild Brassicaceae cover is often higher (Heinen and Harvey 2019). Brassicaceae cover was highest in arable land, in particular cabbage fields, which suggests that (organic) arable land can support *P. brassicae* and *P. rapae* populations. Therefore, it is important to not only examine broad-scale effects of non-crop versus crop habitats, but to also take into account ecological habitat requirements of the species under study.

In our study, arable land area was correlated with the functional landscape variable of cover of brassicaceous plants. Cultivated Brassicaceae fields were part of arable land and represent large and highly concentrated patches of host plants as compared to wild Brassicaceae which are scattered in lower density across the landscape. Therefore, locations with the highest Brassicaceae cover also had the most arable land. Because the brassicaceous crops at these locations were organically grown, we do not expect strong negative effects of farm management practices (e.g. synthetic insecticide applications) on parasitoid populations in these locations (Rusch et al. 2010). However, also non-brassicaceous crops may play a role in supporting parasitoid populations as wild brassicaceous plants were regularly encountered in arable fields (Table 1). Disentangling the confounding effects of brassicaceous and non-brassicaceous crops on parasitism rates merits further research and requires the selection of landscapes with uncorrelated areas of brassicaceous and non-brassicaceous crops.

Studies on HIPVs have paid considerable attention to the use of indirect defence via HIPVs or the use of plants which are better at attracting natural enemies to improve biological control in agricultural fields (Dicke et al. 1990; Cortesero et al. 2000; Kaplan 2012; Penaflor and Bento 2013; Stenberg et al. 2015; Turlings and Erb 2018). At the same time, there has been progress in habitat management at the landscape scale to facilitate natural enemy abundance in agricultural fields and create pest-suppressive landscapes (Tscharntke et al. 2007, 2016; Gurr et al. 2017). Our study shows that although the attractiveness of herbivore-infested plants, most likely via HIPVs, can enhance parasitism rates, landscape characteristics such as the area of arable land, forest and host plant cover are also important determinants of parasitism in the field. Therefore, for enhanced attraction of natural enemies through HIPVs in realistic field situations, it is important to consider the landscape context and the life support functions provided by habitats (Holland et al. 2016). This means that the use of plant varieties with enhanced HIPV blends and habitat management practices are both crucial and interdependent when it comes to improving natural biological control in agricultural fields. It is also important to consider which natural enemies are preferred to be attracted to the field as biological control agents. While generalist natural enemies, such as spiders, may be abundant in a variety of crop and semi-natural habitats (Bianchi et al. 2017), and can switch prey when the pest species is temporarily not available, specialist natural enemies may require more specific habitat types, linked to their specific host plant species.

Structural land-use variables, such as the proportion of arable land and semi-natural habitat, are often used to explain the composition of arthropod communities at the landscape level. However, these metrics usually fail to capture the specific ecological prerequisites of particular organisms. Focal plant traits, such as host-plant cover and attractiveness of natural enemies (i.e. HIPV), which can influence the recruitment of natural enemies, may be useful complementary variables to better understand the structure of arthropod communities at the landscape scale. Our study highlights the importance of integrating local scale processes driven by plant-trait variation with landscape scale processes that determine parasitoid abundance in our understanding of the drivers of the strength of tri-trophic interactions and to better understand and manage parasitism as a tool in biological pest control.

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