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RESEARCH ARTICLE

Contrasting effects of host crops and crop diversity on the abundance and parasitism of a specialist herbivore in agricultural landscapes

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Abstract

Context Landscape complexity affects herbivores in agroecosystems, but consequences on pest control services are variable. Carryover effects of landscape composition in previous years on herbivore control may be important, but have been seldom assessed. Understanding landscape complexity effects at different temporal and spatial scales is important to improve sustainable pest control services.

Objectives We examined the effect of agricultural landscape complexity (e.g., the percentage of semi-natural habitats) on cereal leaf beetle (CLB), *Oulema melanopus* L., and its parasitism by *Tetrastichus julis* (Walker).

Methods From 2014 to 2015, we assessed CLB abundance and parasitism in 54 fields along a gradient of landscape complexity (2–70% of semi-natural habitats) in southern Alberta. We used generalized linear models to test the effects of percentage of crops and semi-natural habitats, and landscape and crop diversity on CLB abundance and parasitism at 0.5, 1, 1.5 and 2 km spatial scales.

Results CLB abundance decreased with higher crop diversity at the 0.5 km scale and increased with CLB host crops in the current and previous years at multiple scales, supporting the resource concentration hypothesis. CLB parasitism increased with CLB abundance and in landscapes with increased canola and alfalfa during a year of low CLB abundance. CLB abundance had contrasting associations with semi-natural habitats: positive with woodlands and negative with pastures.

Conclusions Our study suggests that crop diversity reduces the abundance of this specialist pest in agricultural landscapes likely by a dual effect of reducing host crop area and increasing habitats with resources for parasitoids.

Keywords Landscape complexity · Landscape composition · Semi-natural habitat · Resource concentration hypothesis · Natural enemy hypothesis · Carryover effects · *Oulema melanopus* · *Tetrastichus julis*

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Introduction

Landscape complexity has a major effect on the populations of herbivores, natural enemies, and their interactions (Bianchi et al. 2006; Tscharntke et al. 2007; Chaplin-Kramer et al. 2011). Complex landscapes (i.e. with a high percentage of semi-natural habitats) can increase the abundance of natural enemies by providing alternative foods, overwintering sites, and refuge from insecticides, which in turn increase herbivore suppression in agricultural landscapes (Landis et al. 2000; Bianchi et al. 2006). Increased agricultural intensity has resulted in reductions of semi-natural habitats and more disturbances in agricultural landscapes. The resulting landscape simplification has been associated with declines in pest control from natural enemies (Rusch et al. 2016; Grab et al. 2018). However, a meta-analysis by Chaplin-Kramer et al. (2011) found no clear association of landscape complexity with insect herbivore abundance, despite positive associations with natural enemy abundance, predation and parasitism rate. Using data from 31 countries, Karp et al. (2018) also reported inconsistent associations between pest control and semi-natural habitats in the landscape. Furthermore, spatial and temporal crop diversity (Bosem Baillod et al. 2017; Redlich et al. 2018), and individual crops, including alfalfa (Costamagna et al. 2015) and wheat (Samaranayake and Costamagna 2018) have been associated with increased pest control services, suggesting that the role of crops should also be assessed in landscape studies of biological control.

The resource concentration hypothesis (Root 1973) predicts that herbivore abundance will be higher in landscapes dominated by a suitable host crop due to a higher probability of finding and remaining in the host crop patches, resulting in direct impacts of landscape composition on herbivores (Tscharntke et al. 2012; Maisonhaute et al. 2017). Rand et al. (2014) reported a higher infestation of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae) in landscapes dominated by wheat, supporting this theory. In contrast, Schneider et al. (2015) found a lower abundance of rape pollen beetle, *Meligethes* spp. (Coleoptera: Nitidulidae), in agricultural landscapes dominated by oilseed rape crops, suggesting a dilution effect (Tscharntke et al. 2012). A review by Veres et al. (2013) reported no overall trends in the response of herbivores to the proportion of suitable crops in the landscape, and this variability has been related to the host range, biology, and dispersal potential of different herbivore species (Poveda et al. 2012; Rand et al. 2014). Thus, the effects of host crops on herbivores in the landscape cannot be generalized and deserve further study.

Several studies have reported indirect effects of landscape complexity on herbivores mediated by natural enemies (Bianchi et al. 2006; Chaplin-Kramer et al. 2011), supporting the natural enemies hypothesis (Root 1973). Thies et al. (2003) reported positive associations between the proportion of semi-natural area at 1 to 2 km spatial scales and pollen beetle parasitism. Likewise, Grab et al. (2018) found a high rate of tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) (Hemiptera: Miridae) parasitism in strawberry fields within landscapes with a high proportion of semi-natural habitats at the 0.5 km spatial scale. Other studies at similar scales, however, have reported contrasting and variable responses to landscape complexity by parasitoids (e.g., Menalled et al. 2003; Zaller et al. 2009). It appears that increased semi-natural habitats in the landscape are not always associated with higher herbivore parasitism in agroecosystems.

Carryover effects of host crop area in the landscape from previous years may affect the abundance of herbivores and their parasitoids, but have been poorly studied. Bosem Baillod et al. (2017), found decreased cereal aphid densities in landscapes that had a reduction in host crop area in comparison with the previous year. Berger et al. (2018) reported a positive association between the proportion of previous year's oilseed crops and *Lygus rugulipennis* Poppius (Hemiptera: Miridae) abundance. In contrast, studies of pollen beetle parasitism have reported inconsistent associations with the proportion of previous year's oilseed host crops, including positive (Beduschi et al. 2015), neutral (Riggi et al. 2017), and negative (Rusch et al. 2011) associations. These studies suggest that previous year's host crops may be important in explaining herbivore abundance and parasitism rates in agricultural landscapes, but also that the effect of previous year's crop is unclear and deserves more research.

The cereal leaf beetle, *Oulema melanopus* L. (Coleoptera: Chrysomelidae) (CLB), is a globally important cereal specialist pest, causing up to 40% yield losses in North America (Philips et al. 2011). In southern Alberta, CLB produces one generation per year and is active between April and September with oviposition peaking in mid-May (Kher et al. 2011). CLB larvae are present from May to July with a peak in mid-June, and complete four instars on the same cereal plant before dropping to the soil for pupation (Kher et al. 2011). Wheat, barley, and oats are the preferred hosts for CLB, but rye, triticale and corn can also act as secondary hosts (Kher et al. 2016). CLB overwinters as an adult in cereal field border grasses and nearby woodlands (Casagrande et al. 1977). *Tetrastichus julis* (Walker) (Hymenoptera: Eulophidae), a larval parasitoid of CLB, was imported from Europe and established in several counties in Michigan in 1973 (Philips et al. 2011). *Tetrastichus julis* is the most efficient larval parasitoid of CLB, with up to 60% and 33% parasitism reported in Utah and Alberta, respectively (Dosdall et al. 2011). In Alberta, *T. julis* is active from early May to August, and peak parasitism occurs in mid-June (Kher et al. 2011). *Tetrastichus julis* overwinter as larvae inside CLB pupa within cereal fields (Dysart et al. 1973), therefore, landscapes with cereal fields from the previous year can act as sources of this parasitoid. Understanding how landscape complexity influences CLB abundance and its parasitism is important to improve management strategies for CLB.

In this study, we investigated the effects of landscape complexity in the current and previous years on CLB abundance and its parasitism by *T. julis*. First, we tested the association between agricultural landscape complexity, and the abundance of CLB and its parasitism, and predicted that (a) based on the resource concentration hypothesis, CLB abundance would be higher in landscapes with a high percentage of cereals, and (b) according to the natural enemy hypothesis, CLB parasitism would respond positively to the percentage of semi-natural habitats in the landscape. Second, we assessed the association between the percentage of cereal fields in the landscape in the previous year (*T. julis* overwintering sites, and source of CLB overwintering adults), and the abundance and parasitism of CLB in the current year. We predicted that a higher percentage of cereals in landscapes in the previous year would have positive carryover effects on CLB abundance and parasitism. Finally, we assessed the association between abundance of CLB and its parasitism and, given the high specificity of *T. julis* to CLB, we predicted a density-dependent response of *T. julis* to CLB abundance.

Materials and methods

Study sites

During 2014 and 2015, 27 wheat fields were sampled each year, in the vicinity of the towns of Warner, Lethbridge, Taber, and Vauxhall in southern Alberta. Landscapes were selected to represent a gradient of complexity, ranging from 2 to 77% of semi-natural habitats. The distance between these towns was 50 to 90 km, and the minimum distance between wheat fields was 4 km (except in 3 cases in which fields were separated by approximately 1 km). Except in four cases, fields sampled in 2015 did not overlap with those sampled in 2014. The minimum focal wheat field size was 32 ha (representing ~ 50% of the landscape at the 0.5 km scale, range of 32–128 ha); none of the focal fields were treated with insecticide.

CLB abundance and parasitism levels

CLB abundance and parasitism levels were assessed by collecting six sweep-net samples per field at least 50 m from a corner. Three of these samples were collected along a transect 20 m from the border and the other three at 100 m from the field border. Each sample comprised of 50, 180°-sweeps and was stored individually in 25% ethanol until sorting. Wheat fields were sampled during mid-June to coincide with peak CLB larvae and *T. julis* abundance. CLB larvae were counted in each sample, and CLB abundance (CLB per 50 sweeps) was calculated as an average of the six samples per field. To determine percentage parasitism, up to 10 larvae from each sample were randomly selected and dissected under a microscope (10 ×), for a minimum and maximum of 5 and 60 larvae per field, respectively. Percentage parasitism was estimated at 20 and 100 m by averaging the three samples at each distance to test edge effects and averaging all samples in the field to test landscape effects. In 2014, 235 CLB larvae were reared from subsets of 10 random individuals from each field, and only *T. julis* (n = 457) emerged. Thus parasitism assessed by dissections of CLB larvae was attributed to this species as observed in previous studies from this region (Kher et al. 2014; Hervet et al. 2016).

Landscape quantification

We conducted detailed ground surveys of all crops and habitats within four circular sectors (buffers) of 0.5, 1, 1.5 and 2 km radius from the center of the focal field. We identified 26 land cover types and merged them into 12 categories for analysis based on their relative importance as hosts for CLB and their percentage in the landscape (Online Appendix A). Wheat was analyzed as a separate variable, but also merged with barley into the "major hosts" variable in alternative models. Although oat is a preferred host of CLB, it is rarely grown in the study area (present in two out of 54 landscapes) and was therefore merged with corn and rye in the "minor hosts" category (Online Appendix A). All other crops that were not cereals were merged into a non-cereal crop category with the exception of canola and alfalfa in parasitism models; these crops were tested as separate land-cover types due to their potential role in providing nectar to parasitoids (Idris and Grafius 1997). Pasture was the most abundant semi-natural habitat in our study area and was analyzed as a separate variable. Field border grass and fallow field (fields not seeded for one growing season) land cover types were merged into the grassland category. Trees and riparian vegetation were merged into a woodland category. The minimum mapping unit was approximately 6 m^2. Base geo-referenced maps were obtained from the Alberta Soil Information Viewer website (https://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/sag10372). The percentage of different land cover types and landscape complexity metrics, including Simpson's index of habitat and crop diversity, richness, and evenness were estimated using digital maps made in ARC GIS 10 (ArcGIS 2014) and using the Vegan package (Oksanen et al. 2015).

Data analysis

All statistical analyses were performed in R (version 3.3.5, R Development Core Team 2017). Linear mixed effect models with a normal distribution were used to evaluate the effect of distance from the field border (20 vs. 100 m from the field border) on log transformed CLB abundance and parasitism, with sample location as a fixed factor nested in field, which was considered a random factor (Pinheiro et al. 2012). Since no difference was found due to location (see Results), only one estimate was used for further analyses (i.e. averages of CLB abundance and parasitism per field, n = 6 sweep net samples per field). The F value was calculated using the command test: F in linear mixed models. CLB abundance (average number of CLB/50 sweeps) and percentage parasitism (CLB parasitism/field) were modeled with generalized linear models using negative binomial distributions to account for the over-dispersion observed in models using Poisson distributions and non-normality of residuals. For parasitism models, binomial distribution was initially tested, but due to under-dispersion, final models were constructed using a negative binomial distribution. The explanatory variables were the percentage of major hosts (or wheat separately), minor hosts, non-cereal crops, pasture, grassland, woodland, and habitat and crop diversity (Online Appendix A). A categorical variable "year" and its interaction with other predictor variables were included in all models. Prior to performing model selection, Pearson correlation tests were used to detect potential multicollinearity among independent variables. Separate models were performed at four spatial scales: 0.5, 1, 1.5, and 2 km radius. Variance Inflation Factor (VIF) values were calculated for the independent variables in the final models using the Car package (Fox and Weisberg 2018), excluding variables with VIF > 4 to avoid multicollinearity (Crawley 2013). Simplified models using a single semi-natural habitat variable (woodland + grassland + pasture) were constructed, but were not significant and were not explored further. The effect of cereal crops in the previous year on CLB abundance and percentage parasitism was investigated using similar models. Only the major and minor host variables were included in these analyses since the percentage of semi-natural habitats in the landscape was generally similar between years. Only fields with the presence of CLB larvae were included in the CLB analysis (2014, n = 27; 2015, n = 27). To avoid a biased estimation of parasitism, percentage parasitism was analyzed in fields with ≥ 5 CLB larvae/field (2014, n = 23; 2015, n = 16). Stepwise AIC was used to determine the best-fitted models (models with the lowest AIC value) using the Mass package (Venables and Ripley 2003). At each spatial scale, the sequential Bonferroni method was used to adjust the *P* values for multiple comparisons and only models with table-wide $P < 0.05$ are reported (Rice 1989). The Nagelkerke Pseudo-r^2 values were estimated by comparing the null model (e.g. including only the intercept) with models that included various independent variables, using the R Companion package (Mangiafico 2017). Partial correlations were calculated to assess the association between dependent and independent variables using the rsq package (Crawley 2013), and their unadjusted P values are reported to illustrate their relative importance in each model.

Results

CLB response to landscape complexity in the current year

Average CLB larval abundance was three times higher in 2014 (25.2 ± 10.8 larvae/sample, mean ± SEM, n = 27 fields) than in 2015 (8.2 ± 2.33 larvae/sample, n = 27 fields), resulting in significant overall and interacting effects of year of study with landscape variables (Table 1; Fig. 1a). CLB abundance was similar at 20 and 100 m from the field border ($F_{1,57} = 0.59$, $P = 0.45$); therefore samples from both locations were averaged for further analyses. The model with the strongest support (model 1, Table 1) indicated positive associations between CLB abundance and the percentages of minor hosts and non-cereal crops at the 0.5 km scale (Table 1; Fig. 1b, c). These two cover types had consistent positive associations with CLB abundance at multiple spatial scales (Table 1). The same model indicated negative associations between crop diversity and CLB abundance, which was also found at the 1 km scale (Table 1; Fig. 1d). Crop diversity was negatively correlated with the percentage of wheat at all scales ($r = -0.50, -0.64, -0.56, -0.49$, at the 0.5, 1, 1.5 and 2 km scales, respectively; all $Ps < 0.05$). CLB abundance was negatively associated with parasitism, and showed the same pattern at 1 and 1.5 km scales (Table 1; Fig. 1e). Competing models showed positive associations between CLB abundance and major hosts (2 km scale), but contrasting associations with semi-natural habitats: positive associations with woodland (1–2 km scales) and negative associations with pastures (2 km scale, Table 1).

CLB response to cereal crops in the previous year

The percentage of major hosts during the previous year had consistent positive associations with CLB abundance at all scales (Table 1; Fig. 2a). There were positive associations between the percentage of major hosts in the previous year and the percentage of non-cereal crops in the study year at all scales (r = 0.41, 0.47, 0.50, and 0.52, at the 0.5, 1, 1.5 and 2 km scales, respectively; all $Ps < 0.01$), suggesting a rotation between these groups of crops. Minor hosts showed consistent associations with CLB abundance at the 1, 1.5, and 2 km spatial scales: negative associations in 2013 (preceding a high CLB year) and positive associations in 2014 (Table 1; Fig. 2b).

Parasitism response to landscape complexity in the study year

CLB mean percentage parasitism was lower in 2015 (32.3 ± 5.39, n = 16 fields) than in 2014 (55.7 ± 5.17, n = 23 fields), which resulted in interacting effects of year of study with most landscape variables (models 1–4, Table 2; Fig. 3a). Parasitism was similar at 20 and 100 m from the field border ($F_{1,42} = 0.01$, $P = 0.91$); therefore both locations were combined for subsequent analyses. The model most supported by the data (2 km scale, model 4, Table 2; Fig. 3b–d) indicated positive associations between parasitism and the percentages of CLB major hosts, alfalfa, and canola in 2015 (a low CLB year), but no associations in 2014 (a high CLB year). Similar associations were found at smaller spatial scales (Table 2). Parasitism showed also a consistent positive trend of association with non-cereal crops at the 1.5 and 2 km scales in both years (Table 2; Fig. 3e). Parasitism was positively associated with CLB abundance in 2015 (0.5–1.5 km scales, Table 2).

Parasitism response to cereal crops in the previous year

There was only one model close to the significance level, which suggested a positive association between percentage of major hosts in 2014 and parasitism in 2015 (Pseudo- $r^2 = 0.18$, $P = 0.102$; DF = 34, Log-likelihood = -350.8).

Table 1 A summary of the generalized linear models with best support at various scales evaluating associations between cereal leaf beetle (CLB) abundance (number of CLB/50 sweeps) and multiple landscape variables in the current and previous years, parasitism (% parasitism/field), and the year of the study, in southern Alberta, Canada

Model #	Radius (km)	Model	DF	Log-lik	AIC	Δi	Pseudo-$r2$	P	Partial correlation
Models with current year habitats									
1	0.5 km	CLB ~ I + MNH*** − CD*** + NC*** − Y15** − PP^{PS}	48	− 355.1	369.1	0.00	0.41	0.0001	+ 0.52 (MNH); − 0.50 (CD); + 0.49 (NC); − 0.38 (Y); − 0.22 (PP);
2	1 km	CLB ~ I + MNH*** − Y15*** − CD*** − PP** + Y15:WA* + Y14:WA + NC^{PS}	46	− 356.4	374.4	0.00	0.39	0.0003	+ 0.52 (MNH); − 0.46 (Y); − 0.39 (CD); − 0.30 (PP); + 0.35 (Y:WA); + 0.22 (NC)
3	1.5 km	CLB ~ I − Y15** + MNH** + WA* + MJH** − PP*	48	− 362.8	378.1	0.00	0.32	0.001	− 0.35 (Y); + 0.35 (MNH); + 0.32 (WA); + 0.28 (MJH); − 0.22 (PP)
4	2 km	CLB ~ I + WA** + MJH** + MNH* − Y15* + NC*	48	− 360.4	374.4	0.00	0.35	0.0003	+ 0.40 (WA); + 0.33 (MJH); + 0.32 (MNH); − 0.28 (Y); + 0.26 (NC)
5	2 km	CLB ~ I − PAS*** − Y15** + WA**	50	− 356.7	375.7	1.3	0.28	0.0005	− 0.41 (PAS); − 0.39 (Y); + 0.35 (WA)
Models with previous year cereal crops									
6	0.5 km	CLB ~ I − Y14^{PS} + MJH^{PS}	48	− 358.6	366.6	–	0.15	0.016	− 0.23 (Y); + 0.22 (MJH)
7	1 km	CLB ~ I − Y14* + MJH^{PS} + Y14:MNH* − Y13:MNH^{PS}	46	− 354.7	366.8	–	0.21	0.017	− 0.30 (Y); − 0.27 (Y:MNH); + 0.25 (MJH)
8	1.5 km	CLB ~ I − Y14** + Y14:MNH** − Y13:MNH* + MJH*	46	− 353.7	365.6	–	0.23	0.010	− 0.34 (Y); + 0.30 (Y:MNH); + 0.24 (MJH)
9	2 km	CLB ~ I − Y14** + MJH** − Y13:MNH* + Y14:MNH*	46	− 352.1	364.2	–	0.25	0.005	− 0.35 (Y); + 0.33 (MJH); + 0.27 (Y:MNH)

Model terms consist of the response variable CLB abundance (CLB); intercept (I); landscape variables: canola (CA), major hosts (MJH; wheat and barley), minor hosts (MNH; corn, oat and rye), non-cereal crops (NC; all annual crops that are not host of CLB), pasture (PAS), crop diversity (CD; Simpson diversity index), wooded area (WA); the percentage parasitism of CLB (PP); and the study year (Y, which includes Y14 [2014] and Y15 [2015]). The colon symbol indicates interaction terms. The model reported in bold in the best-fitted model across all scales (smallest AIC across all models). For each scale, the model reported first is the model with the most support by the data, and subsequent models are competing models ($\Delta i < 2$). For each model, we report the degrees of freedom (DF), Log-likelihood (Log-lik), Akaike information criterion (AIC), AIC difference (Δi), Pseudo r^2, and P values for the full model. All models reported are significant using a table-wide significant $P < 0.05$ calculated with the sequential Bonferroni method for models fitted within each scale. Significance levels of partial correlations are indicated as a reference only and were not adjusted for multiple comparisons: ^{PS} $P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; other variables have $P > 0.10$

Discussion

Direct effects of landscape complexity and parasitism on cereal leaf beetle abundance

In our study, increased crop diversity was associated with lower CLB abundance at small spatial scales, but it was not associated with parasitism, suggesting a direct effect on CLB. Our finding was likely due to the lower percentage of major hosts in landscapes with high crop diversity, which was supported by significant negative associations between crop diversity and the percentage of major hosts at all scales. Our finding aligns with the results of a multi-country meta-analysis at the field scale (Lopes et al. 2016) that found that crop diversity (e.g., intercropping) reduced the abundance of herbivores in wheat fields, but had no significant effect on natural enemies. They speculated that visual and volatile cues from non-host crops may disrupt herbivore movement and host finding. Sheng et al. (2017) reported a negative effect of crop diversity on specialist insect herbivores (e.g., cereal aphid) and no significant effect on most generalist insect herbivores (e.g., armyworm), suggesting a species-specific response of herbivores to crop diversity. Other studies found similar reductions of herbivores associated with crop diversity due to indirect effects through natural enemies. Maisonhaute et al. (2017) found lower soybean aphid density in landscapes with high crop richness and diversity, and linked their findings to a lower proportion of soybeans, but also to higher biological control rates. Similarly, Redlich et al. (2018) found increased biological control of cereal aphids associated with crop diversity but not with percentage of semi-natural habitats. Liu and Luo (2019) reported lower damage to cotton in fields with high neighbouring crop diversity, likely due to provision of shelter and resources for natural enemies, which facilitated their movement to cotton fields. The lack of association between crop diversity and CLB parasitism in this study is likely due to the specificity of *T. julis* to CLB, which limits its forage to cereal crops. Crop diversity effects vary for natural enemies (Redlich et al. 2018), suggesting that future studies should also investigate their effects on other CLB natural enemies (particularly generalist predators). Crop diversity was a better predictor of CLB abundance than correlated landscape diversity, which was significant only at the 0.5 km scale, suggesting that crops were the main source of functional landscape heterogeneity (sensu Fahrig et al. 2011). Thus, manipulation of crop diversity can be an effective habitat management strategy against CLB.

The percentage of cereal crops (minor and major hosts) in landscapes surrounding focal fields was positively associated with CLB abundance at multiple scales, providing support for the resource concentration hypothesis. Other specialist herbivores, such as the crucifer flea beetle, *Phyllotreta cruciferae* (Goeze) (Coleoptera: Chrysomelidae) (Root 1973), Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) (Boiteau et al. 2008), the Guatemalan potato moth, *Tecia solanivora* (Povolny) (Lepidoptera: Gelechiidae) (Poveda et al. 2012) and wheat stem sawfly (Rand et al. 2014), all show positive responses to the proportion of host plants in agricultural landscapes, most likely due to higher chances of finding and colonizing host patches in agricultural landscapes (Root 1973). For CLB, this positive association could be due to a combination of increased immigration to and decreased emigration from landscapes with high percentage of cereals. Our results add to the body of research providing empirical support for the prediction of the resource concentration hypothesis that specialist herbivores will increase their abundance in landscapes dominated by their host plants.

Our study is among the few studies (Beduschi et al. 2015; Riggi et al. 2017; Berger et al. 2018) investigating the carryover effect of the percentage of hosts in the landscape in the previous year on herbivore abundance. We found consistent positive associations between percentages of major cereal crops at multiple scales in the previous year and CLB abundance in cereal fields in the current year. Similarly, Berger et al. (2018) reported a positive association between the proportion of previous year oilseed crops and the abundance of *L. rugulipennis* in oilseed fields. Likewise, Colorado potato beetle abundance in newly planted potato fields is explained by distance to potato fields in the previous year because they overwinter in and around potato fields from the previous year (Boiteau et al. 2008; Huseth et al. 2012). In our study, the percentage of non-cereal crops in the current year and the percentage of cereals in the previous year were highly correlated, suggesting that due to crop rotation, most of these non-cereal crops were cereals the year before. This finding suggests that the association

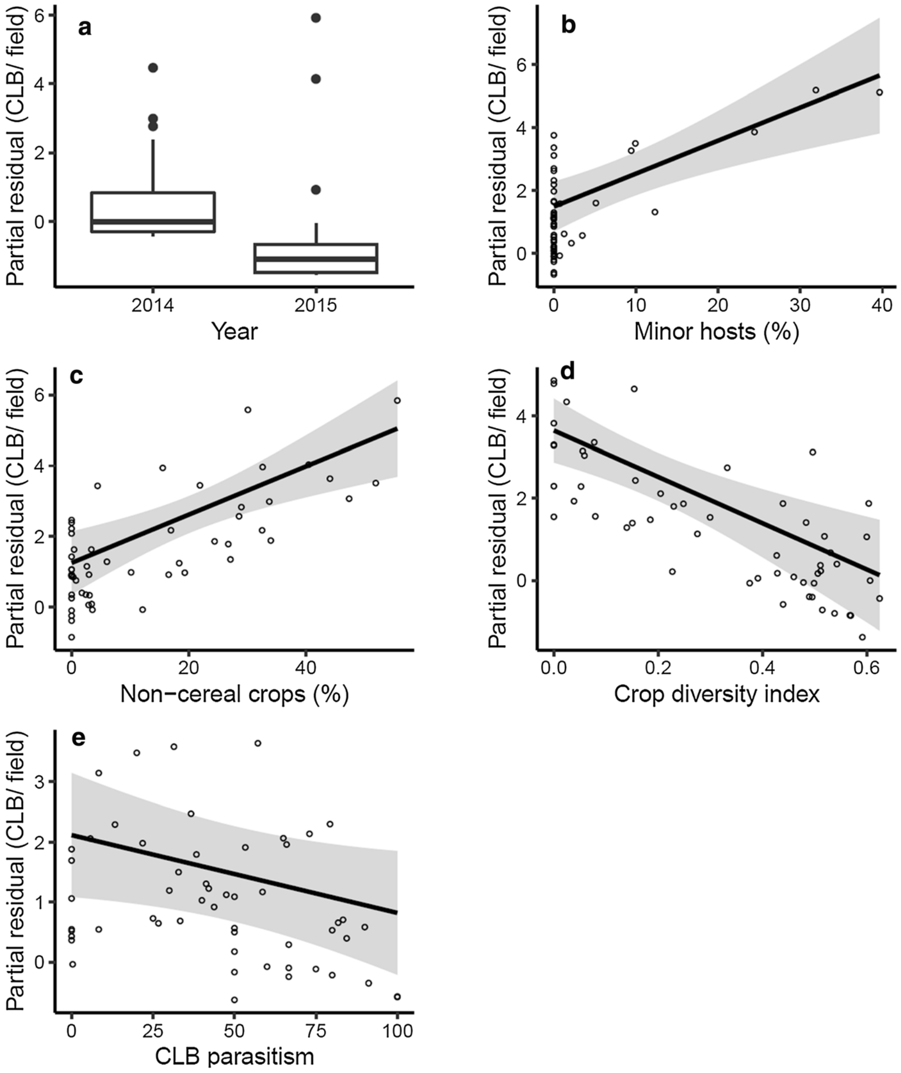

Fig. 1 Average cereal leaf beetle (CLB) abundance (number of CLB/50 sweeps) in focal wheat fields (n = 54) in association with **a** year of the study, **b** % of minor hosts (corn, oats and rye), **c** % of non-cereal crops, **d** crop diversity index, and **e** % parasitism, at the 0.5 km scale. The grey areas are 95% confidence intervals estimated by the Wald confidence interval test using standard errors. See Table 1 (model 1) for statistical details

between non-cereal crops and CLB abundance in the current year may reflect a carryover effect of the percentage of cereals in the landscape in the previous year, rather than a direct positive effect of non-cereal crops on CLB populations. Thus, caution should be taken when interpreting associations between herbivore abundance and annually rotated crops. The percentage of host crops in the landscape in the previous year could be a major factor determining the abundance of specialist herbivores in crops as was found in this study, and deserves further study in other insect pest systems.

The presence of overwintering habitats in agricultural landscapes can explain the abundance of herbivores in agricultural fields (Boiteau et al. 2008; Zaller et al. 2008; Rusch et al. 2013b; Berger et al. 2018). As predicted, woodlands increased CLB abundance in wheat fields due to their role as overwintering sites (Casagrande et al. 1977). Our result is in line with previous studies that reported a positive impact of woodland overwintering sites on the abundance of

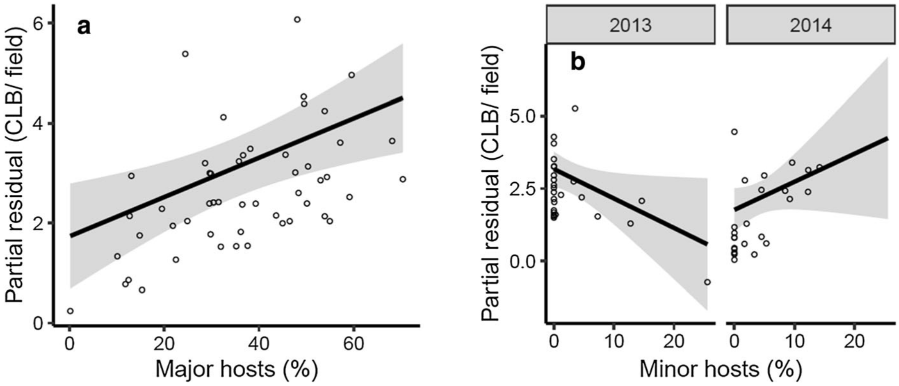

Fig. 2 Average cereal leaf beetle (CLB) abundance (number of CLB/50 sweeps) in focal wheat fields (n = 50) in association with **a** % of major hosts (wheat and barley), and **b** % of minor hosts (corn, rye, and oats) in the previous year's landscapes, and its interaction with year, at the 2 km scale. See Table 1 (model 9) for statistical details

rape pollen beetle at multiple scales (Rusch et al. 2013b), and stem weevil (Zaller et al. 2008) and indicates the potential of specific semi-natural habitats to contribute to ecosystem disservices (i.e. increased pest problems) in some systems.

CLB abundance was negatively associated with a higher percentage of pasture at various spatial scales in the landscape. Perennial grassy areas (e.g., pasture and grassy fallow) have been associated with reductions of specialist herbivore populations in crops through host crop dilution in agricultural landscapes (Huseth et al. 2012; Rusch et al. 2013a). Our findings are consistent with this explanation, as we found negative correlations between the percentage of CLB major hosts and pasture, which resulted in lower percentage of major hosts in these landscapes. Similarly, Huseth et al. (2012) reported negative associations between Colorado potato beetle abundance in potato fields and proportion of grasslands surrounding the field in a 200 m radius due to a potential disruption of beetle dispersal from overwintering habitats. Alternatively, Rand et al. (2014) reported that the proportion of grasslands in the landscape did not affect wheat stem sawfly abundance or parasitism levels in wheat fields in Montana, United States. More studies are needed to determine the specific mechanism behind the negative response of CLB to the percentage of pasture.

The percentage of all semi-natural habitats combined (i.e. grassland, woodland, and pasture) was not associated with CLB abundance and parasitism. This finding is in line with the study by Tschumi et al. (2015), which found no associations between CLB density in wheat fields and the proportion of semi-natural habitats at the 0.75 km scale. However, we found opposite effects of semi-natural habitats when we tested them separately. Thus, one should exercise caution when interpreting patterns resulting from merging all semi-natural variables into one category. In our study, there was an association between landscape complexity and CLB abundance at multiple larger scales, suggesting that the 0.75 km scale tested in the Tschumi et al. (2015) study might have been too small to detect landscape effects. Local diversity enhancements, such as flower strips, resulted in lower CLB abundance in neighboring wheat fields (presumably due to higher predation) in the study by Tschumi et al. (2015) but not in another study (Pollier et al. 2019), further indicating inconsistent effects of semi-natural habitats at a small spatial scales. These results suggest that the role of semi-natural habitats can not always be generalized because habitats within this category might affect herbivores and natural enemies differently and at different spatial scales. Much work remains to elucidate the mechanisms for these patterns.

Our findings indicate strong impacts of *T. julis* on CLB populations, expanding previous studies conducted at local scales (Dysart et al. 1973; Evans et al. 2006, 2015) to the landscape scale. CLB parasitism remained above the 32% minimum threshold for successful classical biological control (Hawkins and Cornell 1994). Because the impact of *T. julis* on CLB larval abundance happens the following year (i.e., parasitism does not decrease CLB abundance until the next generation), we hypothesize that this negative association is due to landscape-scale carryover effects of *T. julis* on CLB populations from previous years. The success of this parasitoid has been linked to its high specificity to CLB (Hervet et al. 2016), and high dispersal ability which resulted in no colonization lag between newly and previously planted wheat fields in disturbed agricultural landscapes (Evans et al. 2015). We conclude that CLB parasitism by *T. julis* has strong negative effects on CLB abundance in agricultural landscapes in southern Alberta.

Indirect effects of landscape complexity on cereal leaf beetle

The percentage of host crops in agricultural landscapes can indirectly influence herbivore parasitism rate due to a density-dependent response by parasitoids (Gunton et al. 2016). In the year with lower CLB abundance (2015), we observed a significant increase of parasitism associated with an increased percentage of major host crops at multiple scales. Contrary to our finding, Grab et al. (2018) reported negative associations between the proportion of crops and tarnished plant bug parasitism by the introduced parasitoid *Peristenus digoneutis* Loan (Hymenoptera: Braconidae). The same authors concluded that the higher proportion of semi-natural habitat in the surrounding landscape was a key factor for explaining tarnished plant bug parasitism. The contrasting findings between Grab et al. (2018) and this study may be due to the parasitoid host specificity. While *T. julis* only attacks CLB (Hervet et al. 2016), *P. digoneutis* can attack several species of *Lygus* and therefore has a wider range of accepted hosts (Mason et al. 2011), which enables this species to exploit resources and alternative hosts from semi-natural habitats. The presence of CLB in high numbers in cereal fields (particularly in 2014) might have reduced *T. julis* searching time and increased parasitism (Stiling 1987). Overall, our results are consistent with a density-dependent response of *T. julis* to CLB abundance, mediated by the amount of host crop available in the landscape.

Natural enemies can benefit from different crops in the landscape if those crops provide supplemental resources (e.g., pollen and nectar), as predicted by the supplementation hypothesis (Dunning et al. 1992). Evans et al. (2010) reported increased *T. julis* longevity and 4–7 times higher CLB parasitism early in the season in cereal fields sprayed with sucrose. We found

Table 2 A summary of the generalized linear models with best support at various scales ($\Delta i < 4$ at each scale) evaluating associations between cereal leaf beetle (CLB) parasitism (% parasitism/field) and multiple landscape variables, CLB abundance (number of CLB/50 sweeps), and the year of the study, in southern Alberta, Canada

Model #	Radius (Km)	Model	DF	Log-lik	AIC	Δ*i*	Pseudo-*r*2	*P*	Partial correlation
1	0.5 km	PP ~ I − Y15*** + Y15:MJH*** − Y14:MJH + Y15:CA*** + Y14:CA + Y15:CLB*** − Y14:CLB	30	− 346.2	364.7	0.00	0.42	0.004	− 0.61 (Y); + 0.59 (Y:MJH); + 0.48 (Y:CA); + 0.54 (Y:CLB)
2	1 km	PP ~ I − Y15*** + Y15:CA*** − Y14:CA + Y15:MJH*** − Y14:MJH + Y15:CLB*** − Y14:CLB − Y15:MNHPS − Y14:MNH	26	− 342.3	367.2	0.00	0.44	0.009	− 0.65 (Y); + 0.54 (Y:CA); + 0.53 (Y:MJH); + 0.45 (Y:CLB); − 0.26 (Y:MNH);
3	1.5 km	PP ~ I − Y15*** + Y15:MJH** − Y14:MJH + Y15:CA** + Y14:CA + Y15:CLB* − Y14:CLB + Y15:ALF^{PS} − Y14:ALF + NC	27	− 345.8	369.8	–	0.43	0.019	− 0.58 (Y); + 0.45 (Y:MJH); + 0.41 (Y:CA); + 0.31 (Y:ALF); + 0.28 (Y:CLB); + 0.27 (NC)
4	2 km								

ALF alfalfa, *CLB* CLB abundance; for all other abbreviations and notes, see Table 1

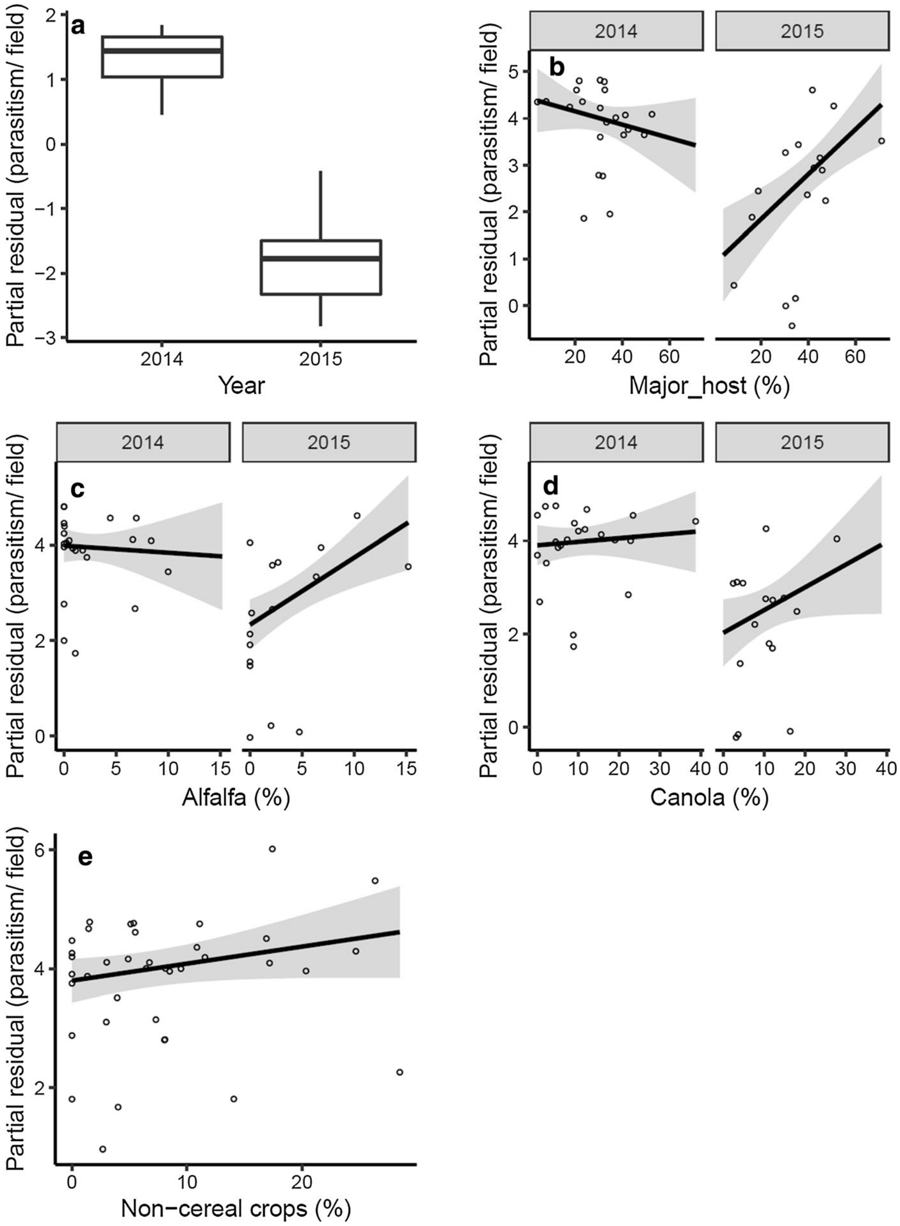

Fig. 3 Average cereal leaf beetle (CLB) parasitism (% parasitism/ field) in focal wheat fields (n = 39) in association with **a** year of the study, **b** % of CLB major hosts (wheat and barley), **c** % of alfalfa, **d** % of canola, and **e** % of non-cereal crops, at the 2 km scale. See Table 2 (model 4) for statistical details

positive associations between CLB parasitism and percentage of cereals, alfalfa, and canola at multiple spatial scales. These positive associations can be due to carbohydrate resource availability for *T. julis*, which include honeydew produced by aphids in cereals and alfalfa, and nectar and pollen produced by flowering canola plants. Given the pro-ovigenic nature of *T. julis* (Dysart et al. 1973), we would expect that under low CLB populations, *T. julis* might have to spend more time locating its host, which results in higher dependency on carbohydrate resources to maximize its foraging ability and parasitism. This pattern is consistent with the positive association of CLB parasitism and these landscape habitats in the low CLB year (2015). Cereals have been associated with increased natural enemies in other systems. In Western Canada, Samaranayake and Costamagna (2018) reported a positive association between cereals and predators in agricultural landscapes, and they attributed it to the presence of aphids and reduced insecticide applications in cereals. Although we did not quantify them, aphids were common in our samples, and pea aphids are ubiquitous in alfalfa in Western Canada (Uddin 2005). Canola nectar improves diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) parasitism by *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) (Idris and Grafius 1997). These findings suggest that CLB parasitism can be enhanced by alternative food resources present in crops (e.g., cereals, alfalfa and canola), which supports the landscape supplementation hypothesis.

Contrary to expectations, we did not find any associations between the percentage of semi-natural habitats (pasture, woodland and grassland) and CLB parasitism. Three possible reasons may explain these unexpected patterns. First, the high specificity of *T. julis* to CLB may limit its foraging in cereal fields where CLB is abundant (Hervet et al. 2016). Second, *T. julis* overwinters inside CLB pupae within cereal fields (Dysart et al. 1973). Unlike other systems such as rape pollen beetle (Thies et al. 2003), a higher percentage of pasture, grasslands, or woodlands in the landscape would not enhance overwintering habitats for *T. julis*. Third, we found a negative correlation between the percentage of pasture and percentage of CLB major hosts in the landscape, which may explain lower CLB abundance in landscapes with a high percentage of pasture. Given the density-dependent response of *T. julis* to CLB (Kher et al. 2014), the lack of positive associations between the proportion of pasture and CLB parasitism might be due to the lower abundance of CLB in these fields. Our findings are in line with a recent study by Karp et al. (2018) that summarized data from 31 countries and found a similar number of positive and negative associations between pest control and semi-natural habitats in the landscape. Furthermore, although we did not account for the effect of predators in this study, positive effects of pastures on predators have been shown in other systems (Rusch et al. 2013a). Kheirodin et al. (2019, 2020) reported several species of predators consuming CLB under laboratory and field conditions, with up to 24.5% predation on CLB eggs over 24 h, suggesting that predators can also be important mortality factors for CLB. Overall, our results suggest that different semi-natural habitats may have diverse roles in host-parasitoid systems and grouping them into one category may mask these roles.

Our study is among the few (Rusch et al. 2011; Beduschi et al. 2015; Riggi et al. 2017) that have investigated the effect of the percentage of host crops in the previous year on current parasitism rates. We found that landscapes with a higher percentage of cereals in the previous year had no significant association with current levels of parasitism. This lack of association may be due to disturbances in cereal fields, such as tillage (regular or reduced), insecticides, and the high dispersal ability of the parasitoid. In our study area, tillage is seldom used (Awada et al. 2014), and insecticide applications are rare in cereals (Meers 2018). Evans et al. (2015) reported a high dispersal ability of *T. julis* that enabled the species to locate CLB over distances up to 600 m in highly disturbed agricultural landscapes. Altogether, these findings suggest that the lack of association between parasitism and percentage of cereal fields in the previous year could be due to the high dispersal ability of *T. julis* that enables this species to locate its host over long distances and mask the potential effects of overwintering sites.

Conclusions

Our study suggests host crops in the current and previous year are positively associated with CLB abundance, and supports the resource concentration hypothesis. CLB parasitism was also positively associated with CLB major host crops, potentially due to a higher abundance of CLB in these landscapes. Percentage parasitism was also higher in landscapes with higher percentage of crops that may potentially provide carbohydrate resources (alfalfa and canola), thus supporting the landscape supplementation hypothesis. Our results suggest that crop diversification at the local landscape scale studied (0.5 km) can be an important factor to reduce CLB numbers in southern Alberta. Altogether, our results suggest that designing agricultural landscapes with increased crop diversity can be an important habitat management strategy to manage CLB, by reducing the percentage of CLB hosts and increasing the proportion of habitats supporting parasitoids.

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