Pollen beetle mortality is increased by ground-dwelling generalist predators but not landscape complexity

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ABSTRACT

Biological control of crop pests by naturally occurring arthropods depends on the entire community of natural enemies, but generalist predators and parasitoids are rarely considered in the same study. Also, the level of biological control in the field is affected by both within-field and landscape scale management. A multi-taxa approach that integrates multiple scales of management is needed to understand drivers for pest mortality. We examined local (weed cover and soil characteristics) and landscape (proportions of semi-natural and oilseed rape habitat) effects on natural enemy communities and biological control of pollen beetles in 15 oilseed rape (OSR) fields in Sweden. We found that agricultural intensification at the local (low weed cover) and landscape scale (low proportion of semi-natural area) increased evenness of generalist predators, but had no effect on the densities of pests and their natural enemies. This suggests that the generalist predators in OSR are well adapted to crop lands, at least within the examined gradient. Increasing OSR in the landscape decreased parasitoid densities and increased pest density, indicating a potential loss of pest control services by specialist natural enemies in landscapes with a high proportion of OSR. Finally, pollen beetle mortality increased with ground-dwelling generalist predator abundance and soil clay content. Parasitism rates did not affect pest mortality, which is interesting as parasitoids have been considered major control agents in OSR. The hypothesis that increasing semi-natural habitat in the landscape enhances natural enemy abundances and species richness in agricultural landscapes was not supported. Local measures targeting generalist predators appear as a reasonable strategy to maximize pollen beetle control.

1. Introduction

Biological control of crop pests is an important ecosystem service delivered by a community of generalist and specialist natural enemies. Biological control is affected by a combination of management interventions and habitat qualities within the field and in the landscape in which the field is embedded (Martin et al., 2013; Rusch et al., 2010; Tylianakis and Romo, 2010). While much research has been performed on single taxon and landscape impacts, few assessments have been made that encompass the impact of both field and landscape scale management on a wider community of generalist and specialist natural enemies, and their actual impact on pest population suppression.

Increasing within-crop plant diversity generally enhances abundance and diversity of natural enemy assemblages (Langellotto and Denno, 2004; Letourneau et al., 2011). It has been hypothesized that within-crop diversification of plants will enhance biodiversity and

ecosystem services more in structurally simple, rather than in cleared (i.e. extremely simplified) or in complex landscapes (Tscharntke et al., 2012). This "intermediate landscape-complexity" hypothesis has been both supported (Concepción et al., 2012, 2007; Jonsson et al., 2015; Midega et al., 2014) and refuted (Phillips and Gardiner, 2016; Rusch et al., 2015b, 2016a; Woltz et al., 2012), but lacks general empirical support in major crops such as oilseed rape.

Interactions among predator functional guilds can increase or decrease the pest predation level through facilitation, intraguild predation or behavioral interference (Letourneau et al., 2009; Martin et al., 2013; Straub et al., 2008). There is increasing evidence that abundance, species richness and community evenness of different taxa of biological control agents respond differently to landscape complexity with implications for pest control services (Gardiner et al., 2010; Rusch et al., 2014; Woodcock et al., 2010). However different natural enemy groups are rarely examined simultaneously. In a meta-analysis on natural

enemy response to landscape complexity only two out of 46 studies simultaneously examined parasitoid and generalist natural enemies and only one estimated actual impact of multiple natural enemies on pest mortality (Chaplin-Kramer et al., 2011). These two studies confirm that the relationship between landscape context and arthropod abundances in crops are taxon specific with generalist predators responding more to woody habitats than specialists (Bianchi et al., 2005; Perović et al., 2010).

In addition, body size is a critical life-history trait determining the type and the strength of interactions among species (Schneider et al., 2012; Woodward et al., 2005; Rusch et al., 2015a). It is hypothesized that species with larger body sizes would be more vulnerable to landscape simplification because of higher disturbance (ie. short crop rotations) (Blake et al., 1994; Ewers and Didham, 2006). However, investigation across predator taxa has found increased mean body size with landscape complexity for rove beetles but not for carabids and spiders in barley fields (Rusch et al., 2014). It is expected that landscape simplification will reduce natural pest control (Rusch et al., 2016b). However, studies to ascertain which components of the natural enemy community (abundance, species richness, evenness, mean body size) respond to landscape complexity and affect pest mortality are lacking.

The pollen beetle (*Meligethes aeneus* Fabricius 1775; Coleoptera, Nitidulidae) is among the major insect pests in OSR (*Brassica napus* L.) in Europe (Ekbom, 2010). Landscape composition, influences pollen beetle abundance directly by affecting its dispersal and mortality (Rusch et al., 2013; Schneider et al., 2015; Zaller et al., 2008a) and indirectly by affecting parasitism rates (Beduschi et al., 2015; Rusch et al., 2011; Schneider et al., 2015; Thies et al., 2008, 2003; Thies and Tscharntke, 1999; Zaller et al., 2009). Generally, increasing cover of semi-natural habitat in the landscape has a positive effect on both pollen beetle abundances and parasitism rates in OSR crops. Generalist natural enemies have been suggested to be important pollen beetle predators (Büchi, 2002; Haschek et al., 2012; Öberg et al., 2011), but little is known about their actual impact on pollen beetle population dynamics or how they respond in OSR to within field and landscape complexity. In addition, mortality of different life stages of the pollen beetle has rarely been considered. Abiotic factors such as increasing percent of clay in soil (Marrone and Stinner, 1984; Simelane, 2007; Turpin and Peters, 1971) and decreasing pH (Johnen et al., 2010; Li et al., 2007) are known to increase other coleopteran larval survival in the laboratory. Despite the fact that pollen beetles spend larval and pupal stages in the soil (Osborne, 1960) the effect of soil texture and pH on net pollen beetle mortality in the field remains unknown.

We investigated how pest mortality in OSR was affected by natural enemy communities, and how characteristics at the local and landscape scale in combination influence the pest and its natural enemies (Fig. 1). Firstly, we hypothesized that generalist predator (spiders, carabids, and rove beetles) abundance, species richness, and community evenness and mean body size, as well as abundance of parasitoids and parasitism rates would increase with increasing coverage of semi-natural habitat in the landscape. Second, we expected within-field weed cover to have a positive effect on predator abundance, richness, mean body size, and evenness; and that this effect would be stronger in landscapes with low cover of semi-natural habitat (Tscharntke et al., 2012). Third, we examined the effect of natural enemy community and soil characteristics on pollen beetle mortality to investigate the biological control potential at the field scale. We expected specialist and generalist natural enemy abundances to additively enhance pollen beetle mortality, and pest mortality to increase with generalist predator community richness, evenness, and mean body size. Finally, because part of the pollen beetle life cycle is spent in the soil we expected mortality to be affected by soil properties.

2. Material and methods

2.1. Experimental design

The study was carried out in 2013 in 15 conventionally managed winter OSR fields in the Swedish province of Västra Götaland (Figure A and Table A, Supplementary material). Average temperature and precipitation for the months of May and June were 13 °C (min = −1.5, max = 24) and 77 mm (min = 32, max = 100). The landscape of this region is dominated by arable land (46%) comprising mostly cereals (47%), pastures (6%) and woodlands (48%) (Statistics Sweden 2013: http://www.scb.se/sv). To ensure variation in landscape composition among fields, they were chosen along a gradient of agricultural intensity measured as percentage arable land in a circular landscape sector of 1.5 km diameter encompassing the field (Zaller et al., 2008b). Percentage arable land in the landscape varied between 38% and 93.62%. Within each field, we selected a plot, 40 × 70 m, of unsprayed (insecticides, herbicides and fungicides) area located at the edge of the field. The field edge was adjacent to a grassy strip in all fields. Observations of invertebrates and weed coverage were made along two transects parallel to the field edge 3 and 30 m within the field. Each transect included five sampling points 5 m apart (Figure A, Supplementary material). In each point we sampled densities of the pest, the natural enemies, and the weed coverage in a similar spatial arrangement among sites.

The landscape characterization was obtained from the Integrated Administrative and Control System (IACS) database and interpreted with MATLAB R2012b. The land use was measured in a circular sector around each field of 500 m and 1000 m radius. Pollen beetle abundance and parasitism are found to be affected by landscape components at scales ranging from 750 m (Thies et al., 2003) to 1250 m or larger (Zaller et al., 2008a, 2008b). Here, we defined a radius of 1000 m, as the mean between the distances reported in the literature. We also tested 500 m radius as non-crop features at this scale can have an effect on generalist predators (Maisonhaute and Lucas, 2011). The landscape variables investigated at each scale were: proportion of winter OSR in 2013 (OSR_{t0}), proportion of past year winter and spring OSR (OSR_{t-1}) and proportion of semi-natural habitat (including pasture, ley, grasslands and forest) (SN). These variables have been found to affect pollen beetles dynamics and parasitism rates (Rusch et al., 2011; Schneider et al., 2015; Thies et al., 2008).

2.2. Study organisms

Pollen beetles produce one generation per year and adults usually overwinter outside the field in semi-natural habitats (Rusch et al., 2011). In the spring, the beetles migrate to OSR fields where they feed on and oviposit in the buds. The larvae feed on pollen and when fully grown drop to the soil for pupation. The next generation of adult beetles emerges in the middle of the summer and these will overwinter. *Meligethes aeneus* is the dominant species in Sweden. Pollen beetle damage and effects on yield in the studied system are published (Gagic et al., 2016).

2.3. Sampling

2.3.1. Weed and soil sampling

Weed cover in the OSR crop was used as a measure for within-field complexity. Weed cover was visually estimated using quadrats (1 × 1 m), measurements were replicated four times at each sampling point. Each quadrat was given a rank from 1 to 6 corresponding to a percent weed coverage category (1: < 1%; 2: 1–5%; 3: 5–12.5%; 4: 12.5–25%; 5: 25–50%; 6: > 50%) (Winqvist et al., 2011). To measure soil properties, we collected five random soil cores of 15 cm depth and 6 cm diameter at each site. Cores were mixed and transported at 5 °C and protected from sunlight. We determined pH (SS-ISO 10390) and
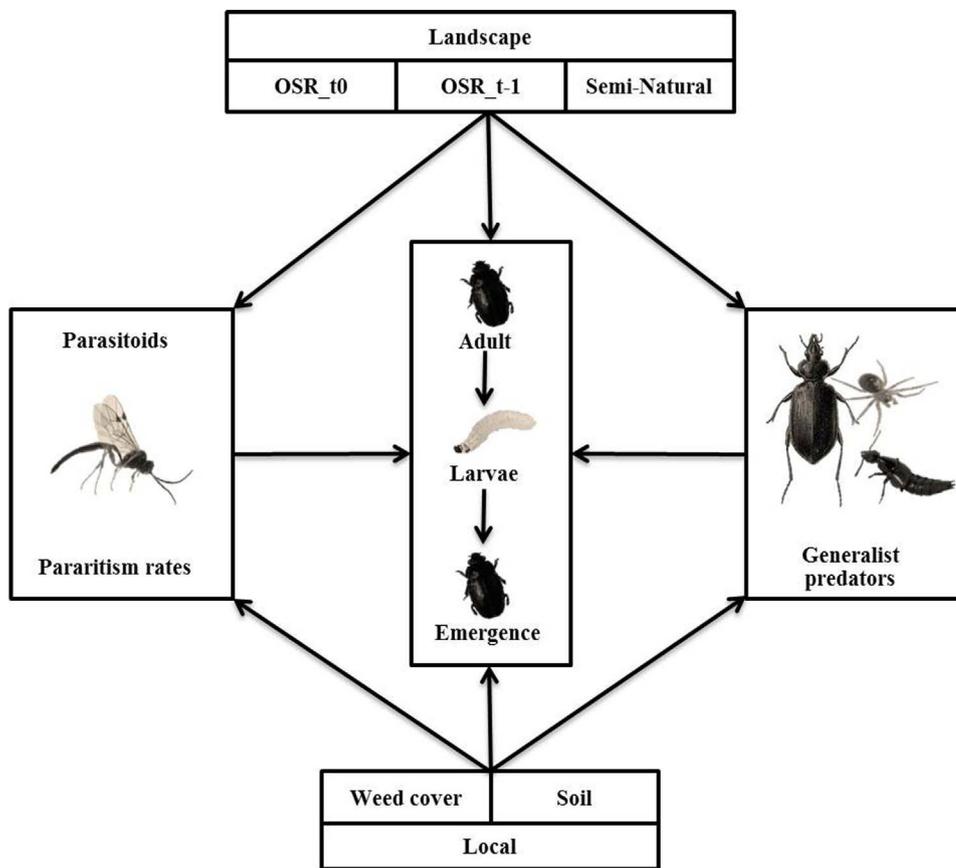
Fig. 1. Diagram illustrating the tested hypotheses. Abbreviations: OSR_{t0} − present year OSR, OSR_{t-1} − past year OSR.

soil texture, measured by percent clay and sand particles in mineral soil material after sieving and sedimentation (SS-ISO 11277). All soil analyses were made by Agrilab, Uppsala (http://www.agrilab.se).

2.3.2. Invertebrate sampling

Adult pollen beetles were counted on ten plants at each sampling point (100 plants per field in total). Counts were made three times during the season, from pollen beetle colonization at OSR green bud stage until OSR flowering period (GS 51 − 69) (Lancashire et al., 1991). Average abundance per plant per sampling point was multiplied by OSR plant density per m^2 to give a measure of pollen beetle abundances per m^2. To estimate abundances of parasitoids we placed 10 yellow pan traps per field at the canopy level at OSR green bud stage and collected samples before pollen beetle larvae pupation (22–31 May). Activity-density of generalist natural enemies in the field was estimated using 10 pitfall traps during pollen beetle larvae dropping period (12–20 June). All predators and parasitoids were stored in 70% alcohol and identified to species when possible otherwise to genus. Average sizes for generalist predator species of carabids and spiders and for genera of staphilynids were gathered from the literature (Almquist, 2007, 2005; Landin, 1970; Lindroth, 1989; Roberts, 1993). Adult and sub-adult spiders were sexed and sexual dimorphism in spider size was accounted for by considering female and male as different species in the analysis. Community-weighted mean (CWM) of body size, which is the abundance weighted mean body size value in the community, were calculated for the entire predator community and separately for carabids, spiders and staphylinids. The CWM for predator body size was calculated with the function dbFD in package FD in R (Laliberté and Legendre, 2010).

2.3.3. Estimation of pollen beetle parasitism and mortality

We used 10 funnel traps (30 cm diameter) per field to catch pollen beetle larvae falling from OSR flowers. Funnels were placed in small plastic pots which were dug in the soil before larval dropping period. To control for variation in plant density between the sites, the flowering parts of two plants were bound together above each funnel. Funnels were emptied regularly and removed after the flowering period. Larvae collected in the funnels were placed in 70% alcohol and counted to estimate larval density which was then adjusted to a density of larvae per m^2. Twenty larvae per sampling point were dissected in the laboratory to estimate parasitism rates (in total 200 larvae per field). A larva was noted as parasitized if a parasitoid egg was found in the larvae. Percent parasitism was calculated as percentage of parasitized larvae from all dissected larvae.

To estimate mortality of pollen beetle larvae and pupae, 10 metal cylinders (30 cm diameter) per field were placed beside the funnels and dug a few centimeters into the soil during larval dropping period, but before adult emergence from the fields. Cylinders were paired with funnels and placed simultaneously to allow for comparison. Two plants were bound together above each cylinder. Yellow sticky traps were placed in the cylinders to catch emerging pollen beetles, and a nylon gauze was placed on the top of the cylinders to allow pollen beetle larvae passage but prevent adult pollen beetles escape (Figure B, Supplementary material). After emergence of adults, yellow sticky traps were collected and captured emerging pollen beetles were counted. Total mortality (M) was calculated as percentage of larvae that did not emerge, $M = ((L − E)/L)*100$, where L is the number of larvae falling in the funnels and E the number of adults emerging in the cylinders. Because of possible intraguild predation, mortality due to parasitoids is confounded with mortality due to generalist predators. We were interested in investigating the interaction of natural enemies guilds on net pollen beetle mortality therefore we did not distinguish between mortality due to parasitoids and mortality due to predators and other abiotic factors as in Büchi (2002).

2.4. Statistical analyses

2.4.1. Pollen beetle, parasitoid abundances and parasitism rates

Density-dependence tests on parasitism rate, parasitoid abundance and pollen beetle larvae abundance were performed with Linear Mixed-Effects (LME) models. For parasitism rates, parasitoid and pollen beetle larvae abundances and their interaction were included in the model. For parasitoid abundance we included pollen beetle larvae abundance as the fixed factor. Finally, for pollen beetle larvae abundances, adult abundance was included as a fixed factor. If an effect was detected the significant variable(s) was(were) also included as a fixed effect in all models testing for landscape scale effects. Within-field position (Edge and Center transect) was nested within Field and included in the random structure of all models.

We used LME models to analyze the effects of local complexity (measured as weed cover) and landscape variables at 500 m or 1000 m, i.e. OSR_{t0}, OSR_{t-1}, and SN, on pollen beetle adult and larvae abundance, parasitoid abundance and parasitism rates. To test intermediate landscape complexity hypothesis interactions between weed cover and semi-natural habitat were included in all models. Weed cover did not correlate with any of the landscape variables (see Table 2 for a detailed list of models).

2.4.2. Generalist predator community measures

Models for generalist predator abundance, species richness, evenness (measured as Pielou's evenness index) and CWM body size were run for all predators taken together and for spiders, carabids, and staphylinids separately. The effect of landscape and local variables were also tested on the abundances of the dominant species in each taxon (Table 1). Fixed factors in the models included pollen beetle larvae abundance, semi-natural habitat, weed cover and the interaction between weed cover and semi-natural habitat. For the generalist predators' models, we assumed that generalist predators would be influenced by the proportion of total arable habitat in the area rather than by the proportion of only OSR. Hence, for generalist predator models, proportion of total arable land rather than proportion of OSR in the

landscape was included in the model. Proportion of arable land was negatively correlated with the proportion of semi-natural habitat at both scales (1000 m: rho = −0.72, *p*-value < 0.001 and 500 m: rho = −0.77, *p*-value < 0.001), therefore only semi-natural habitat was kept as landscape variable in the predators models (see Table 2 for a detailed list of models).

2.4.3. Pollen beetle mortality

To assess the effects of natural enemies and soil variables on pollen beetle mortality, we used linear mixed-effects models with field position nested within Field as random factor. The explanatory variables were weed cover, soil pH, % clay in the soil, parasitism rate, generalist predator abundance, CWM body size, richness, evenness and the interaction between parasitism and predators abundances to test for intraguild predation. Percent clay in the soil was used as a proxy for soil texture, percent sand was highly correlated with clay (rho = −0.85, *p*-value < 0.001) and not included in the model. Multiple models were run for pest mortality including as fixed factors either overall predator abundances (i.e. the sum of spider, carabid and staphylinid abundances) or abundances of spiders, carabids and staphylinids analysed separately to investigate whether a taxon had a stronger influence on pest mortality.

2.4.4. Model checks

A visual validation procedure was applied to check that model assumptions were satisfied. To achieve homoscedasticity, we used logarithmic or square root transformation when necessary. All variables were standardized (to a mean of zero and a standard deviation of one) beforehand to improve model convergence and to make effect sizes easier to compare and interpret (Zuur et al., 2009). The collinearity among independent variables in the models was low, with a variance inflation factor (VIF) lower than 2 for all models (Zuur et al., 2009). Because non-linear interaction between landscape and within-field complexity could be expected, we compared models including either the quadratic or the linear polynomial term of semi-natural habitat. Non-linear terms and their interactions with within-field complexity were never significant and model fits (assessed using AIC) were never improved in LMEs including non-linearity terms. Only LMEs without non-linear terms are therefore presented. We used multi-model inference (Burnham and Anderson, 2004) in package "MuMIn" (Barton, 2015), to test our hypotheses. This approach allows for comparisons among multiple models with different combinations of predictors, and identification of the most parsimonious model according to the second order Akaike information criterion corrected for a small sample size (AICc) (Zuur et al., 2009). For each model we calculated its Akaike weights (w_i) and used unconditional (or 'zero method') model averaging procedure of models with $\Delta w_i < 2$ (Burnham and Anderson, 2004; Grueber et al., 2011). Marginal and conditional pseudo-R-squared were calculated using the r.squaredGLMM function in package "MuMIn" (Nakagawa and Schielzeth, 2013) (Table 2). We used spline correlograms in the package "ncf" and found no spatial autocorrelation in the model residuals. All analyses where performed in R (version 2.15.1, R Development Core Team 2012). Variables are summarized in Table 1.

3. Results

3.1. Local and landscape effects

3.1.1. Pollen beetle

For both investigated scales, proportion of current year OSR had a positive effect on pollen beetle adult abundances (*p*-value < 0.05) (Fig. 2a). On the other hand, the relative importance values (w_i) for adult pollen beetle abundance of weed cover, the proportion of semi natural habitat and OSR_{t-1} were consistently low (Table 2). Pollen beetle adult density positively affected larvae density (*p*-value < 0.01)

Table 1
Summary of the mean, the standard error of the mean (SE), the minimum (min) and maximum (max) values for the investigated variables.

	Variable	Total	Mean	SE	Min	Max
Biotic	Adult pollen beetle (ind m^{-2})	1019	115	9	0	615
	Larvae pollen beetle (ind m^{-2})	27676	2610	126	141	6804
	Mortality (%)	–	88	1.9	75	96
	Parasitism rates (%)	–	16	1.8	0	90
	Tersilochus (ind)	719	4.8	1	0	123
	Phradis (ind)	1034	6.6	0.8	0	59
	Pred Ab (ind) [a]	25871	6.7	7.3	10	423
	Carabid Ab (ind)	9216	61	3.7	1	213
	Spider Ab (ind)	9028	60	3.4	2	212
	Staph. Ab (ind)	7627	52	3.4	1	169
	Pred Richness (ind)	–	29	0.5	7	47
	Pred evenness	–	0.8	0.005	0.5	0.8
	Pred CWB (mm)	–	6.5	0.09	3.2	9
Local	Weed cover	–	2.8	0.1	1	5.75
	Soil clay (%)	–	17	0.9	1	30
	pH	–	6.3	0.05	5.6	7.6
Landscape	Semi-natural 500 m (%)	–	39	2.5	1.2	89
	Semi-natural 1000 m (%)	–	43	1.9	14	87
	OSR_{t-1} 500 m (%)	–	5	0.6	0	27
	OSR_{t-1} 1000 m (%)	–	5.5	0.3	0	15
	OSR 500 m (%)	–	20	0.7	3.4	32
	OSR1000 m (%)	–	7.1	0.3	1	16

[a] Predatory carabids (48 spp), spiders (118 spp) and staphylinids (19 genera) were collected between 12 − 20 June. The dominant carabid species were *Poecilus cupreus* (17%), *Agonum muelleri* (14%), *A. dorsale* (13%), *Loricera pilicornis* (13%), and *Bembidion aeneum* (7%). The dominant spider species were *Erigone atra* (18%), *Pardosa prativaga* (17%), *Oedothorax apicatus* (12%), *P. agrestis* (11%) and *Pachygnatha degeeri* (8%). The dominant staphylinid genera were *Philonthus* (59%) and *Tachinus* (15%).

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Table 2

Summary of the best models after multimodel inference for pollen beetle (Pb) adults and larvae, Parasitism rates and Parasitoid and Predators abundances (Ab). Presented are the results from the **"unconditional" (zero) average** model (wi – relative variable importance, E – estimate and Se – standard error). Abbreviations: NI: variable not included in the analysis, OSR$_{t0}$: present year OSR, OSR$_{t-1}$: past year OSR, SN: semi-natural (including woodland, pasture and lay), R²m: marginal coefficient of determination, R²c: conditional coefficient of determination, *: interaction and −: variable not present in models with Δ wi < 2. P-values:. = 0.05, * < 0.05, ** < 0.01. Significant results are shown in bold.

Scale (m)	Response	OSR$_{t0}$ (%)	OSR$_{t-1}$ (%)	SN (%)	SN* Weed cover	Pb larvae	Pb adult	Pb larvae * Parasitoid Ab	Parasitoid Ab	Weed cover	#models Δ wi < 2	R²m	R²c
500	Pb adults[a]	**wi = 1*; E = 0.46; Se = 0.16**	wi = 0.52; E = 0.13; Se = 0.17	wi = 0.25; E = −0.03; Se = 0.10	–	NI	NI	NI	NI	wi = 0.23; E = 0.014; Se = 0.04	6	0.31	0.73
1000		**wi = 1***; E = 0.53; Se = 0.15**	wi = 0.24; E = 0.03; Se = 0.10	wi = 0.18; E = −0.02; Se = 0.07	–	NI	NI	NI	NI	wi = 0.16; E = 0.006; Se = 0.04	4	0.34	0.73
500	Pb larvae	**wi = 1**; E = 0.36; Se = 0.13**	–	wi = 0.29; E = −0.03; Se = 0.08	–	NI	**wi = 1**; E = 0.25; Se = 0.08**	NI	NI	wi = 0.21; E = 0.01; Se = 0.05	3	0.29	0.58
1000		wi = 0.78; E = 0.23; Se = 0.18	–	–	–	NI	**wi = 1**; E = 0.23; Se = 0.08**	NI	NI	wi = 0.23; E = 0.02; Se = 0.06	3	0.31	0.59
500	Parasitoid Ab[a]	wi = 0.88; E = −0.35; Se = 0.22	wi = 0.54; E = 0.17; Se = 0.21	–	–	NI	NI	NI	NI	wi = 0.40; E = 0.06; Se = 0.10	5	0.19	0.73
1000		**wi = 1*; E = −0.43; Se = 0.19**	wi = 0.35; E = 0.09; Se = 0.17	wi = 0.24; E = −0.04; Se = 0.11	wi = 0.11; E = −0.01; Se = 0.05	NI	NI	NI	NI	wi = 0.69; E = 0.13; Se = 0.12	6	0.20	0.72
500	Parasitism[b]	**wi = 1*; E = 0.22; Se = 0.10**	wi = 0.22; E = −0.01; Se = 0.05	–	–	wi = 1; E = −0.02; Se = 0.02	NI	**wi = 1*; E = 0.08; Se = 0.32**	**wi = 1*; E = 0.10; Se = 0.37**	wi = 0.21; E = 0.003; Se = 0.02	3	0.29	0.83
1000		**wi = 1*; E = 0.22; Se = 0.10**	–	–	–	wi = 1; E = −0.03; Se = 0.03	NI	**wi = 1**; E = 0.08; Se = 0.03**	**wi = 1*; E = 0.09; Se = 0.04**	wi = 0.28; E = 0.006; Se = 0.02	4	0.31	0.83
500	Pred Ab	NI	NI	wi = 0.66; E = 0.041; Se = 0.16	wi = 0.66; E = −0.19; Se = 0.16	wi = 0.48; E = −0.05; Se = 0.08	NI	NI	NI	wi = 0.66; E = −0.03; Se = 0.08	4	0.10	0.64
1000		NI	NI	wi = 0.65; E = 0.05; Se = 0.15	wi = 0.65; E = −0.18; Se = 0.15	wi = 0.47; E = −0.05; Se = 0.07	NI	NI	NI	wi = 0.65; E = −0.04; Se = 0.09	4	0.10	0.63
500	Spider Ab[b]	NI	NI	wi = 0.82; E = −0.07; Se = 0.07	wi = 0.82; E = −0.09; Se = 0.05	wi = 0.37; E = −0.01; Se = 0.02	NI	NI	NI	wi = 0.82; E = 0.008; Se = 0.03	3	0.14	0.63
1000		NI	NI	wi = 0.69; E = −0.07; Se = 0.07	wi = 0.39; E = −0.03; Se = 0.05	wi = 0.42; E = −0.01; Se = 0.02	NI	NI	NI	wi = 0.39; E = 0.0005; Se = 0.02	6	0.13	0.62
500	Carab Ab	NI	NI	wi = 0.29; E = 0.03; Se = 0.12	wi = 0.29; E = −0.05; Se = 0.09	wi = 0.12; E = −0.003; Se = 0.09	NI	NI	NI	wi = 0.55; E = −0.06; Se = 0.08	4	0.06	0.75
1000		NI	NI	wi = 0.49; E = 0.07; Se = 0.16	wi = 0.49; E = −0.09; Se = 0.11	–	NI	NI	NI	wi = 0.72; E = −0.09; Se = 0.09	3	0.07	0.75
500	Staph Ab	NI	NI	wi = 0.53; E = 0.12; Se = 0.18	wi = 0.30; E = −0.06; Se = 0.11	wi = 0.59; E = −0.07; Se = 0.08	NI	NI	NI	wi = 0.38; E = 0.01; Se = 0.06	7	0.11	0.71
1000		NI	NI	wi = 0.64; E = 0.16; Se = 0.20	wi = 0.37; E = −0.08; Se = 0.12	wi = 0.55; E = −0.07; Se = 0.08	NI	NI	NI	wi = 0.37; E = 0.008; Se = 0.06	6	0.12	0.71
500	Pred Evenness	NI	NI	**wi = 0.99**; E = 0.36; Se = 0.12**	**wi = 0.91**; E = 0.31; Se = 0.14**	NI	NI	NI	NI	wi = 0.93; E = 0.03; Se = 0.09	1	0.24	0.47

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Table 2 (*continued*)

Scale (m)	Response	OSR_{t0} (%)	OSR_{t-1} (%)	SN (%)	SN* Weed cover	Pb larvae	Pb adult	Pb larvae * Parasitoid Ab	Parasitoid Ab	Weed cover	#models Δ wi < 2	R^2m	R^2c
1000		NI	NI	wi = 0.95**; E = 0.36; Se = 0.13	wi = 0.87.; E = 0.24; Se = 0.12	NI	NI	NI	NI	wi = 0.90; E = 0.05; Se = 0.09	1	0.24	0.47

[a] Response variable was transformed (log) to homogenize residuals.
[b] Response variable was transformed (sqrt) to homogenize residuals.

and was therefore included in all models testing for landscape effects on pollen beetle larvae (Table 2, Fig. 3). Current year OSR had a high probability to appear in the best model for larvae abundances, but this was only true for the smaller spatial scale of 500 m radius landscape (*p*-value < 0.01) (Table 2, Fig. 2b).

3.1.2. Natural enemies

There was no effect of pollen beetle larvae abundances on parasitoid abundances (*p*-value = 0.17), therefore this factor was not included in the model investigating landscape effects. Proportion of current year OSR had a negative effect on parasitoid abundances at larger spatial scales (*p*-value < 0.05) (Table 2). Parasitism rates increased with increasing parasitoid abundances but only when pollen beetle densities were low as suggested by a positive interaction term (*p*-value = 0.01). Therefore the interaction was included in all models testing for landscape effects on parasitism rates. Overall parasitism rate was negatively affected by increasing proportion of current year OSR at both spatial scales (*p*-value < 0.05) (Fig. 4, Table 2). Current year OSR was the only landscape variable to have a high probability to be selected in the best model for parasitism.

Predator species richness and CWM body size were affected neither by local nor landscape variables, all variables had a low probability to be in the best model (w_i < 0.45) (R^2 < 0.05) (data not shown). For predator community evenness only one best model with Δ w_i < 2 was selected for which the relative importance values obtained for the proportion of semi-natural habitat and its interaction with weed cover were high for both spatial scales (Table 2). Generalist predators community evenness decreased with increasing proportion of semi-natural habitat at both spatial scales (*p*-value < 0.01) but only when local weed cover was low (*p*-value ≤ 0.05) (Table 2). For generalist predator abundances, four models with Δ w_i < 2 out of 16 possible model combinations were selected. For all scales, the relative importance values (w_i) obtained for proportion of semi-natural habitat, weed cover, and interaction between these values were high (w_i = 0.66) but non-significant, the interaction factor appeared in 2 out of the 4 best models selected (Table 2). A similar result was found for spider abundances but only at small spatial scales, where the interaction term had a high importance (w_i = 0.82), appearing in 2 out of the 3 selected best models, but was not significant. There were no significant effects of landscape and local variables on the abundance of the dominant predator species/genus in each taxon (data not shown).

3.1.3. Pollen beetle mortality

The model for mortality with highest explanatory power contained clay%, and generalist predator abundance (Table 3). Mortality was higher when soil clay% was high (*p*-value < 0.001) and when generalist predator abundance increased (*p*-value < 0.05) (Fig. 5). In addition, a combination of all taxa contributed synergistically to pollen beetle mortality. Indeed, no effects of predator abundances on pollen beetle mortality were found when including predator abundances for each group separately (spiders, carabids and staphylinids) or abundances of the dominant species/genus within each order (data not shown). The effective mortality caused by parasitoids was low, on average 0.017% (min = 0% and max = 0.24%) compared to mortality due to predators and other abiotic factors (see Büchi, 2002 for calculations of effective parasitoid mortality).

4. Discussion

We found that pest abundance increased with increasing host crop area in the landscape while parasitism rates declined, indicating a lower pest control by specialist natural enemies in landscapes with a high proportion of OSR. Increasing proportion of semi-natural habitat in the landscape did not enhance local pest or natural enemy abundances. More even communities of generalist predators were found in landscapes with low proportion of semi-natural habitats and low local weed
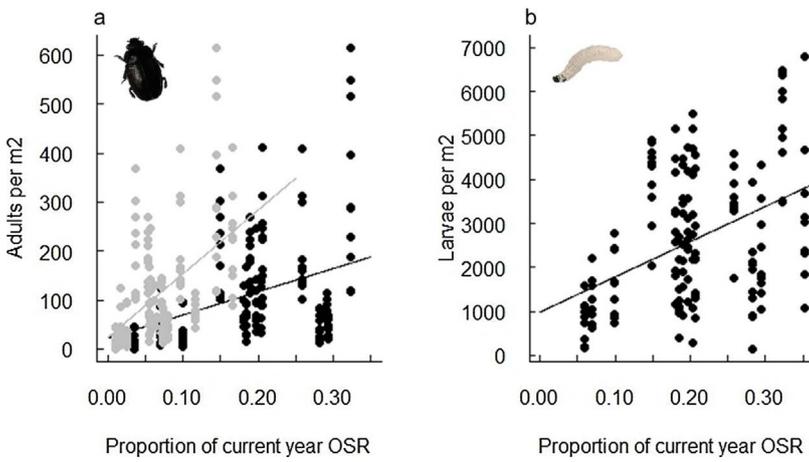
Fig. 2. Model prediction showing the relationship between a. pollen beetle adult abundance per m², b. pollen beetle larvae abundance per m² and the proportion of oilseed rape in the current year of study habitat at 500 m radius (black) and at 1000 m (grey).
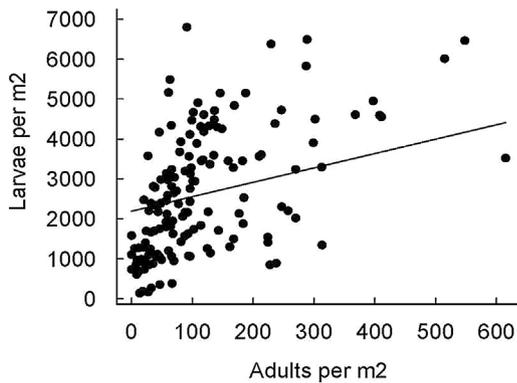

Fig. 3. Model prediction showing the relationship between pollen beetle larvae per m² and pollen beetle adult per m².
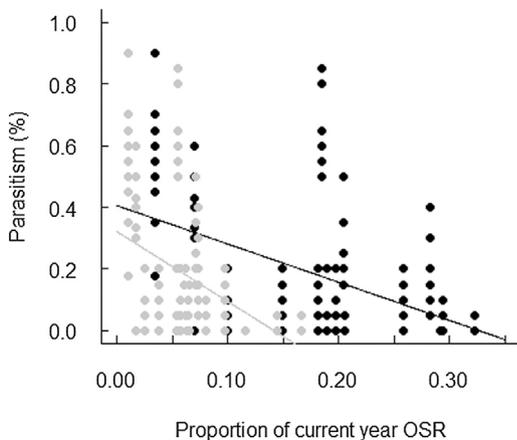

Fig. 4. Model prediction showing the relationship between proportion of parasitized larvae and current year oilseed rape at scale 500 m (black) and 1000 m (grey).

cover. This suggests that the generalist predator communities do not depend on the species pool provided by semi-natural habitats. Finally, we show that pollen beetle mortality increased when overall abundance of ground-dwelling generalist predators was high and when soil clay content was high. In contrast we found no effect of parasitism rates on net pollen beetle mortality.

4.1. Local and landscape effects on pollen beetle and their natural enemies

Proportion of current year OSR enhanced both adult and consequently larval stages of the pollen beetle, supporting the resource concentration hypothesis (Tahvanainen and Root, 1972; Thies et al., 2003). However, negative relationships between current year OSR and pollen beetle densities have also been found (Frank et al., 2010; Schneider et al., 2015; Zaller et al., 2008b). One explanation for this difference is that when there is inter-annual OSR reduction in the landscape, pollen beetles crowd, whereas when there is expansion pollen beetles dilute (Schneider et al., 2015). We did not detect inter-annual effects at the investigated scales (data not shown). However, at the regional scale of Västra Götaland, the proportion of OSR decreased between years, with $OSR_{(spring + winter)}$ = 3.2% of total arable land in 2012, and $OSR_{(winter)}$ = 1.1% in 2013 (Agricultural statistics, http://scb.se/sv). High densities of pollen beetles, due to high OSR resources in the previous year, coupled with decreased resources in the year of sampling may have led to a concentration of pollen beetles in landscapes with high OSR. This corroborates the resource concentration hypothesis which states that specialist herbivorous insects will become more abundant with increasing host plant patches because the insects are more likely to find and stay longer in those patches.

Contrary to the effect on the pollen beetles, current year OSR had a negative effect on parasitoids and parasitism rates. This is in line with indications of a dilution effect of parasitism rates in landscape with high OSR (Schneider et al., 2015; Thies et al., 2008). Dilution of parasitism rate with increasing OSR could also be an indirect effect via increased pollen beetle larvae density in the field which in turn could have decreased the positive link between parasitoid abundance and parasitism

Table 3

Summary of the best models after multimodel inference for pollen beetle mortality (%). Presented are the results from the full average model (w_i – relative variable importance, E – estimate and Se – standard error). Abbreviations: R2m: marginal coefficient of determination, R2c: conditional coefficient of determination, *: interaction and –: variable not present in models with Δ wi < 2. P-values: * < 0.05, *** < 0.001. Significant results are shown in bold.

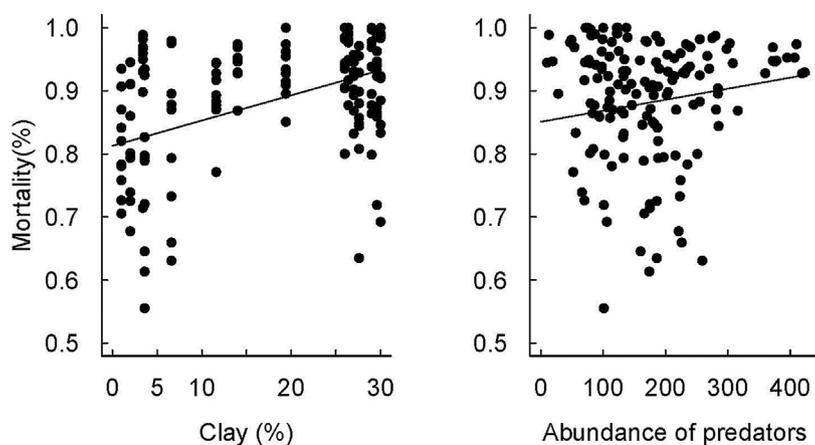| Response	Clay (%)	pH	Parasitism	Pred Ab	Pred Ab * Parasitism	Pred Richness	Pred Evenness	CWM body size	# models Δ wi < 2	R2m	R2c
Mortality	**wi = 1***;** **E = 0.37;** **Se = 0.10**	wi = 0.58; E = 0.09; Se = 0.10	wi = 0.28.; E = 0.02; Se = 0.05	**wi = 1*;** **E = 0.22;** **Se = 0.09**	–	wi = 0.58.; E = −0.07; Se = 0.08	–	–	7	0.24	0.46

Fig. 5. Model predictions showing the effect of% clay in the soil and predator abundance on pollen beetle mortality (%).

rates in landscape with high OSR habitat. The opposite direction of the effects of current year OSR on parasitism rates and host abundances suggests that parasitoids are not as effective at controlling pollen beetle in landscapes with a large OSR crop area, in particular when host densities are high. Therefore, current landscape management promoting uniform large OSR patches across large scales promotes unstable dynamics between parasitoids and their host, benefiting the pest and undermining biological control by parasitoids. Parasitoid abundances did not respond to previous year OSR area. This was unexpected as parasitoids overwinter as pupae in these habitats (Beduschi et al., 2015; Rusch et al., 2011). This discrepancy may be due to low cover of previous year OSR in the region (0–15%) compared with other studies (0–45%) (Beduschi et al., 2015). Insecticide exposure and soil tillage also affects parasitoid survival rate (Hanson et al., 2015; Rusch et al., 2011). Large amounts of pesticides known to be applied for pollen beetle control were sold across Sweden in 2012 and 2013 (Table B, Supplementary material). Therefore, insecticide application may have had a greater impact than landscape composition on parasitoid abundances but not on pollen beetle abundances because of widespread insecticide resistance in the studied region (Riggi et al., 2015).

We found no positive effect of semi-natural habitats on pollen beetle abundances and their natural enemies. This is in contrast to previous works in OSR where positive effects of non-crop area in the landscape on pollen beetle abundance (Rusch et al., 2013, 2012; Zaller et al., 2008b), parasitoid abundance and parasitism rates (Beduschi et al., 2015; Rusch et al., 2011; Thies et al., 2003; Thies and Tscharntke, 1999), and spider and carabid abundances (Drapela et al., 2008; Haschek et al., 2012) were found. However a recent study by Schneider et al. (2015) also found no positive effect of semi-natural habitats on pest control by specialist natural enemies. The reason for these discrepancies may be twofold:

First, the parameter semi-natural area *per se* encompasses various land-uses such as ley, meadows and woody areas that can individually have contrasting effects on abundance of a pest and its natural enemies. For instance, in our study the proportions of woodland areas necessary for pollen beetle overwintering were low, between 0 and 28% compared with 0 and 47% in another study (Rusch et al., 2011). In addition, grassland elements were composed of ley and pastures while, in other studies, the grassland elements comprised mainly fallows and meadows (Rusch et al., 2011; Thies et al., 2003; Thies and Tscharntke, 1999). A finer functional description of these habitats in terms of resources for species will provide improved mechanistic understanding of the effects of semi-natural habitats in the landscape (Sarthou et al., 2014).

Second, the taxonomic scale, in particular for ground-dwelling predators, might be insufficient to unravel landscape effects (Drapela et al., 2008; Haschek et al., 2012; Schmidt et al., 2005). Functional or species level analyses are better able to distinguish responses of predators to landscape due to specific preferences (Butterfield and Suding,

2013; Rusch et al., 2014). When analysed individually, however, carabids, spiders and rove beetles dominant species/genus abundances were not affected by landscape or local variables. Furthermore overall abundance and richness of generalist predators did not respond positively to increasing landscape complexity as initially hypothesized. This suggests that generalist predators in OSR are true crop inhabitants and that there is little exchange between semi-natural habitats and OSR (Tscharntke et al., 2016). This is in line with a recent study that found that top-down control of aphid in cereal fields was not generally higher in landscapes with low intensity agriculture across five European regions (Thies et al., 2011).

The intermediate landscape-complexity hypothesis was not supported in OSR crops. This is in opposition to recent findings where provision of alternative resources via plant diversity in annual crops (kale, maize and other cereals) enhanced natural enemies in simple but not in complex landscapes (Concepción et al., 2007; Jonsson et al., 2015; Midega et al., 2014). The two reasons described above of insufficient landscape and/or taxonomic resolution might explain this. An alternative, non-exclusive, hypothesis is that OSR provides greater resource availability and shelter compared to other annual crops (Westphal et al., 2003). Therefore practices increasing within crop plant diversity might not benefit local arthropods communities in OSR fields. In addition, contrary to expectations we found that the community of generalist predators was more even when local and landscape scale complexity was low, suggesting that overall, these communities are rather well adapted to crop habitats (Tscharntke et al., 2016).

4.2. Pollen beetle biological control

Higher abundances of ground-dwelling predators correlated with decreased pollen beetle emergence (Table 1). This is in line with a previous exclusion experiment showing that arthropod predation can reduce pollen beetle larvae numbers by about 22% across three years (Büchi, 2002). Interestingly, our results did not support the idea that high evenness of natural enemy communities, high natural-enemy species richness, and communities with on average larger predators improved pest control (Ewers and Didham, 2006; Letourneau et al., 2009; Crowder et al., 2010). We found a cumulative effect of all ground-dwelling predator abundances on pest mortality rather than any specific dominant species or taxon having a stronger impact on pollen beetle mortality. This suggests that at high pest density there is an additive or even a synergistic effect of spiders, carabids and staphylinds on pest mortality (Schmidt et al., 2003; Snyder et al., 2006). Surprisingly, parasitism rates did not affect pollen beetle mortality. Parasitoids remain in the egg stage until the pollen beetle larvae enter the soil to pupate (Osborne, 1960). Thus it can be assumed that predators do not distinguish between parasitized and unparasitized larvae. This is in line with the finding of low effective mortalities from parasitoids in OSR

(1–2%) despite high rates of parasitism (Büchi, 2002).

We could not distinguish between predation and other causes of mortality in the soil. However, we found a positive effect of soil texture on pollen beetle mortality. An increase in clay of 30% (corresponding to a 5% increase in total clay content) increased pollen beetle mortality by 10%. One reason could be that soils with higher clay content have greater water holding capacity (Cosby et al., 1984), and this is known to enhance the development of entomopathogenic fungi (Luz and Fargues, 1999). However, studies on this aspect are few (Hokkanen, 2008; Meyling et al., 2012; Rusch et al., 2012) and further research investigating interactions between soil properties and pollen beetle mortality is required to be able to generalize these observations.

5. Conclusions

Our results suggest that increasing resource concentration in the landscape has the potential to undermine biological control of pollen beetles by specialist natural enemies. However, overall generalist predator abundances in OSR crops were not affected by landscape context, suggesting that they are well adapted to arable habitats at least within the gradient investigated. Therefore, predation by generalist ground-dwelling predators could offset the detrimental effects of increasing OSR in the landscape on specialist pest control in OSR systems. Direct investigations of pollen beetle mortality in the soil are necessary to unravel whether the observed pattern is linked to entomopathogenic fungi as hypothesized. Moreover, longer-term investigations of both local and landscape context effects on pollen beetles and their natural enemies are needed to confirm the observed patterns in our study.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.06.039.

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