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Using multi-level generalized path analysis to understand herbivore and parasitoid dynamics in changing landscapes

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Abstract

Context In patchy environments, such as agricultural landscapes, both spatial and temporal scales of habitat heterogeneity can affect population dynamics and trophic interactions. As a result of crop rotation, landscapes and local resource availability may change dramatically within and between years.

Objectives We used a tritrophic interaction constituted by pollen beetles, their host plant oilseed rape, and their parasitoids, as a model system to investigate how the effect of landscape composition on insect abundance changes with time and whether system dynamics showed carry-over effects of previous years. We employ path analysis models that allow us to study whole networks of hypotheses rather than univariate cause–effect relationships.

Methods We exposed pan traps in a 5×5 grid design within 10 landscapes in June 2011 (after oilseed rape flowering) and May 2012 (at peak oilseed rape flowering). Additionally, we assessed parasitism rates of pollen beetle larvae in May 2011 and measured changes in landscape composition.

Results The effect of the oilseed rape proportion on beetle abundance changed with time from negative (during flowering) to positive (after flowering). Parasitism had a negative effect on the number of newly emerged pollen beetles, but only in landscapes with a low proportion of oilseed rape. Interestingly, our path analysis showed that landscape composition affected herbivore abundance 1 or 2 years later, mediated by changes in parasitism.

Conclusions Our results suggest that plant–herbivore–parasitoid interactions in dynamic agricultural landscapes can show interannual carry-over effects, as they are affected by landscape composition and top-down effects in previous years.

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Introduction

Agricultural landscapes are characterized by rapid changes in composition as a result of crop rotations (Wissinger 1997; Thies et al. 2005). From an insect herbivore perspective, the availability of suitable host plants may change drastically even within the course of a year (Wissinger 1997).

Effects of landscape context on a given insect herbivore or whole insect communities have often been studied using landscape sectors around individual sampling locations based on sampling only one season (Steffan-Dewenter et al. 2002; Chust et al. 2003; Tscharntke et al. 2005; Concépcion et al. 2008; but see Thies et al. 2008). While these studies have yielded a wealth of insights, they have not evaluated the complex relationships through time and space, but rather focused on either space or time.

Both spatial and temporal scales are important to understand trophic interactions and population dynamics (Kareiva et al. 1990; Fahrig 1992; Pickett and Cadenasso 1995; Roland and Taylor 1997; Thies et al. 2005). Patterns of distribution and abundance of a species might be different when viewed broadly in time and space instead of at a fine scale over a short time period (Wiens et al. 1985). Nonetheless, most studies have focused only on the effect of spatial scale and one habitat type. Therefore, in this study, we performed a comprehensive analysis which included a larger temporal scale, replicated in 1 × 1-km landscape grids. This allowed us to assess a possible carry-over effect, where past years' landscape composition remains influential through long-lasting, interannual effects on insect abundance. Carry-over effects have been observed for soil microorganisms and precipitation (Kardol et al. 2007; Reichmann et al. 2013), as well as for landscape components that affected the abundance and species richness of solitary bees in the following year (Le Féon et al. 2013).

In Central Europe, cropped land is dominated by cereals such as wheat and barley; increasingly, other crops such as maize and oilseed rape are grown. Locally, root crops such as sugar beet are widespread (Eurostat 2013). In addition, most landscapes contain up to 40 % forest and 10 % semi-natural habitats such as extensively managed grassland (Keil et al. 2010). While amounts of forest and grassland remain relatively stable, cropped land is characterized by strong internal changes in crop identity over time (Tiemann et al. 2015). Many groups of insects, such as pollinators, herbivores or parasitoids, may change in abundance in response to changes in crop composition. In particular, mass-flowering crops such as oilseed rape have been shown to strongly shape insect abundance (Westphal et al. 2003; Holzschuh et al. 2011).

Oilseed rape (Brassica napus L.) is a highly subsidized crop and the increasing demand for the oil produced with its seeds has been followed by an increase in acreage (Alford 2003; BMBF 2012) and a growth of pest populations (Hokkanen 2000). Many pests attack oilseed rape crops, but the pollen beetle (Meligethes aeneus F.) is the one that causes the most pronounced negative impacts on oilseed rape flowers (Zaller et al. 2008a) and also requires the most control measures (Williams 2010). Due to the different feeding phases, the great capacity of dispersal (Fritzsche 1957) and the possibility of parasitism, pollen beetle abundance can be affected by different landscape components, mainly at large scales (Thies et al. 2003; Zaller et al. 2008a; Rusch et al. 2013a).

Nevertheless, it is still not clear how these components, especially the proportion of oilseed rape, influence beetle abundance. It has remained uncertain if the percentage oilseed rape in a landscape is negatively (Zaller et al. 2008a), positively (Valantin-Morison et al. 2007) or neutrally (Thies et al. 2003; Rusch et al. 2013a) related to pollen beetle abundance. The discrepancies in the results may arise from unknown differences among the study regions (Rusch et al. 2013a), but they could also represent the result of the temporal dynamics in the relationship between pollen beetles, their parasitoids and oilseed rape.

Parasitism rate has been shown to be influenced by soil tillage, insecticide use and landscape composition (Nilsson 1985; Thies and Tscharntke 1999; Ulber et al. 2010). While the positive effect of the proportion of non-crop has been shown (Thies and Tscharntke 1999; Thies et al. 2003; Rusch et al. 2011), the role of oilseed rape fields in the surrounding areas is still unclear. Evidence published so far indicates that the proportion of this crop in the previous year could be an important determinant (Thies et al. 2008; Rusch et al. 2011). However, this possibility has never been directly tested, since the studies considered either the difference in percentage of oilseed rape between years (Thies et al. 2008) or the proportion of previous year oilseed rape fields with conventional soil tillage (Rusch et al. 2011).

Even though previous studies have investigated how landscape features influence pollen beetle abundance and parasitism, to our knowledge, no study so far has examined the effects on the whole trophic interaction at once. While multiple regression approaches allow deep insights, they may fail in complex interacting systems (Grace et al. 2014). Here, we employ generalized multilevel path analysis

(Shipley 2002) to study changes in herbivore abundance over time and how it is affected by parasitism in changing landscapes. We used a grid-based sampling approach (following Scherber et al. 2012) in 10 replicated landscapes over two field seasons and aimed to answer the following questions:

- Is parasitism rate more strongly affected by host plant abundance (the proportion of oilseed rape) in the previous or in the current year?
- Can we observe a change in the effect of different landscape components on herbivore abundance between two study years?
- Is beetle abundance driven by carry-over effects that span over 1 or 2 years?

Methods

Study system

We used pollen beetle (*M. aeneus*) as a model system because this is one of the numerically most abundant insect herbivores in Central Germany (Ryszkowski et al. 2001). Moreover, previous studies have suggested the existence of an interannual effect on this tritrophic interaction (e.g. Thies et al. 2008; Rusch et al. 2011). The pollen beetle emerges in early spring, after overwintering in the soil of field margins or woodlands, and feeds on pollen of various species of plants before migrating into oilseed rape fields (Nilsson 1988; Williams 2010). They arrive in the fields during bud stage and will feed on pollen by chewing into the buds, where they also oviposit (Nilsson 1988; Cook et al. 2004). The main damage caused by pollen beetles happens during the bud stage, since feeding and oviposition cause bud abscission and may reduce yield (Zaller et al. 2008b; Williams 2010). The larvae feed on pollen and eventually drop to the soil to pupate. The development from egg to adult takes about 1 month (Cook et al. 2004; Williams 2010). The newly emerged pollen beetles feed on the pollen of different flowers when spring oilseed rape is not available, since the flowering of winter oilseed rape fields will have ended (Hokkanen 2000). Adults of the first generation die after egg laying and, in late summer, the new generation of beetles seek overwintering sites and will only reproduce in the following year (Nilsson 1988; Williams 2010). During the larval stage, pollen beetles are susceptible to attack by specialized parasitoids. The three most common species are *Tersilochus heterocerus* (Thomson), *Phradis interstitialis* (Thomson) and *Phradis morionellus* (Holmgren) (Ulber et al. 2010). The parasitoid egg is laid inside the pollen beetle larvae and hatch once these drop to the soil to pupate (Ulber et al. 2010). In the soil, the parasitoid larva completes its feeding and pupates. Parasitoids overwinter as diapausing adults in the soil of the oilseed rape fields and emerge in the following spring (Jourdheuil 1960; Nilsson 2003).

Sampling procedures

Sampling was performed in 2011 and 2012 in ten landscapes in the surroundings of Göttingen (51°32′N, 9°56′E) in Central Germany. The region mainly consists of cropped land interspersed with semi-natural non-crop areas like meadows, calcareous grasslands and woodlands. Landscapes were approximately 1 km × 1 km wide (mean area ± SD = 0.93 ± 0.23 km^2) and represented orthogonal gradients of the proportions of winter oilseed rape and non-crop area, selected at random from a larger set. Yellow pan traps (150 mm × 60 mm, 750 ml) were placed at vegetation height throughout each landscape following a 5 × 5 grid and exposed for 3 days in June 2011 (after oilseed rape flowering) and May 2012 (at peak oilseed rape flowering) in order to collect pollen beetles and their parasitoids. The sampling grid was laid out over the landscapes in such a way to always include forest margins and grasslands (non-crop areas) as well as crop fields, while excluding cities or villages. The number of points located in each habitat type and an example of a sampling landscape can be found in the Supplementary Material (Table S1; Fig S1, respectively). Overall, 250 pan traps were exposed per sampling round. Given that some traps were damaged or vandalized, and that a pan trap could only be included in the model when it was present in both years, the final number of samples was 237 per round. The beetles collected when oilseed rape fields were no longer flowering represent mainly the new generation of beetles of 2011 (Williams et al. 2007). These beetles were still in their larval stage during oilseed rape blooming and, therefore, could have been attacked by parasitoids. The beetles collected in May 2012 were the same beetles; mature adults that had emerged in the previous year and had overwintered, possibly in nearby forest margins.

In May 2011 (at the peak oilseed rape flowering), the flowers of five oilseed rape plants were collected in each grid point located in an oilseed rape field (N = 58) to estimate parasitism rates. Wild flowers in non-crop areas were also inspected, but no pollen beetle larva was found outside oilseed rape flowers. The identity of the flowers was not recorded in detail but included *Taraxacum* spp. (most abundant genus), *Belis* sp., *Papaver rhoeas* and *Cardamine* sp. Other species were present in lower abundances. All larvae located within the sampled flowers were counted and, in each sample, 20 individuals were dissected in order to determine the parasitism rate. In the grid points where no larvae were present, the parasitism rate was defined as zero.

Landscape parameters

We used satellite-based image classification (RapidEye[TM] multispectral imagery, level 3A, 5 bands, resolution 5 m/pixel; classified using ENVI EX 4.8, Exelis VIS, Boulder, Colorado, USA) to measure proportions of oilseed rape fields and non-crop areas, which include meadows, pastures and forests. Percentage of non-crop area has been shown to be a robust criterion for the quantification of habitat complexity as it tends to be closely correlated with other landscape metrics such as habitat diversity (Thies and Tscharntke 1999). These measurements were done for the years of 2010, 2011 and 2012 and for all study areas using the software ArcGis 10.1 (ESRI Redlands, CA, USA). While the proportion of oilseed rape fields changed greatly through time, due to crop rotation, the proportion of non-crop area did not change in the studied years. Only winter oilseed rape is considered, given that no spring oilseed rape fields were observed in the study areas or in the surroundings.

According to the literature, pollen beetle abundance and parasitism are affected by landscape components at larger scales, ranging from 750 m (Thies et al. 2003) to 1250 m or larger (Zaller et al. 2008a, b). For this reason, we defined a radius of 1000 m around each of the 237 sampling points. This value is a mean between the distances reported in the literature and presented a low correlation between explanatory variables (i.e. the proportions of oilseed rape and non-crop area, Supplementary Material Table S2).

Data analyses

To evaluate how landscape features and parasitism rates affect pollen beetle abundance over time, we used generalized multilevel path analysis (Shipley 2009). In contrast to classical structural equation modelling, this approach can accommodate nonlinear relationships and non-normal error distributions. Additionally, it is possible to take into account the hierarchical structure of the data, which would, otherwise, violate the assumption of independence among observations.

The model we tested proposes that landscape components affect pollen beetle abundance differently through time both directly and indirectly, through parasitism (Fig. 1). We hypothesized that parasitism rates in 2011 were affected by the proportion of oilseed rape fields in 2010 and 2011 as well as the proportion of non-crop area within the 1000 m buffer. Moreover, pollen beetle abundance in June 2011 would be determined by parasitism rates in the same year, along with the proportions of oilseed rape and non-crop area. These landscape components could also influence pollen beetle abundance in 2012, together with the habitat where each yellow pan trap was located (local scale) and pollen beetle abundance from the previous year. Based on the path diagram constructed following these hypotheses, we generated all possible independence claims, i.e. directional separations (Supplementary Material Table S4). A directional separation (d-sep) comprises a pair of variables that, according to a given path model, are expected to be statistically independent upon conditioning on some other set of variables. In order to test the full causal hypothesis represented by the path diagram, we performed a simultaneous test of all four independence claims. That was done by combining the null probabilities of each independence test according to:

$$C = -2 \sum_{i=1}^{k} \ln(p_i)$$

where k is the number of d-sep tests and p_i are the p values obtained in each d-sep test. Model fit was evaluated by comparing C to a χ^2 distribution with $2k$ degrees of freedom.

The model path coefficients were estimated by fitting generalized mixed models with random intercepts for each sampling landscape. Binomial and Poisson error distributions were used when the response variable was parasitism rate and pollen beetle abundance, respectively. In order to account for
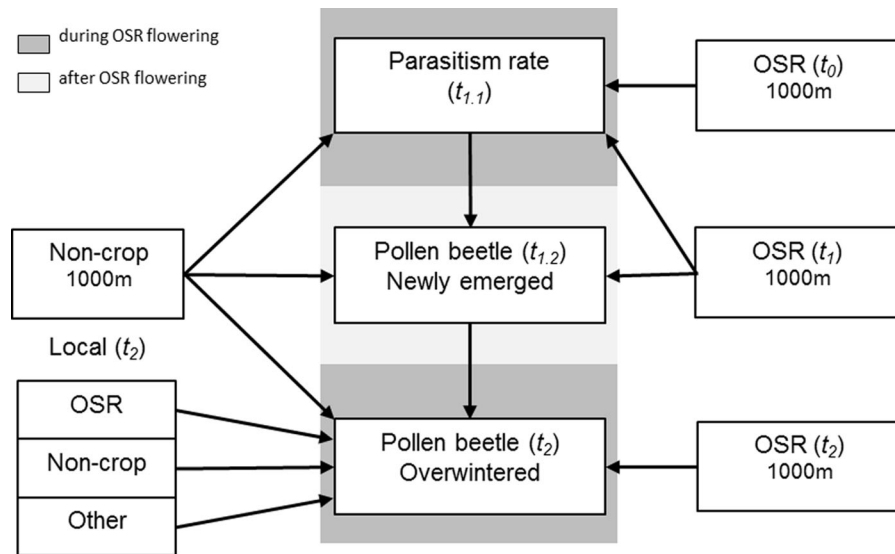
Fig. 1 Conceptual structural equation model illustrating hypothesized effects of landscape components on pollen beetle abundance and parasitism through time. "OSR" indicates proportion of area occupied by oilseed rape fields and "Non-crop" the proportion of non-crop area in the surroundings, both within a 1000 m buffer from each sampling point. "Local" represents the sampling habitat: non-crop areas (Non-crop), oilseed rape fields (OSR) or other crop fields (Other). Time steps are represented by "t". t_0 = 2010; t_1 = 2011; t_2 = 2012; $t_{1.1}$ = May 2011; $t_{1.2}$ = June 2011

overdispersion in the beetle abundance data, we added an observation-level random effect (Elston et al. 2001). When used as an explanatory variable, pollen beetle abundance was log transformed to reduce the influence of outliers and to match the log link applied in generalized mixed models. Independence claims were tested in the same way. Interactions were kept in the model when they were both significant ($p < 0.05$) and provided an improvement in Akaike's Information Criterion (AIC) higher than 3 (Burnham and Anderson 2002). Residuals were tested for spatial autocorrelation using Moran's Autocorrelation Coefficient (Bivand et al. 2008). However, after the inclusion of a random intercept for each landscape, there was no remaining spatial pattern in the residuals. The conditional R-squared was calculated following Nakagawa and Schielzeth (2013). In order to increase clarity, we did not include the correlations between exogenous variables in the model shown in the results section. These can be seen in the supplementary material (Fig S2) and do not influence the relationships presented in Fig. 2.

To establish the determinants of parasitoid abundance in May 2012 (at peak flowering), we fit a linear mixed-effects model. The response variable was log transformed to reduce the influence of outliers and to achieve appropriate distribution of the residuals. The

initial explanatory variables were percentage of oilseed rape in 2011 and 2012, percentage of non-crop area around the sampling point and the type of crop (habitat) present in the sampling location in 2011 and 2012. The inclusion of habitat type, while not necessary to answer the proposed question, was important to guarantee the accuracy of the results. The use of attractive yellow pan traps may cause values to be higher in semi-natural habitats and cereal fields during oilseed rape flowering. Therefore, not accounting for the difference between habitat types could have masked the effect of landscape components. The model was simplified to achieve the smallest possible Akaike's Information Criteria (AIC) using forward and backward stepwise selection procedures. According to this method, all parameters remaining after model simplification had relevant explanatory power (Crawley 2013).

All statistical analyses were conducted with R 3.0.2 (R Core Team 2013). To fit the parasitoid abundance model we used the package "nlme" (Pinheiro et al. 2013). The hierarchical models were fit using the package "lme4" 1.0-6 (Bates et al. 2014). The package "spdep" 0.5-71 (Bivand and Piras 2015) was used to calculate the Moran's I. The package "effects" (Fox 2003) was used to create interaction graphs.
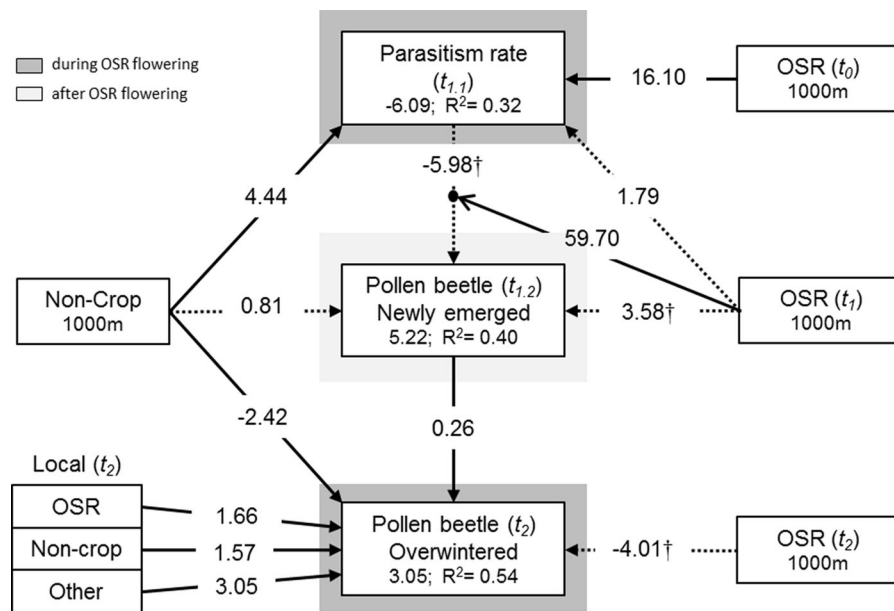
Fig. 2 Multilevel path analysis showing effects of different landscapes components on pollen beetle abundance and parasitism through time. "OSR" indicates the proportion of area occupied by oilseed rape fields within a 1000 m circle. "Non-crop" represents the proportion of non-crop area in the same *circle*. "Habitat" specifies the local land use where sampling was performed: non-crop areas (Non-crop), oilseed rape fields (OSR) or other crop fields (Other). This model was well supported (Chi square = 6.01, df = 8, $p = 0.64$). Path coefficients are unstandardized partial regression coefficients obtained from generalized mixed models. Path coefficients explaining parasitism rate are "logit" transformed. All other coefficients are "log" transformed. *Arrows* ending in other *arrows* represent interactions. Numbers before semicolons are the model intercepts. *Dotted arrows* represent non-significant relationships ($p < 0.05$). [†]Marginal significance ($p < 0.1$). Time steps are represented by "t". $t_0 = 2010$; $t_1 = 2011$; $t_2 = 2012$; $t_{1.1} = $ May 2011; $t_{1.2} = $ June 2011

Results

Data summary

The percentage of oilseed rape ranged from 0 to 26 % in 2010, 0–45 % in 2011 and 0–35 % in 2012. The proportion of non-crop area remained almost constant within each area throughout the years varying from 0 to 73 %. Mean pollen beetle abundance per trap was 1180 (SD = ±2565; min = 2; max = 33,006) in June 2011, and 62.81 (SD = ±142; min = 0; max = 1418) in May 2012 (more details can be found in the Supplementary Material Table S3). Mean parasitism rate was 2 % (SD = ±10 %; min = 0 %; max = 70 %). In May 2012, we collected 501 parasitoids, of which 95.8 % were *T. heterocerus*, followed by *P. interstitialis* (2.8 %), *P. morionellus* (0.8 %) and *Diospilus capito* (0.6 %). Since only seven parasitoids were collected in June 2011, these data were not analyzed.

Path analyses

Effects on parasitism: during oilseed rape flowering (2011)

Even though some paths were not significant, the hypothesized model was well supported by the data (Chi square = 6.01; df = 8; $p = 0.64$). The proportion of oilseed rape in the previous year ($p < 0.001$) and the proportion of non-crop area ($p < 0.01$) was positively related to parasitism rates, while oilseed rape in the same year had no significant effect ($p = 0.54$) (Fig. 2).

Effects on newly emerged pollen beetle: after oilseed rape flowering (2011)

Even though parasitism rate and the proportion of oilseed rape had marginally significant effects on newly emerged pollen beetle abundance in June 2011

($p = 0.06$ and $p = 0.09$, respectively), only their interaction was significant ($p < 0.01$). This indicates that parasitism only influenced pollen beetle abundance negatively in landscapes with lower proportions of oilseed rape (Fig. 3). Once these proportions were higher, pollen beetle abundance increased with parasitism rate. The proportion of non-crop area did not significantly affect the number of pollen beetles ($p = 0.40$).

Effects on overwintered pollen beetle: during oilseed rape flowering (2012)

Abundance of newly emerged pollen beetles, in turn, positively affected the number of beetles found in the next year during oilseed rape blooming ($p < 0.001$). Furthermore, this number was negatively affected by the proportion of non-crop area ($p < 0.05$) and a strong trend suggested a negative relationship between abundance of overwintered beetles in 2012 and the oilseed rape proportion. The sampling habitat influenced the amount of beetles per trap (oilseed rape fields $p < 0.05$; non-crop area $p < 0.05$; other fields $p < 0.001$). In the habitats named "other" (i.e. cereal and beet fields) significantly more beetles were collected in comparison to oilseed rape fields and non-crop area, which presented similar numbers.

Parasitoid abundance

The only remaining parameters in the parasitoid model were the sampling habitats from 2011 and 2012, which means that only these parameters had explanatory power. It was possible to observe that significantly more parasitoids were sampled in former oilseed rape fields, occupied in 2012 by other crops (Fig. 4; $p < 0.05$). Some parasitoids were also collected in oilseed rape fields, that had been other crops in the year before, but almost no parasitoids were sampled in non-crop areas.

Discussion

Our results show that the effect of oilseed rape fields and non-crop areas on pollen beetle abundance changed with time. Furthermore, the landscape composition had interannual consequences, constituting a carry-over effect.

Landscape components and parasitism rate

The strong positive effect of the proportion of oilseed rape in the previous year (2010) on parasitism rates in the following year (2011) had not been directly observed so far. It has been shown that the proportion of non-ploughed oilseed rape fields from the previous year can be an important determinant of parasitism rate (Rusch et al. 2013a) but, although all the fields in our study site were ploughed, this parameter still had the greatest effect. This is probably due to the fact that parasitoids of pollen beetles overwinter in oilseed rape fields (Jourdheuil 1960). The positive relationship between non-crop area and parasitism rate concurs with the literature (Thies and Tscharntke 1999; Thies et al. 2003; Rusch et al. 2011). The lack of ploughing in these environments may enable parasitoid populations to build up over years (Nilsson 1985; Thies et al.

Fig. 3 Effect of the interaction between parasitism rate and the proportion of oilseed rape in 2011 on the abundance of newly emerged pollen beetles. From *left* to *right*, graphs show low, intermediate and high percentage of oilseed rape within a 1000 m radius. *Gray-shaded areas* represent 95 % confidence intervals
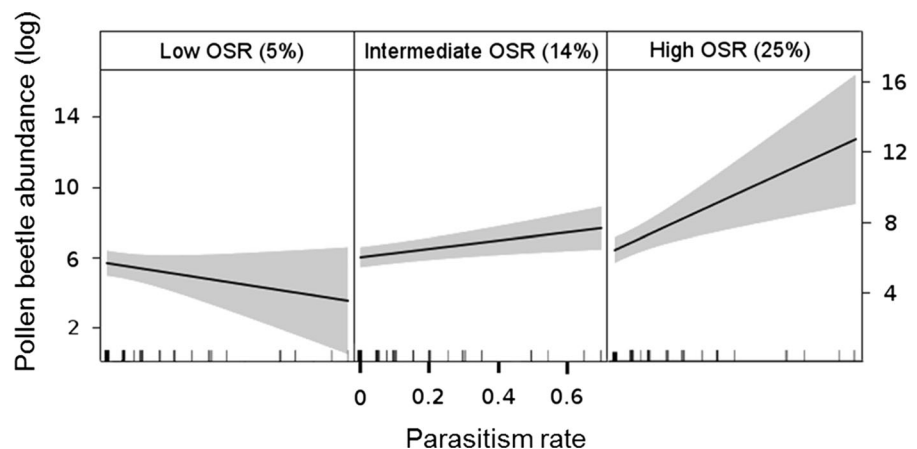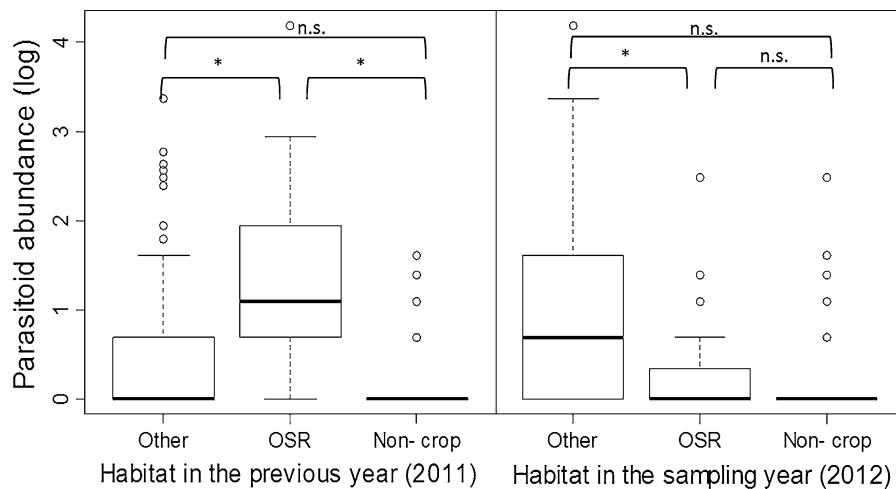
Fig. 4 Parasitoid abundance at oilseed rape peak flowering according to the kind of habitat found in the sampling location in the current (*right*) and in the previous year (*left*). "OSR" and "Other" represent oilseed rape and other crops (i.e. cereal and beet fields), respectively. *Asterisks* denote significant differences

2003). Likewise, these areas might provide alternative hosts or additional nectar resources (Wratten and Van Emden 1995; Frenzel and Brandl 1998). This supplementary food supply could facilitate the migration from hibernation sites to oilseed rape fields, given that, after hatching, the parasitoids are very limited in energy (Nilsson 2003; Rusch et al. 2013b).

Moreover, it is important to notice that parasitism rates were generally low, as was parasitoid abundance in 2011. This is possibly a consequence of the use of insecticides that year, which was intensified due to the high abundance of pollen beetles. It has been reported that insecticides can reduce parasitoid abundance by approximately 50 % and, therefore greatly affect parasitism rates (Ulber et al. 2010).

Effects of parasitism rate and oilseed rape on newly emerged pollen beetles

Even though the proportion of oilseed rape in 2011 did not affect parasitism rate, it did influence its efficiency. Parasitism rates only had a negative effect on subsequent abundance of newly emerged pollen beetles (2011) when the current proportion of oilseed rape in the landscape was low. Once the prevalence of this crop increased, pollen beetle abundance was positively related to parasitism rates. Similar results were reported by Gladbach et al. (2011), who found a positive relationship between pollen beetle larval abundance and parasitism rate and there are two reasons why this could be happening. The first is that parasitoids follow olfactory and visual cues coming from oilseed rape fields and are specially attracted by plants infested with pollen beetle (Williams et al. 2007; Jönsson and Anderson 2007) and the second is that the probability of a female encountering a host larva can increase with host density (Williams and Cook 2010). Our study indicates that the proportions of oilseed rape play a more important role in increasing pollen beetle offspring than parasitism in reducing it. This is possibly because a higher abundance of host plants can reduce intraspecific competition among pollen beetle larvae (Hokkanen 2000), accounting for the higher number of newly emerged pollen beetles in areas with higher proportions of oilseed rape.

Landscape components and overwintered pollen beetles

Conversely, during blooming the relationship between the proportion of oilseed rape in the current year and overwintered pollen beetles (2012) was negative. Even though oilseed rape fields attract pollen beetles (e.g. Williams et al. 2007; Williams and Cook 2010) it seems that, during flowering, the local pest pool, formed by the beetles that overwintered within the landscape, is an important limiting factor of pollen

beetle abundance. The strong dilution trend caused by oilseed rape area also indicates that in spite of the potential of large oilseed rape areas to attract over-wintered beetles from other landscapes, the populations were not large enough to exploit fully the short-term increase in flower resources. The negative influence of non-crop habitats on abundance of overwintered beetles could also represent a weaker dilution effect, as they would also spillover to these areas. Pollen beetles respond not only to volatiles emitted by oilseed rape but also to the odour of several plant species, including rye (*Secale cereale* L.) (Ruther and Thiemann 1997), and are often found in wild flowers (Ahmed et al. 2013; Honěk et al. 2013). Additionally, almost the same number of overwintered beetles (2012) was collected in oilseed rape and in non-crop areas, and even more were found in other crops. These results do not represent local abundance of pollen beetles, given that yellow pan traps will be less attractive when placed against the yellow background of the flowering oilseed rape in comparison to being placed in other crops. However, these results provide evidence that the pollen beetles will spillover from oilseed rape fields to surrounding habitats when a stimulus is provided. These results contrast with those of Gladbach et al. (2011) who found spillover from oilseed rape onto wild cruciferous plants only for parasitoids, but not pollen beetles. Possibly, this difference arises from the fact that in their study, only larvae sampled after flowering were considered and not adults. Once the oilseed flowers have faded, the number of adults and larvae can be uncorrelated, since many of the adults are newly emerged and unable to reproduce and most of the larvae will have already dropped to the soil to pupate (Williams et al. 2007; Williams 2010).

Overall, our study indicates that percentage of oilseed rape in the landscape can be an important driver of pollen beetle abundance. This is in line with a series of other studies (Valantin-Morison et al. 2007; Zaller et al. 2008a), but in contrast to Rusch et al. (2013a), in which the proportion of oilseed rape fields was considered to be much less relevant than non-crop area. In their study, sampling took place while oilseed rape fields were in the bud stage, when pollen beetles are still emerging from overwintering sites (i.e. non-crop area) and can still be largely influenced by the proportion of these sites. In our study, sampling was performed only during and after flowering.

Carry-over effects of landscape components

Our results showed an interannual carry-over effect of landscape components. For example, percentage of oilseed rape in 2010 affected overwintered pollen beetle abundance in 2012 by increasing parasitism rates in 2011 and, consequently, reducing the new generation of that year. These new beetles then partly comprised the pollen beetle population in the following year.

Given that agricultural landscapes are prevalent in Central Europe (Keil et al. 2010), this kind of carry-over effect from landscape components could commonly influence insect populations that benefit from farming areas. Recent history of land use has been shown to affect solitary bee diversity and abundance (Le Féon et al. 2013), as the inclusion of grasslands in crop rotation promoted a durable benefit to the bee community. Long lasting effects of landscape components can possibly also be observed in other pest populations, such as aphids, which are affected by processes acting at landscape scale (Thies et al. 2005).

The scale at which these effects can be observed will probably depend on the mobility of the organism and on landscape configuration. For example, in more compartmented regions, covered by large semi-natural habitats in one part and cropped land in the other, regional scale migrations of the mobile pollen beetles can occur (Rusch et al. 2013a). This would increase the spatial scale of the interannual carry-over effects or possibly overthrow them.

Recommendations for landscape managers

We propose that breaking off oilseed rape cultivation in a large area for one year, as suggested by Ekbom (2010), would be a more efficient strategy to control pollen beetles than keeping oilseed rape area constant (Zaller et al. 2008b; Frank et al. 2010). Avoiding dramatic fluctuations in oilseed rape area would probably enable the beetle population to build up through time, while the approach proposed by Ekbom (2010) could dramatically reduce the number of new generation beetles. Given that parasitoids would also be negatively affected, it is recommendable to create "parasitoid conservation" areas containing another possible host plant species, such as white mustard. With this setting, pollen beetles would be allowed to

lay eggs and parasitoids could reproduce. Ideally, such areas would be placed near to fields expected to have overwintering parasitoids.

Conclusions

We found that the effect of oilseed rape on pollen beetle abundance changed with time. It was negative during flowering on overwintered beetles and positive after flowering on new generation beetles. Additionally, it was possible to observe a carry-over effect of oilseed rape, given that the proportion of this crop in 2010 indirectly affected the abundance of overwintered pollen beetles in 2012. This effect was mediated by changes in parasitism rates, which then affected the abundance of newly emerged pollen beetles. Carry-over effects of landscape components could affect other insect populations in agricultural areas, but further studies are necessary to define how prevalent these effects are in other landscapes and organisms. Our study showed that parasitoid-host interactions and the host's population dynamics can be much more complex in the annually changing cropped land landscapes than usually thought. Generalized multilevel path analysis can be an important tool to study such cascading effects, given that this approach allows the analyses of networks of causal processes, while bivariate analyses are limited to simpler models (Grace et al. 2014).

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