Markó, V., Elek, Z., Kovács-Hostyánszki, A., Kőrösi, Á., Somay, L., Földesi, R., Varga, Á., Iván, Á., Báldi, A. (2017) Landscapes, orchards, pesticides–Abundance of beetles (Coleoptera) in apple orchards along pesticide toxicity and landscape complexity gradients. - Agriculture, Ecosystems and Environment, 247, pp. 246-254. DOI: 10.1016/j.agee.2017.06.038

Landscapes, orchards, pesticides – abundance of beetles (Coleoptera) in apple orchards along pesticide toxicity and landscape complexity gradients

Viktor Markó[1,4,*], Zoltán Elek[2,3,*], Anikó Kovács-Hostyánszki[2], Ádám Kőrösi[3], László Somay[2], Rita Földesi[2], Ákos Varga[1], Ágnes Iván[1], András Báldi[2]

[1]- *Department of Entomology, Szent István University, H-1118, Budapest, Ménesi út 44, Hungary*

[2]- *Lendület Ecosystem Services Research Group, Institute of Ecology and Botany, MTA Centre for Ecological Research, H-2163 Vácrátót, Alkotmány utca 2-4, Hungary*

[3]- *MTA-ELTE-MTM Ecology Research Group, c/o Biological Institute, Eötvös Loránd University and Hungarian Natural History Museum, Budapest, H-1117 Pázmány Péter sétány 1/C, Hungary*

*- The authors equally contributed to this paper

[4]- *Corresponding author:*

Viktor Markó Ph.D.

Szent István University, Faculty of Horticultural Sciences, Department of Entomology

H-1118, Budapest Villányi út 29–43, Hungary; tel.: +3613057672, fax: +3613057672, e-mail: Marko.Viktor@kertk.szie.hu

Abstract

Landscape composition may influence biodiversity and ecosystem services in agricultural fields. Hitherto, most studies have focused on annual crops and the available information on the impacts of landscape structure in orchards is sparse. In this study, we evaluated the effects of pesticide use as cumulative toxicity on pest and predatory beetle (Coleoptera) assemblages in the canopy of apple orchards surrounded by different proportion of semi-natural vegetation, crop fields and settlements in Hungary. Laboratory data suggest that increasing pesticide toxicity negatively affects predators (coccinellids), but we did not find such a pattern. Supposedly, the effect of pesticides was masked by the continuous recolonisation of orchards from the surrounding landscape. On the contrary, for the less mobile pest species [*Anthonomus pomorum*, *Phyllobius oblongus* (Curculionidae)] we did find a decline in abundance along the gradient of increasing pesticide toxicity. Landscape composition around the orchards significantly influenced the abundance of predatory, fungivorous and tourist species, but had no effect on pests. Contrary to expectations, however, semi-natural habitats had a minor effect compared to arable fields, orchards and settlements which habitat types had various effects on the abundance of different coleopteran groups and species. For example, *Harmonia axyridis* (Coccinellidae) abundance was positively affected by its overwintering sites, i.e. human settlements in spring, semi-natural forests in summer, and arable fields in autumn. The mass immigration of other predatory, fungivorous and tourist species from the surrounding arable fields into the orchards started from July with senescence and harvesting of arable crops. These results suggest that arable fields, other orchards and settlements might be more important sources of colonisation for natural enemies in orchards than certain semi-natural habitats.

Keywords: Coleoptera; Dispersal; Ecosystem service; Land-use systems; Perennial crops; Pest control

1. Introduction

Apple is by far the most widely grown fruit crop in the temperate zone and following banana ranks the second in world fruit production (FAOSTAT, 2016). It accounts for 35% of the total European orchard area (1.3 million hectares) with 10–14 million tons of apple production per year (Eurostat, 2015). Pests cause substantial losses in apple production, which could reach up to 80–90% in some years without adequate pest control (Cross et al., 2015; Sutton et al., 2014). Naturally occurring predators and parasitoids, however, can substantially contribute to the biological control of apple pests and thus bring economic benefits to growers (Cross et al., 2015). Although numerous studies have focused on the effects of landscape composition on pests and natural enemies in annual cropping systems, considerably less attention has been paid to perennial crops such as apple (e.g. Herrmann et al., 2012; Inclán et al., 2015; Maalouly et al., 2013).

Landscape composition plays a key role in determining insect dispersal in agricultural landscapes (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Thies and Tscharntke, 1999; Veres et al., 2013). Semi-natural habitats provide shelter, reproduction and overwintering sites for agricultural insects, thus serve as sources of cyclic recolonisation of agricultural fields after soil cultivation, pesticide applications or harvest (Holland et al., 2016; Miliczky and Horton, 2005; Wissinger, 1997). Conversely, pests and their natural enemies reaching high abundances in agricultural fields can also disperse in opposite direction into semi-natural habitats (Tscharntke et al., 2012). These patterns of dispersal might show similarities but also considerable differences in perennial and annual systems. Perennial crop systems like apple orchards persist for multiple growing seasons and might offer more stable, abundant and diverse resources for insects dispersing from semi-natural habitats than arable fields. Moreover, the landscape-moderated concentration and dilution hypothesis suggests that spatial and temporal changes in habitat availability in the landscape drives the local arthropod abundances, and hence predicts that arthropods emigrating from arable fields after harvest will also concentrate in orchards (Schellhorn et al., 2015; Tscharntke et al., 2012). Thus, we presume that both natural and anthropogenic habitats can support orchard insect assemblages, with a greater contribution of undisturbed habitats. Furthermore, in general, orchards are exposed to high level of pesticides compared to arable fields (Eurostat, 2007; Roßberg, 2013), and they might be exposed to a wide range of pesticide regimes with organic and intensively managed orchards at the two endpoints (Simon et al., 2011; Dib et al., 2016). In spite of the importance of pesticides in regulating arthropod populations, most landscape-scale studies have not covered their impact or it was taken into account by using cumulative management indices, which incorporate, along with the number of pesticide treatments, the intensity of soil preparation, weed control, grazing, pruning, and harvesting (e.g. Bailey et al., 2010; Grez et al., 2013, but see Monteiro et al., 2013).

Different arthropod species and guilds respond differently to pesticide use and landscape composition. Pesticide applications may have a greater impact on natural enemies than on pests, because natural enemies have a lower level of pesticide resistance and any decline in their prey and hosts may also influence their abundance negatively (Biddinger et al., 2009; Jonsson et al., 2012; Krauss et al., 2011; Lövei et al., 1991; Markó et al., 2009; Whalon et al., 2016). On the other hand, species at higher trophic levels, such as predators and parasitoids, could be more vulnerable to habitat loss, fragmentation and isolation than those at lower levels and are therefore less able to colonise the orchards from semi-natural habitat islands and recover less rapidly after pesticide applications (Bailey et al., 2010; Herrmann et al., 2012; Holt, 1996; Tscharntke et al., 2012). Thus species traits, pesticide applications and landscape composition may interact in shaping the arthropod communities in apple orchards. Increasing pesticide pressure and landscape degradation might shift the insect communities toward pests. Conversely, with decreasing pesticide pressure and increasing amount of semi-natural habitats in the landscape insect assemblages might shift toward natural enemies.

The availability of resources necessary for pests and natural enemies vary spatially and temporally in the landscape. Resource requirements of insects (e.g. for feeding, reproduction and overwintering) and their dispersal ability (e.g. only adults can disperse over long distances) may also change during the season. Thus the temporally overlapping resources can form species-specific resource chains (Schellhorn et al., 2015). Different insect species might disperse along different resource chains, i.e. they might show species- and season-specific responses to landscape composition (Raymond et al., 2015; Schellhorn et al., 2014, 2015). Identification of these habitat use patterns is essential for understanding how different landscape elements influence natural enemies and pests, and for gaining knowledge about how to manage landscapes and agricultural fields to maximise biocontrol services (Schellhorn et al., 2015).

Apple orchards harbour species rich and abundant beetle assemblages with several pest and predatory species (Markó et al., 1995; Sutton et al., 2014). Pests might cause damage to roots, trunk, branches, leaves, buds, flowers and fruits of apple trees, while predatory beetles, mainly coccinellids, are important contributors to the control of spider mites, aphids, psyllids and scale insects (Biddinger et al., 2009; Cross et al., 2015; Sutton et al., 2014). In this study, we tested how different landscape elements (proportion of arable fields, orchards, grasslands, human settlements, forest plantations, and semi-natural forests) and management profiles (pesticide use, weed control) can influence the abundance of coleopteran species in apple orchards throughout the growing season. We hypothesized that (i) pesticide use in apple orchards has higher impact on the abundance of predatory beetles than that of pests, (ii) semi-natural habitats in the landscape faciliate colonisation of apple orchards by predatory beetles better than agricultural fields, and (iii) beetle species show different responses to landscape composition during different periods of the season.

2. Material and methods

2.1. Sampling area

Twelve apple orchards with contrasting landscape context were selected as sampling sites in Szabolcs-Szatmár-Bereg County, Hungary (Supplementary Fig. 1, Table 1). In all orchards, trees were 10-years old and the main cultivar was 'Relinda' followed by the cv. 'Rewena' in some. Orchard size varied between 3.9 and 6.9 ha (mean ± S.D., 4.8 ± 0.9 ha).

Landscape composition around each orchard was estimated in a 1 km-radius circle based on CORINE land cover maps and aerial photographs using ArcGIS 10.2 (ESRI, 2013). The 1 km buffer distance is within the spatial range where the relative proportion of habitat types is known to be stable (Marini et al., 2012).

We used the following habitat types, which covered 95–100% (on average 98.7%) of the total study area: arable fields (mostly corn, wheat and sunflower), deciduous forest plantations [mostly black locust (*Robinia pseudoacacia*) and poplar (*Populus x euramericana*)], semi-natural grasslands (meadows and pastures), human settlements (houses, gardens and streets), orchards (almost exclusively apple orchards, but also some sour cherry and walnut orchards) and semi-natural forests (mostly native riverine willow-poplar forests dominated by *Salix alba*, *S. fragilis*, *Populus alba* and *P. nigra*, hedgerows and tree lanes) (Table 1, Supplementary Fig. 2). Proportions of all these habitat types were uncorrelated with each other, except for the significant negative correlation between 'semi-natural forests' and 'forest plantations' (Kendall rank correlation tests, τ-a: -0.682, $p=0.002$) (Supplementary Table 1).

Insecticides were applied 2–5 (on average: 3.6 ± 1.2) and fungicides 0–8 (on average: 3.7 ± 2.6) times in the orchards during the growing season. The most frequently applied insecticide compounds (number of applications in brackets) were tau-fluvalinate (15), acetamiprid (6) and thiacloprid (5); the most often used fungicides were the copper-based compounds (16) and sulphur (9). The pesticide load of orchards was estimated using data from the International Organization for Biological Control (IOBC) Pesticide Side Effect Database (http://www.iobc-wprs.org/) where the acute toxicity of pesticides for non-target organisms is divided into four risk categories from harmless (score 1) to harmful (score 4). The calculation of pesticide (insecticide and fungicide) load was based on the toxicity of the applied pesticide compounds to ladybirds (Coccinellidae), but the toxicity scores were rescaled to a 0–3 scale (range from harmless to harmful). Cumulative IOBC toxicity scores were calculated for all orchards separately by summing the toxicity scores of each insecticide and fungicide application for either a month, or several months, or the whole growing season, regarding the activity pattern of the studied Coleoptera species. The pesticides were applied between April and August in 2012, and within this period the cumulative toxicity scores were between 0–15 (in average: 8.4 ± 4.1) per orchard; while the monthly cumulative toxicity scores for all the 12 orchards were as follows: April: 21, May: 26, June: 32, July: 22 and August: 6.

Weed height (cm) was measured in the alleys of each orchard two times in the season, and it was 4–22 cm (13 ± 5 cm) in May and 2–30 cm (20 ± 9 cm) in September. Cumulative toxicity scores and weed height did not correlate with each other and with the habitat types, except for the positive correlation between ‘cumulative toxicity scores from April to June’ and ‘proportion of settlements’ (τ-a: 0.515, $p=0.020$) (Supplementary Table 2a, 2b and 3).

2.2. Sampling methods

Beetles were collected from the whole canopy of 20 apple trees per orchard by beating method (Muther and Vogt, 2003) with a beating funnel 35 cm radius, 50 cm depth, and a 70-cm-long beating stick at approximately 3-week intervals in eight occasions between 21st May and 11th October, 2012. In each orchard, samples were collected from five plots (at least 25 m apart) of four designated trees (within 10 m) and were pooled within each plot. Plots were located 12–60 m from the edge of the orchard and the same trees were sampled repeatedly. All individuals were identified to species level, voucher specimens were deposited at the Department of Entomology of the Szent István University. Each species was classified into one of four major feeding guilds: predators, apple-feeders, tourists (non-apple feeder herbivorous species; in sensu Moran and Southwood, 1982) and fungivores. In order to study the effect of seasonality on the abundance of beetles, and avoid potential biases caused by the low number of individuals per sampling occasions, we pooled the data bi-monthly (May-June, July-August and September-October). In those cases where the total abundance was greater than 60 individuals in both months, the analyses were also performed on the monthly data (results are shown separately in Supplementary Tables 6 and 7). In case of the group 'other apple-feeders' we pooled the abundance data for six months, due to their low abundance.

The number of aphids was counted on 20 annual shoots of apple trees (two shoots per tree for ten trees) in four occasions (in May, June, July and September) in every orchard. The most abundant aphids (Hemiptera: Aphididae) in May and June were *Aphis pomi* (De Geer) and *Aphis spiraecola* (Patch), while *Dysaphis plantaginea* (Passerini) and *Dysaphis devecta* (Walker) were less common. Canopy dwelling mites (Acari) were counted on 20 leaves per orchard (2 leaves from 10 trees in each apple orchard) in eight occasions (on the same dates as beetles). The most abundant mite groups (in decreasing order) were as follows: Family Eriophyidae, Tarosnemidae, Phytoseiidae, Stigmaeidae, Tetranychidae and the superfamily Tydeoidea, and individuals from the families Eriophyidae and Tarosnemidae accounted for 50% of the total catch.

2.3. *Data analysis*

General linear mixed-effect models (GLMM with identity link, Bolker et al., 2009) were used to study the relationship between the assumed explanatory variables and the seasonal (between April and October) abundance data for individual beetle species and for the group 'other apple feeders' (Supplementary Table 4.). We added orchard as a random effect to the models. Response variables were log(x+1) transformed to fulfil the normality requirement for model residuals. We built sets of single-argument models, where only one explanatory variable was considered in each model to avoid collinearity (Burnham and Anderson, 2002).

The models were divided into two main groups based on the set of explanatory variables:

(1) Orchard model family, where the most important orchard management attributes were tested: (1a) cumulative IOBC toxicity scores; (1b) estimated weed height in the alleys (where weed data from May were used for beetle abundance in May and June and those from September for beetle abundance in July and afterwards); (1c) total mite abundance data (for predatory beetles only); (1 d) abundance of aphids (for predatory beetles only).

(2) Landscape model family, where the effect of percent proportion of most important habitat types was tested: proportion of (2 a) arable fields; (2 b) forest plantations; (2 c) semi-natural grasslands; (2 d) human settlements; (2 e) orchards; (2 f) semi-natural forests.

For each species, we fit a null model first in order to model variance structure for responses and then we added this item to the models using 'varPower’ function (Pinheiro and Bates, 2000). With this approach we controlled overdispersion in the data for each species separately and assumed a species-specific error distribution to handle the potential bias caused by the occasionally low species abundance values (sensu Warton, 2005). We used a model selection based on information criterion corrected for small samples sizes (Akaike Information Criterion - AICc) to rank the above models per model family in terms of their ability to explain species abundances (Burnham and Anderson, 2002). In this way, the ‘best approximating’ model was selected as the most parsimonious explanation of the data, when Δ AICc > 2. In other cases, when the models differed in their AICc values less than 2, we applied a model averaging approach to account for model selection uncertainty and obtain robust parameter estimates (Grueber et al., 2011). During model averaging, we built all the possible models with the given set of explanatory variables and parameter estimates of the best models (Δ AICc > 2) were averaged with the models' AICc weights.

Model estimates were obtained using maximum likelihood method and diagnostics included the AICc and checking model residuals. We estimated the model parameters using the 'nlme' package (Pinheiro et al., 2011), performed model averaging with the package 'MuMIn' (Barton 2013) and applied the 'graphics' package for graphical outputs in R 3.1.2 (R Core Team, 2014). Some preliminary statistics and the interdependence of explanatory variables were tested by the software *ROPstat* (Vargha et al., 2015).

3. Results

A total of 8207 individuals of 177 canopy-dwelling beetle species were collected from the studied apple orchards. The number of species varied between 30 and 55 (43 ± 10) per orchard, and the number of individuals varied between 239 and 1646 (684 ± 404). Nine species comprised 86% of the total abundance: *Anthonomus pomorum* (Linnaeus) (Curculionidae, 112 individuals) and *Phyllobius oblongus* (Linnaeus) (Curculionidae, 90) as the most abundant apple feeders; *Stethorus pusillus* (Herbst) (Coccinellidae, 1148), *Coccinella septempunctata* Linnaeus (Coccinellidae, 209), *Propylea quatuordecimpunctata* (Linnaeus) (Coccinellidae, 179) and *Harmonia axyridis* (Pallas) (Coccinellidae, 151) as the most common predatory beetles; *Phyllotreta vittula* (Redtenbacher) (Chrysomelidae, 2074) as the most abundant tourist species; and *Cortinicara gibbosa* (Herbst) (Lathridiidae, 2988) and the mildew feeder *Psyllobora vigintiduopunctata* (Linnaeus) (Coccinellidae, 116) as fungivorous species.

The seasonal activity pattern of these species suggests that the highest activity of *A. pomorum* and *P. oblongus* was in May and June, while harlequin ladybird *(Harmonia axyridis)* and *C. gibbosa* occurred throughout the whole growing season with two activity peaks, one in early summer and one in autumn. Other predatory species *(S. pusillus, C. septempunctata, P. quatuordecimpunctata)* and *P. vittula* were abundant in the orchards from July onwards, while *P. vigintiduopunctata* occurred in great numbers in September and October (Fig. 1).

3.1. Effects of orchard management practices

In the orchard models, we detected guild-specific responses of beetles to pesticide applications (Fig. 2, Table 2). Increasing pesticide toxicity caused a steep decline in the abundance of apple feeders, such as *A. pomorum*, *P. oblongus* and the group ‘other apple feeders’ [in order of decreasing abundance: *Pogonocherus hispidus* (Linnaeus) (Cerambycidae), *Otiorhynchus ovatus* (Linnaeus) (Curculionidae), *Scolytus rugulosus* (Müller) (Curculionidae), *Peritelus familiaris* Boheman (Curculionidae), *Rhynchites bacchus* (Linnaeus) (Rhynchitidae) and six other species, Fig. 2, Table 2]. However, predatory beetles such as *S. pusillus*, *H. axyridis*, *C. septempunctata* and *P. quatuordecimpunctata*, the tourist *P. vittula* and the fungivorous *C. gibbosa* appeared to be unaffected by pesticide load (see three examples in Fig. 2; effect of pesticide toxicity on *S. pusillus* in May and June, t=0.32, *p*=0.75; on *H. axyridis* in May and June, t=0.79, *p*=0.44; and on *C. septempunctata* in July and August, t= -0.04, *p*=0.96). The detailed analyses are presented in Supplementary Table 4 and 6.

Weed height (for all beetle species) and the generally low abundance of aphids (for predatory species) in May and June did not influence the abundance of beetles, while the abundance of the acariphagous species, *S. pusillus* increased with the increasing number of mites in May and June and showed a negative correlation with their number in September and October (Fig. 3, Table 2, Supplementary Table 4).

3.2. Effects of landscape composition

Abundance of apple feeders was not influenced by the landscape composition (Supplementary Table 5). In contrast, some habitat types had a major impact on the abundance of predatory, fungivorous and tourist species, and these effects had a characteristic seasonal pattern.

The abundance of *H. axyridis* in May and June correlated positively with the proportion of settlements; in July and August with the proportion of semi-natural forests; and in September and October with the proportion of arable fields in the landscape (Fig. 3, Table 3). Accordingly, the number of *H. axyridis* adults was 4.0-times greater in May and June, 2.1-times greater in July and August and 6.3-times greater in September and October in the six orchards with higher than in the six ones with lower proportion of settlements, semi-natural forests and arable fields, respectively.

Abundance of *S. pusillus* in May and June was not affected by landscape composition, but in July and August it showed negative correlation with orchards (i. e. positive correlation with non-orchard habitats, mainly arable fields and forest plantations) and its abundance increased with the proportion of arable fields in the surrounding landscape in September and October (Fig. 3. and Table 3; Supplementary Table 5 and 7). *Coccinella septempunctata* and *P. quatuordecimpunctata* were either absent or present in low numbers in the canopy of apple trees in May and June (Fig. 1). Later in the season, *C. septempunctata* was positively affected by the amount of surrounding orchards (1.8-times more individuals in the six orchards with higher amount of orchards in the surrounding landscape compared to the other six orchards), and *P. quatuordecimpunctata* was positively affected by surrounding arable fields (Fig. 4, Table 3). *Phyllotreta vittula* was most abundant during the second half of the season from July to October and its abundance was positively correlated with the proportion of arable fields (Fig. 4, Table 3, Supplementary Table 7 and Supplementary Fig. 3). The fungivorous species, *C. gibbosa* was not affected by landscape composition with the exception of October, when its abundance showed nearly significant positive correlation with arable fields and significant negative correlation with forest plantations (Supplementary Table 5 and 7). The other fungivorous species, *P. vigintiduopunctata* was not affected by landscape composition (Supplementary Table 5). Altogether, in September and October the six orchards with higher proportion (45–67%) of arable fields harboured 3.5-times more predatory, 3.5-times more tourist and 2.2-times more fungivorous beetles than the six orchards with lower proportion (14–30%) of arable fields. The same values for each species were as follows: *H. axyridis* (6.3), *S. pusillus* (3.3), *P. quatuordecimpunctata* (4.4), *P. vittula* (5.0), *P. vigintiduopunctata* (3.3) and *C. gibbosa* (2.1). However, in spite of their high proportion in the landscape, forest plantations and grasslands did not alter any of the beetle species in the canopy of apple orchards (Table 3).

4. Discussion

4.1. Effects of orchard management

Our study revealed that canopy-dwelling beetle species show a guild-specific response to pesticide regimes in apple orchards. The abundance of apple feeders such as *A. pomorum*, *P. oblongus* and ‘other apple feeders’ decreased with the increasing pesticide pressure. By contrast, the abundance of predatory (*H. axyridis*, *S. pusillus*, *C. septempunctata*, *P. quatuordecimpunctata*), tourist (*P. vittula*) and fungivorous (*C. gibbosa*) beetles was unaffected by pesticide use (Fig. 2, Table 2).

Since pesticide applications are often detrimental to arthropods, they are among the main drivers of insect abundance in croplands (e.g. Biddinger et al., 2009; Jonsson et al., 2012; Kovács-Hostyánszki et al., 2011; Krauss et al., 2011; Lövei et al., 1991; Markó et al., 2010). However, species with high dispersal ability recolonise the agricultural fields more easily after pesticide applications and thus are able to compensate for the mortality caused by pesticides (Markó et al., 2009). In this study, the evaluation of pesticide pressure based on the toxicity of the applied compounds to beetles (coccinellids), and their negative effect on the apple feeder species was in accordance with our expectations. Similarly, it is highly probable that the pesticide treatments, in line with the previous laboratory based results, greatly increased the mortality of predatory species such as coccinellids (Biddinger et al., 2009; IOBC Pesticide Side Effect Database; Lövei et al. 1991). Therefore the detected differences between apple feeders and predatory beetles in their response to increasing toxicity of pesticides could not be explained simply by their different sensitivity to the pesticides applied. More probably, phytophagous beetles were not able to compensate for the mortality due to the increasing pesticide toxicity, whereas predatory beetles such as ladybirds had greater dispersal ability and re-colonized the orchards after pesticide applications. As a consequence, with increasing pesticide toxicity the beetle assemblages shifted toward species with higher dispersal capacity i.e. toward species that are able to colonise orchards from greater distances.

Beside pesticides, a number of local-scale factors such as prey availability and ground cover vegetation can influence insect abundance in orchards and some of them may override the others (Elliott et al., 2002; Markó et al., 2013; Schüepp et al., 2014). In our study, instead of cumulative pesticide toxicity, the number of the acariphagous coccinellid, *S. pusillus*, was determined by their aggregation response to prey (mite) abundance in the period of the highest pesticide pressure, in May and June (Fig. 3). However, lower abundance of mites in the orchards with greater number of *S. pusillus* in September and October suggests that *S. pusillus* not only follows, but, in some cases, suppress the abundance of mites (Biddinger et al., 2009). The abundance of aphidophagous ladybirds remained independent not only from the cumulative pesticide toxicity, but also from the generally low prey (aphid) abundance and the varying weed height in the orchards (Supplementary Table 4). Altogether, the abundance of predatory beetles in this study was only weakly influenced by prey availability, but rather was determined by their dispersal capacity and by availability of source habitats (Elliott et al., 2002; Schüepp et al., 2014).

4.2. Effects of landscape composition

The apple feeder beetles such as *A. pomorum*, *P. oblongus*, and the group 'other apple feeders' did not respond to landscape composition around the orchards (Supplementary Table 5). Instead, their abundance and distribution was driven by pesticide use. Previous studies proved that forests adjacent to apple orchards provide overwintering habitats for *A. pomorum*, while the semi-open woody vegetation in the landscape around the orchards affects positively the abundance of *P. oblongus* (Bailey et al., 2010; Brown et al., 1993).

For predatory, tourist and fungivorous beetles, we found that the habitats with high anthropogenic disturbance such as human settlements (*H. axyridis*), orchards (*C. septempunctata*) and arable fields (*H. axyridis*, *S. pusillus*, *P. quatuordecimpunctata, P. vittula, C. gibbosa*) had a strong positive effect on the abundance of beetles in the canopies of apple orchards (Figs. 3 and 4). However, in contrast to our second hypothesis, semi-natural habitats played only a limited role in the colonisation of orchards. Neither the proportion of forest plantations (mainly consisting of exotic tree species to Hungary) nor the proportion of grasslands influenced the number of beetles, and only the natural forests showed some positive effect on the abundance of *H. axyridis* in the orchards (Table 3). Forest plantations of exotic trees provide less diverse and suitable resources for most of the native insect species than native forests and therefore probably take little part in the maintenance of ecosystem services (Bremer and Farley, 2010; Moran and Southwood, 1982; Tscharntke 2017).

Most of the studies that have assessed the impact of landscape elements on coccinellids focused on annual crop systems such as soybean, maize and wheat, or on perennial herbaceous crops such as alfalfa. Contrary to our results, these studies reported that greater amount of grasslands and meadows (Elliott et al., 2002; Woltz and Landis, 2014) and semi-natural habitats (Gardiner et al., 2009; Raymond et al., 2015; Woltz et al., 2012; Woltz and Landis, 2014) in the landscape affects coccinellids positively, whereas the greater amount of croplands (arable fields and orchards) affects them negatively (Grez et al., 2013). Our results obtained in perennial crop systems (apple orchards) are more consistent with the observations in natural habitats (Rand et al., 2006), where coccinellids colonized the natural grasslands and nettle patches from the adjacent cropland habitats (spillover) (Rand and Louda, 2006; Rand and Tscharntke, 2007). Thus, arable fields may not only receive, but also provide ecosystem services in the mosaic agricultural landscapes.

Altogether, our results suggest a possible explanation for the general observation supported by meta-analyses, that in agricultural fields natural enemies show stronger response to landscape complexity than pests (Chaplin-Kramer et al., 2011; Veres et al., 2013). Pesticide use in agricultural fields can obscure the influence of landscape composition on arthropods, and this obscuring effect could be stronger in the case of pests than in the case of natural enemies. On the one hand, insecticide applications are directed against pests, and therefore, growers choose compounds and decide on timing and frequency of applications according to the targeted pest species. On the other hand, pests might be more specialised to particular habitats than their generalist natural enemies, might have lower dispersal capacity and therefore are less able to compensate for the mortality caused by pesticides.

4.3. Seasonality in the landscape

In accordance with our third hypothesis, the role of landscape composition in determining the abundance of beetles showed a marked seasonal pattern. *Harmonia axyridis* was positively affected by human settlements in May and June, by semi-natural forest in July and August and by arable fields in September and October (Fig. 3). The *harlequin ladybird* has three generations a year in Hungary, overwinters predominantly in aggregations in buildings, develops on tall herbs, and in the canopy of shrubs and trees (Koch 2003; Markó and Pozsgai, 2009). Thus, the greater abundance of the overwintered and first-generation adults in orchards close to settlements can be explained by its synanthropic overwintering nature, while the greater abundance of the second- and partly third-generation adults around semi-natural forests by its largely arboreal character (Koch, 2003). According to former studies, the yearly total abundance of harlequin ladybirds in soybean fields was found to be positively affected by the amount of grasslands and settlements (Woltz and Landis, 2014), while that in alfalfa fields was positively influenced by the amount of settlements (Grez et al., 2014).

The abundance of *C. septempunctata* increased with the increasing proportion of orchards from July (Fig 4, Table 3). This species is predominantly univoltine, its larvae develop on herbs in grasslands, croplands and their weedy edges, and adults emerge in July (Sárospataki and Markó, 1995). The positive effect of orchards might be explained by the presence of weeds and the associated aphid prey (Supplementary Table 4) (Burgio et al., 2006). *Coccinella septempunctata* exhibits higher level of habitat fidelity compared to *H. axyridis* and *P. quatuordecimpunctata*, which readily disperse between alfalfa, soybean and maize fields (di Lascio et al., 2016; Forbes and Gratton, 2011).

Most of the studied species had strong positive response to the increasing amount of arable fields during the second half of the growing season. The mass immigration of adults into the orchards started in July *(P. vittula, P. quatuordecimpunctata)*, and August *(S. pusillus)*, and became more pronounced in September and October *(H. axyridis, S. pusillus, P. quatuordecimpunctata, C. gibbosa)* (Figs. 3, 4; Table 3; Supplementary Table 7). Maize fields maintain abundant *H. axyridis*, *S. pusillus, P. quatuordecimpunctata, P. vigintiduopunctata* (Ácsné Szekeres, 2011; Radwan and Lövei, 1983; Vandereycken et al., 2013), *P. vittula* (Szénási and Markó, 2015) and *C. gibbosa* (Rauschen et al., 2010) populations, and these species occur in large numbers in other arable crops as well. Arable fields accounted for 44% of the study region, and in 2012, maize, sunflower and wheat shared 41%, 19% and 12% of the total area of arable fields, respectively (Hungarian Central Statistical Office, 2013). The harvest of wheat, barley and rape started from late June and was followed by the harvest of maize for forage and silage from early August. Maize and sunflower were harvested from early September till end of October. Therefore from the middle of the growing season, arable fields gradually became unsuitable habitats for most of the beetles due to senescence, dry-out *and harvesting of crops*. This decline in habitat quality, in accordance with the 'landscape-moderated concentration and dilution hypothesis' might have induced a vast mass emigration of beetles (i.e. spillover) from the arable fields to orchards and probably to other suitable habitats (Tscharntke et al. 2012). As a consequence, we found a 3–6-fold increase in the abundance of predatory beetles in the orchards with high amount (45–67%) of arable fields in the surrounding landscape in autumn compared to those with low amount (14–30%) of arable fields. Increased abundance of coccinellids and their predation on apple aphids in autumn may reduce the number of aphid females laying overwintering eggs and, indirectly, the aphid abundance in spring (Kehrli and Wyss, 2001). Similarly, a number of integrated pest management and augmentative release studies demonstrated that increased abundance of *Stethorus* species can provide effective control of spider mites in woody perennial systems (Biddinger et al., 2009; Hoy, 2011).

5. Conclusions

Orchards are permanent habitats that are surrounded by a variety of land-use types and exposed to high level of pesticide input. This study suggests that in commercial apple orchards pesticide use drives the abundance of beetle species with low dispersal capacity (pests), while landscape composition is the major driver of the abundance of well-dispersing beetles (mainly predatory coccinellids). For orchard colonisation by well-dispersing beetles, semi-natural habitats such as forests, grasslands and forest plantations played only a limited role as source habitat, suggesting that the quality of these habitats might be an important limiting factor in provision of ecosystem services. By contrast, anthropogenic landscape elements such as human settlements, orchards, and especially arable fields showed a strong positive influence on the abundance of predatory and tourist beetles. To sum up, in apple orchards we observed a pattern that is opposite to what have been reported from annual crops (arable fields) where semi-natural habitats are the main landscape drivers of the abundance of predatory beetles. This reverse pattern might be common in perennial crops in the regions with low landscape diversity and large amount of arable fields.

In our study the effect of landscape composition on beetle abundance in apple orchards showed a strong temporal pattern. Habitats in the resource chain such as settlements in spring-early June, semi-natural forests in summer, and arable fields in autumn provide *H. axyridis* individuals for apple orchards. The mass immigration of other predatory and tourist species from arable fields into the orchards starts in July and becomes more pronounced in September and October in correspondence with the life cycle of the beetle species and senescence, dry-out and harvesting of arable crops. Therefore, orchards act as sink habitats for predatory beetles in the earlier part of the growing season when pesticides are typically applied and, they provide reservoirs for them in the later part of the growing season when the agricultural landscapes offer only limited resources.

Further studies are necessary to examine whether the patterns found for beetles in apple orchards can be generalised to other arthropod groups, and to determine to what extent natural enemies immigrating from annual crops are able to contribute to pest suppression in perennial crop systems.

Acknowledgements

We are grateful to the growers for their cooperation during this study and to Katinka Nyisztor and Veronika Szilágyi for their assistance in field and laboratory work. We also thank Károly Vig and László Ádám for the identification of *Phyllotreta vittula* and *Cortinicara gibbosa* individuals. This study was supported by the Hungarian Scientific Research Fund (OTKA NN 101940) and by the MTA 'Lendület' program. A K-H. was a Bolyai and a MTA Postdoc Fellow.

References

Ácsné Szekeres D., 2011. Assessment of the impact of Bt (MON 810, Cry1Ab) maize on selected non-target Coleoptera (Carabidae, Coccinellidae). PhD. thesis, Szent István University, Gödöllő.

Bailey, D., Schmidt-Entling, M.H., Eberhart, P., Herrmann, J.D., Hofer, G., Kormann, U., Herzog, F., 2010. Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. J. Appl. Ecol. 47, 1003–1013.

Barton, K. 2013. MuMIn: Multi-model inference. R package version 1.9.5. http://CRAN.R-project.org/package=MuMIn

Bianchi, F.J.J.A., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. London, Ser. B Biol. Sci. 273, 1715–1727.

Biddinger, D.J., Weber, D.C., Hull, L.A., 2009. Coccinellidae as predators of mites: Stethorini in biological control. Biol. Control 51, 268–283.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H. White, J.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135.

Bremer, L.L., Farley, K.A., 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodivers. Conserv. 19, 3893–3915.

Brown, M.W., Szentkirályi, F., Kozár, F., 1993. Spatial and temporal variation of apple blossom weevil populations (Col., Curculionidae) with recommendations for sampling. J. Appl. Entomol. 115, 8–13.

Burgio, G., Ferrari, R., Boriani, L., Pozzati, M., van Lenteren, J., 2006. The role of ecological infrastructures on Coccinellidae (Coleoptera) and other predators in weedy field margins within northern Italy agroecosystems. Bull. Insectology 59, 59–67.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information theoretic approach. Springer-Verlag, New York, USA.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol. Lett.. 14, 922–932.

Cross, J., Fountain, M., Markó, V., Nagy, C., 2015. Arthropod ecosystem services in apple orchards and their economic benefits. Ecol. Entomol. 40, 82–96.

di Lascio, A., Madeira, F., Costantini, M.L., Rossi, L., Pons, X., 2016. Movement of three aphidophagous ladybird species between alfalfa and maize revealed by carbon and nitrogen stable isotope analysis. BioControl 61, 35–46.

Dib, H., Sauphanor, B., Capowiez, Y., 2016. Effect of management strategies on arthropod communities in the colonies of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in south-eastern France. Agric. Ecosyst. Environ. 216, 203–206.

Elliott, N.C., Kieckhefer, R.W., Beck, D.A., 2002. Effect of aphids and the surrounding landscape on the abundance of Coccinellidae in cornfields. Biol. Control 24, 214–220.

ESRI, 2013. ArcGys vers. 10.2 Environmental Systems Research Institute Inc. Redlands, CA, USA.

Eurostat, 2007. The use of plant protection products in the European Union. Data 1992–2003. Luxembourg: Office for Official Publications of the European Communities 2007.

Eurostat, 2015. Agriculture, forestry and fishery statistics 2014 edition. Luxenburg: Publication office of the European Union.

FAOSTAT, 2016. Food and Agricultural Organization of the United Nations (FAO), FAO, Statistical Database, http://faostat.fao.org (accessed: 25.04.2016.)

Forbes, K.J., Gratton, C., 2011. Stable isotopes reveal different patterns of inter-crop dispersal in two ladybeetle species. Ecol. Entomol. 36, 396–400.

Gardiner, M.M., Landis, D.A., Gratton, C., DiFonzo, C.D., O'neal, M., Chacon, J.M., Wayo, M.T., Schmidt, N.P., Mueller, E.E., Heimpel, G.E., 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. Ecol. Appl. 19, 143–154.

Grez, A.A., Rand, T. A., Zaviezo, T., Castillo-Serey, F., 2013. Land use intensification differentially benefits alien over native predators in agricultural landscape mosaics. Divers. Distrib. 19, 749–759.

Grez, A.A., Zaviezo, T., Gardiner, M.M., 2014. Local predator composition and landscape affects biological control of aphids in alfalfa fields. Biol. Control 76, 1–9.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711.

Herrmann, J., Kormann, U., Schüepp, C., Stocker, Y., Herzog, F., Entling, M., 2012. Effects of habitat isolation and predation pressure on an arboreal food-web. Community Ecol. 13, 82–87.

Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A.C., Smith, B.M. and Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: A review of European studies. Pest Manage. Sci. 72, 1638–1651.

Holt, R.D., 1996. Food webs in space: an island biogeographic perspective. in: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns and Dynamics. Chapman & Hall, New York, NY, USA, pp. 313–323.

Hoy, M.A. 2011. Agricultural Acarology - Introduction to Integrated Mite Management. CRC Press, Boca RatonInclán, D.J., Cerretti, P., Marini, L., 2015. Landscape composition affects parasitoid spillover. Agric. Ecosyst. Environ. 208, 48–54.

IOBC Pesticide Side Effect Database. Available online: http://www.iobc-wprs.org/ip_ipm/IOBC_Pesticide_Side_Effect_Database.html (accessed: 25.01.2015.).

Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., Didham, R.K., 2012. Agricultural intensification drives landscape-context effects on host–parasitoid interactions in agroecosystems. J. Appl. Ecol. 49, 706–714.

Kehrli, P., Wyss, E., 2001. Effects of augmentative releases of the coccinellid, Adalia bipunctata, and of insecticide treatments in autumn on the spring population of aphids of the genus Dysaphis in apple orchards. Entomol. Exp. Appl. 99, 245–252.

Koch, R. L., 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. J. Insect Sci. 3, 1–16.

Kovács-Hostyánszki, A., Batáry, P., Báldi, A., 2011. Local and landscape effects on bee communities of Hungarian winter cereal fields. Agric. For. Entomol. 13, 59–66.

Hungarian Central Statistical Office, 2013. Statistical Report Szabolcs-Szatmár-Bereg Country 2012/4. www.ksh.hu/docs/hun/xftp/megy/124/szab124.pdf (accessed 06.11.2016.).

Krauss, J., Gallenberger, I., Steffan-Dewenter, I., 2011. Decreased functional diversity and biological pest control in conventional compared to organic crop fields. Plos One 6(5), p.e19502.

Lövei, G.L., Sárospataki, M., Radwan, Z.A., 1991. Structure of ladybird (Coleoptera: Coccinellidae) assemblages in apple: changes through developmental stages. Environ. Entomol. 20, 1301–1308.

Maalouly, M., Franck, P., Bouvier, J.C., Toubon, J.F., Lavigne, C., 2013. Codling moth parasitism is affected by semi-natural habitats and agricultural practices at orchard and landscape levels. Agric. Ecosyst. Environ. 169, 33–42.

Marini, L., Quaranta, M., Fontana, P., Biesmeijer, J.C., Bommarco, R., 2012. Landscape context and elevation affect pollinator communities in intensive apple orchards. Basic Appl. Ecol. 13, 681–689.

Markó, V., Merkl, O., Podlussány, A., Vig, K., Kutasi, C., Bogya, S., 1995. Species composition of Coleoptera assemblages in the canopies of Hungarian apple and pear orchards. Acta Phytopathol. Entomol. Hung. 30, 221–246.

Markó, V., Keresztes, B., Fountain, M. T., Cross, J. V., 2009. Prey availability, pesticides and the abundance of orchard spider communities. Biol. Control 48, 115–124.

Markó, V., Pozsgai, G., 2009. Spread of harlequin ladybird (*Harmonia axyridis* Pallas, 1773) (Coleoptera, Coccinellidae) in Hungary, and the first records from Romania and Ukraine. Növényvédelem 45, 481–490.

Markó, V., Bogya, S., Kondorosy, E., Blommers, L.H., 2010. Side effects of kaolin particle films on apple orchard bug, beetle and spider communities. Int. J. Pest Manage. 56 189–199.

Markó, V., Jenser, G., Kondorosy, E., Ábrahám, L., Balázs, K., 2013. Flowers for better pest control? The effects of apple orchard ground cover management on green apple aphids (*Aphis* spp.) (Hemiptera: Aphididae), their predators and the canopy insect community. Biocontrol Sci. Technol. 23, 126–145.

Miliczky, E.R., Horton, D.R., 2005. Densities of beneficial arthropods within pear and apple orchards affected by distance from adjacent native habitat and association of natural enemies with extra-orchard host plants. Biol. Control 33, 249–259.

Monteiro, L.B., Lavigne, C., Ricci, B., Franck, P., Toubon, J.F., Sauphanor, B., 2013. Predation of codling moth eggs is affected by pest management practices at orchard and landscape levels. Agric. Ecosyst. Environ. 166, 86–93.

Moran, V.C., Southwood, T.R.E., 1982. The guild composition of arthropod communities in trees. J. Anim. Ecol. 51, 289–306.

Muther, J., Vogt, H., 2003. Sampling methods in orchard trials: a comparison between beating and inventory sampling. IOBC WPRS Bulletin 26, 67–72.

Pinherio, J., Bates, D., 2000. Mixed-effects models in S and S-plus. Springer, New York.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Development Core Team, 2011. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-98, URL http: //CRAN.R-project.org/package=nlme.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Radwan, Z., Lövei, G.L., 1983. Structure and seasonal dynamics of larval, pupal, and adult coccinellid (Col., Coccinellidae) assemblages in two types of maize fields in Hungary. J. Appl. Entomol. 96, 396–408.

Rand, T.A., Tylianakis, J.M., Tscharntke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecol. Lett. 9, 603–614.

Rand, T.A., Louda, S.M., 2006. Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. Conserv. Biol. 20, 1720–1729.

Rand, T.A., Tscharntke, T., 2007. Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. Oikos 116, 1353–1362.

Rauschen, S., Schaarschmidt, F., Gathmann, A., 2010. Occurrence and field densities of Coleoptera in the maize herb layer: implications for environmental risk assessment of genetically modified Bt-maize. Transgenic Res. 19, 727–744.

Raymond, L., Ortiz-Martínez, S.A., Lavandero, B., 2015. Temporal variability of aphid biological control in contrasting landscape contexts. Biol. Control 90, 148–156.

Roßberg, D., 2013. Erhebungen zur Anwendung von Pflanzenschutzmitteln in der Praxis im Jahr 2011. (Survey on application of chemical pesticides in Germany). J. Kulturpflanz. 65, 141–151.

Sárospataki, M., Markó, V., 1995. Flight activity of *Coccinella septempunctata* (Coleoptera: Coccinellidae) at different strata of a forest in relation to migration to hibernation sites. Eur. J. Entomol. 92, 415–419.

Schellhorn, N.A., Bianchi, F.J.J.A., Hsu, C.L., 2014. Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. Annu. Rev. Entomol. 59, 559–581.

Schellhorn, N.A., Gagic, V., Bommarco, R., 2015. Time will tell: resource continuity bolsters ecosystem services. Trends Ecol. Evol. 30, 524–530.

Schüepp, C., Uzman, D., Herzog, F., Entling, M.H., 2014. Habitat isolation affects plant–herbivore–enemy interactions on cherry trees. Biol. Control 71, 56–64.

Simon, S., Brun, L., Guinaudeau, J., Sauphanor, B., 2011. Pesticide use in current and innovative apple orchard systems. Agron. Sustainable Dev. 31, 541–555.

Sutton, T.B., Alswinckle, H.S., Agnello, A.M., Walgenbach, J.F. (Eds.), 2014. Compendium of apple and pear diseases and pests. American Phytopathological Society.

Szénási, Á., Markó, V., 2015. Flea beetles (Coleoptera: Chrysomelidae, Alticinae) in Bt-(MON810) and near isogenic maize stands: Species composition and activity densities in Hungarian fields. Crop Prot. 77, 38–44.

Thies, C., Tscharntke, T., 1999. Landscape structure and biological control in agroecosystems. Science 285, 893–895.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P. et al., 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biol. Rev. 87, 661–685.

Vandereycken, A., Brostaux, Y., Joie, E., Haubruge, E., Verheggen, F. J., 2013. Occurrence of *Harmonia axyridis* (Coleoptera: Coccinellidae) in field crops. Eur. J. Entomol. 110, 285–292.

Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., et al. 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. Biol. Conserv. 204, 449–458.

Vargha, A., Torma, B., Bergman, L.R., 2015. ROPstat: A general statistical package useful for conducting person-oriented analyses. J. Pers. Oriented Res. 1, 87–98.

Veres, A., Petit, S., Conord, C., Lavigne, C., 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. Agric. Ecosyst. Environ. 166, 110–117.

Warton, D. I. 2005. Many zeros does not mean zero inflation: comparing the goodness-of-fit of parametric models to multivariate abundance data. Environmetrics, 16, 275-289.

Whalon, M.E., Mota-Sanchez, D., Hollingworth, R.M., Duynslager, L., 2016. Arthropod pesticide resistance data base, Available at http://www.pesticideresistance.org/. (accessed 20.03.2016).

Wissinger, S.A., 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. Biol. Control 10, 4–15.

Woltz, J.M., Isaacs, R., Landis, D.A., 2012. Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. Agric. Ecosyst. Environ. 152, 40–49.

Woltz, J.M., Landis, D.A., 2014. Coccinellid response to landscape composition and configuration. Agric. For. Entomol. 16, 341–349.

Table 1. Landscape characteristics (%) around twelve apple orchards in a 1-km radius circle.

Orchards	Arable fields	Forest plantations	Settlements	Grasslands	Orchards	Semi-natural forests
Győrtelek	67	0	1	4	21	5
Kocsord	62	2	22	4	4	5
Demecser	62	8	7	12	5	3
Gelénes	46	1	2	14	19	13
Gulács	46	9	5	6	22	11
Zsurk	45	1	10	23	7	13
Nagydobos	30	59	1	2	7	1
Eperjeske	26	38	18	10	5	3
Mándok	21	19	41	10	7	2
Rohod	18	33	14	20	11	4
Csaroda	15	0	25	26	7	27
Nyírmada	14	71	0	4	8	0

Table 2. Summary of the best orchard models. Coefficient and z values correspond to average model, while estimated (beta), t values and S.D. (random) are for the best models. Only significant results are shown.

Species and month	Best models	Variables	Estimated	S.E.	D.f.	t	*P*	S.D. (random)
Anthonomus pomorum	Toxicity	intercept	1.70	0.38	48	4.47	<0.0001	0.30
May & June		toxicity	-0.18	0.05	10	-3.57	0.005	
Phyllobius oblongus	Toxicity	intercept	1.45	0.37	48	3.90	0.0003	0.31
May & June		toxicity	-0.15	0.05	10	-3.13	0.010	
Other apple feeders	Toxicity	intercept	1.37	0.21	48	6.36	<0.0001	0.51
May-October		toxicity	-0.09	0.02	10	-4.17	0.001	
Stethorus pusillus	Mite	intercept	0.03	0.21	47	0.15	0.87	0.35
May & June		log mite	0.13	0.06	47	2.19	0.030	
September & October	Mite	Intercept	2.73	0.26	47	9.15	<0.0001	0.54
		log mite	-0.0091	0.0036	47	-2.49	0.010	

Table 3. Summary of the best landscape models. Coefficient and z values correspond to average model, while estimated (beta), t values and S.D. (random) are for the best models. Only significant results are shown.

Species and months	Best models	Variables	Coefficient/ estimated	S.E.	D.f.	Z/t	*P*	S.D. (random)
Harmonia axyridis	Average	**(intercept)**	**0.066**	**0.157**	**48**	**4.180**	**0.0001**	0.41
May & June		**settlement**	**0.020**	**0.040**	**10**	**4.250**	**0.002**	
		arable field	**-0.012**	**0.003**	**10**	**-3.990**	**0.003**	
July & August	Forest	intercept	0.140	0.092	48	1.520	0.134	0.36
		semi-natural forest	**0.023**	**0.008**	**10**	**2.660**	**0.020**	
September & October	Arable field	intercept	-0.272	0.240	48	1.130	0.263	0.37
		arable field	**0.019**	**0.005**	**10**	**3.368**	**0.007**	
Coccinella septempunctata	Orchard	intercept	0.285	0.170	48	1.670	0.100	0.46
September & October		**orchard**	**0.045**	**0.014**	**10**	**3.197**	**0.009**	
Propylea quatuordecimpunctata	Average	(intercept)	-8.119	10.08	48	0.803	0.421	
July & August		**arable field**	**0.195**	**0.049**	**10**	**3.027**	**0.002**	
		forest	**0.190**	**0.048**	**10**	**2.997**	**0.002**	
		grassland	**0.202**	**0.052**	**10**	**2.954**	**0.003**	
September & October	Arable field	intercept	-0.159	0.228	48	-0.698	0.488	0.41
		arable field	**0.022**	**0.005**	**10**	**4.081**	**0.002**	
Stethorus pusillus	Average	(intercept)	0.778	3.15	48	0.247	0.805	
July & August		**orchard**	**-0.077**	**0.02**	**10**	**2.517**	**0.011**	
Sept. & October	Arable field	intercept	0.734	0.372	48	1.947	0.054	0.56
		arable field	**0.036**	**0.008**	**10**	**4.075**	**0.002**	
Phyllotreta vittula	Arable field	intercept	0.356	0.455	48	0.781	0.438	0.57
July & August		**arable field**	**0.056**	**0.01**	**10**	**5.181**	**0.0004**	
Sept. & October	Arable field	intercept	0.244	0.369	48	0.662	0.51	0.5
		arable field	**0.037**	**0.008**	**10**	**4.22**	**0.001**	

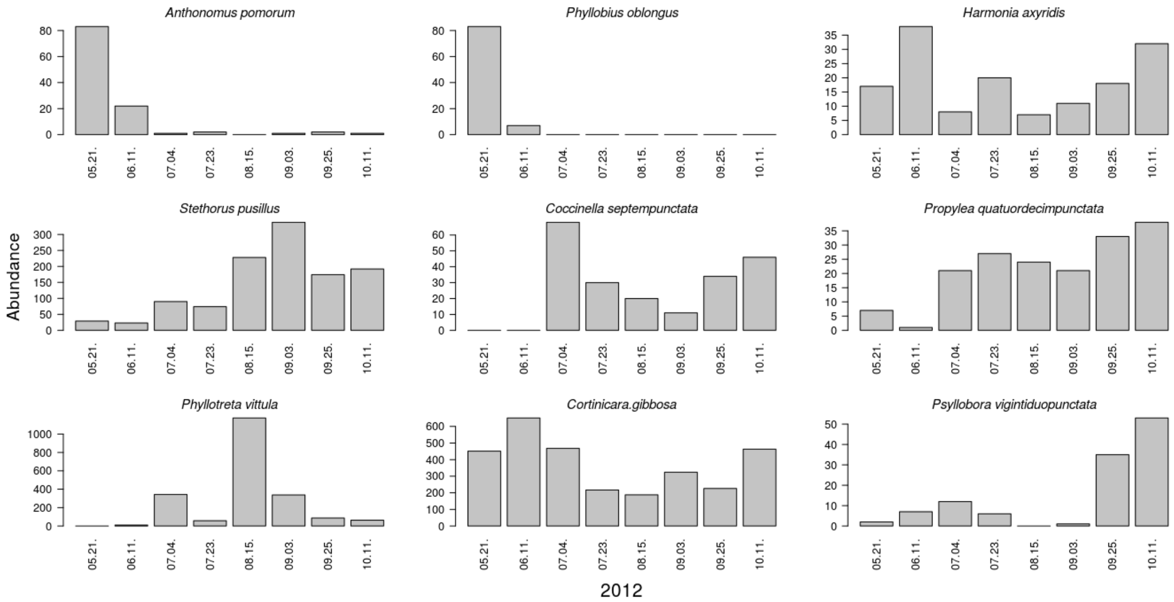

Fig. 1. Seasonal abundance (total abundance across all orchards) of beetles in the canopy of the studied apple orchards, in 2012. Note the different scales on the y-axes.

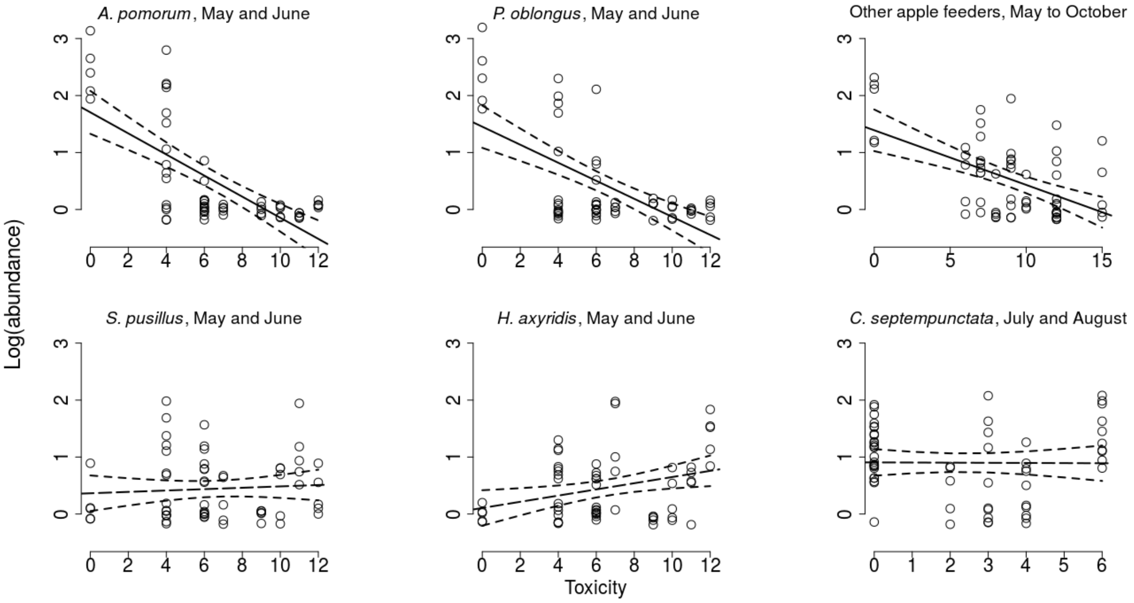

Fig. 2. Effects of the cumulative toxicity of pesticides on the abundance of apple feeder (*A. pomorum, P. oblongus* and the group 'other apple feeders') and predatory (*S. pusillus*, *H. axyridis* and *C. septempunctata*) beetles. Non-significant effects are designated by dashed lines.

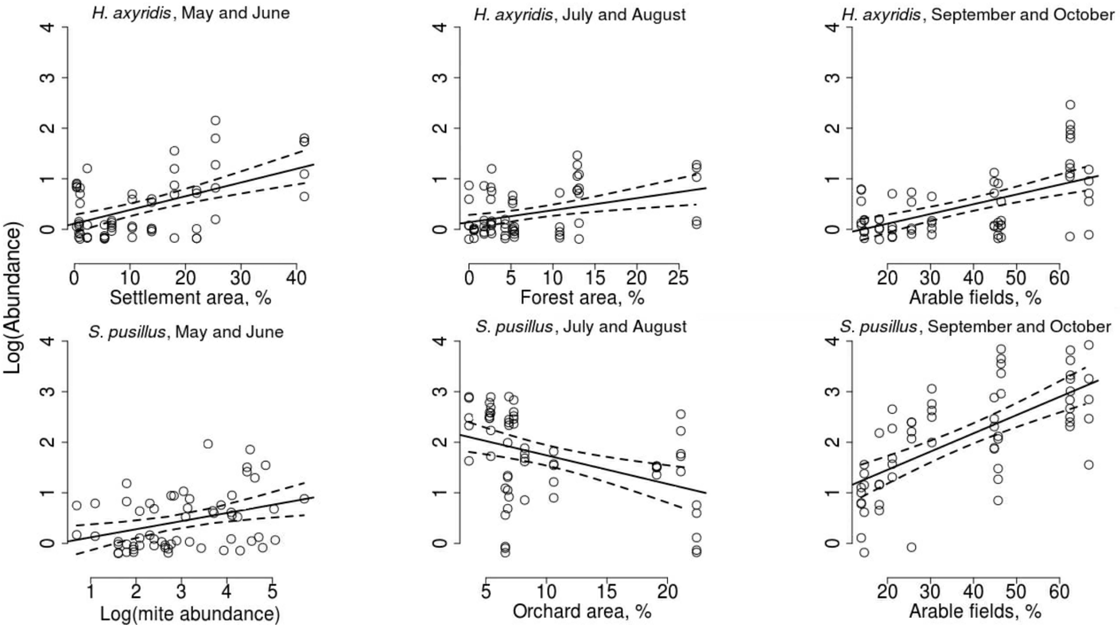

Fig. 3. Abundance of *H. axyridis* and *S. pusillus* in relation to the most influential landscape elements and mite density.

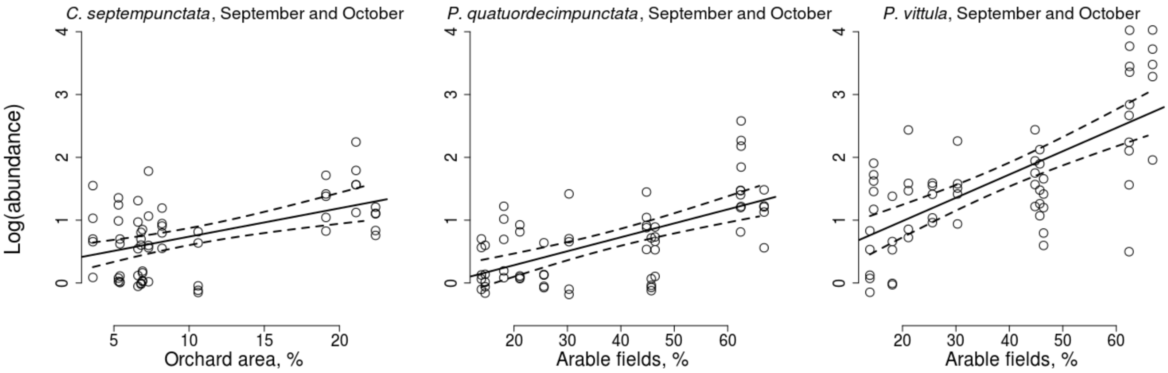

Fig. 4. Effects of orchards on the abundance of *C. septempunctata* and effects of arable fields on the abundance of *P. quatuordecimpunctata* and *P. vittula* in September and October.