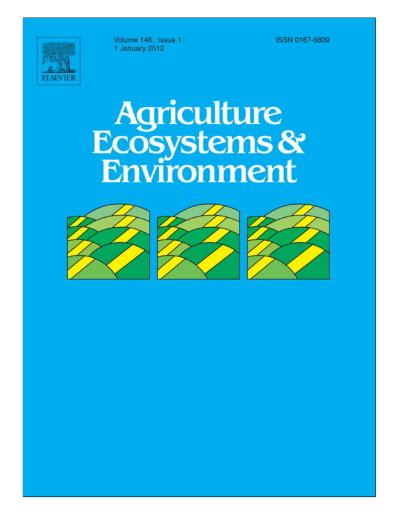
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Spatio-temporal dynamics of *Orius* spp. (Heteroptera: Anthocoridae) abundance in the agricultural landscape

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ABSTRACT

Predators of the genus *Orius* are widely released as control agents against *Frankliniella occidentalis*, however they can also colonize crops spontaneously, and conservation biological control can potentially take advantage of the presence of semi-natural areas in the agricultural landscape. A three-year study was conducted in Hungary in order to evaluate the *Orius* species spatial pattern at landscape scale, and to link their eventual aggregation, i.e. higher abundance, to the presence of semi-natural areas, which has been shown to benefit conservation biological control in general. Results show that *Orius* species population size and spatial pattern are related to semi-natural areas, and that influences with other agro-environmental factors exist. *Orius niger* abundance is likely to be associated with semi-natural areas, where it can successfully overwinter, but also with other resources in the landscape, especially in warm years. As a consequence of *O. niger* being a habitat generalist we suggest that at landscape scale its abundance pattern is driven by resource patterns and availability of both semi-natural and cultivated areas. Furthermore, their population dynamics is influenced by crop management intensity rather than crop composition of cropping systems.

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1. Introduction

Sustainable pest management implies the control of pests by natural enemies (conservation biological control, Jonsson et al., 2008), which has been linked to landscape patterns (With et al., 2002). The positive effect of semi-natural areas on the abundance and diversity of natural enemies and on pest control is recognized (Bianchi et al., 2006; Tscharntke et al., 2007; Veres et al., 2011), however the efficiency of conservation biological control has not yet been clearly related to the dynamic resource pattern of agricultural landscape. Temporal shifts in resource availability between

crop and non-crop habitat may result in shifts in the direction of predator dispersal over time (Rand et al., 2006). While semi-natural areas are more stable in time (Burel and Baudry, 1990; Petit et al., 2002), most crops provide extreme quantities of food resources in certain phenological stages and are also subject to frequent disturbances that make them periodically unsuitable. Species that might provide effective conservation biological control are expected to be adapted to these dynamics, to tolerate disturbance in crops, and take comparative advantage of the high amount of resources in cultivated areas (Wissinger, 1997). The importance of spillover from the cropland "matrix" in driving the pattern of predator abundance was shown for coccinellid beetles (Rand and Louda, 2006), but requires further study.

A primary requirement for occurrence and importance of predator spillover across cropland-semi-natural habitat edges is that the predators are habitat generalists which exploit prey resources within both habitat types (Rand et al., 2006). Predators of the genus *Orius* are polyphagous and are part of various agro-ecosystems worldwide (e.g. cotton, Atkan, 2006; Lucas and Rosenheim, 2011; soybean, Lundgren et al., 2009; faba bean, Atkan, 2010; potato, Fathi, 2009; wheat and alfalfa, Bokina, 2008; maize, Albajes et al.,

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2010; Mészáros et al., 1984; Rácz, 1989; orchards, Brown and Schmitt, 2001; Whalon and Croft, 1986; other vegetables an ornamental crops, Bosco and Tavella, 2008; Tommasini, 2004; Perdikis et al., 2011). They are produced by commercial insectaries and widely released to control western flower thrips, *Frankliniella occidentalis* Pergande (Baez et al., 2004; Weintraub et al., 2011); however naturally occurring *Orius* species can colonize crops spontaneously (Bán et al., 2009; Bosco et al., 2008) and augment pest control. Consequently, the potential of this conservation biological control might depend on the abundance of *Orius* in the surrounding landscape. Thus, identification of the resources required and bottlenecks in the *Orius* lifecycle are prerequisites for understanding the interaction between landscape structures and the success of conservation biological control.

Spatially-aggregated abundance patterns can be explained by distributions of resource sources or sinks in the landscape (Petit et al., 2010). Orius species require overwintering sites to complete their life cycle in Palaearctic climates (Saulich and Musolin, 2009). Fertilized females enter overwintering diapause under fallen leaves, in litter, beneath tree bark or on plant stems, particularly in semi-natural areas. During the growing season, the dynamics of flowering resources drive both the population size and distribution pattern of Orius (Péricart, 1972), because these species are highly mobile (Montserrat et al., 2004), actively search prey and respond to odors from prey-infested plants (Carvalho et al., 2011). Flowering plants in semi-natural areas provide more balanced but limited resources over the season in comparison to mass-flowering crops. Arable fields have great potential for supplying resources required by Orius (i.e. pollen and prey) (Blitzer et al., 2012; Lundgren et al., 2009; Veres et al., 2011). Cultivated areas can, however, prove to be sinks at landscape scale especially where insecticides are applied frequently during the entire growing season (Ricci et al., 2009).

Orius adults do not appear in crops at early crop growth stages before pest populations have built up, then Orius enter the crop fields, particularly overwintering females, and aggregate to highdensity patches (Bokina, 2008; Montserrat et al., 2004). In the arable cropping systems of Central-Eastern Europe (see Section 2.1 and Vasileiadis et al. (2011) for details), winter wheat fields are colonized initially, depending on cereal aphid and thrips densities (Bokina, 2008), and it is only later that maize fields provide pollen and prey and are colonized (Albajes et al., 2010; Mészáros et al., 1984; Rácz, 1989). Maize silk is an optimal food resource for both Orius adults and juveniles. It has been also shown that Orius species are more abundant in weedy fields (Lundgren et al., 2008, 2009). Sunflower is the last mass flowering crop in this cropping system that can provide a large range of prey, pollen and nectar. Only oilseed-rape fields are sprayed against pollen beetle and weevils, in which Orius has been shown to be less abundant (Bosco and Tavella, 2008), however it is not clear whether oilseed rape is a resource or a sink for Orius species.

In a 10 years agro-ecosystem survey in maize in Hungary, the Orius abundance was shown to be strongly positively correlated to the amount of prey and to the average temperature in the growing season (Rácz, 1989). Low temperature increases Orius species mortality during overwintering, extends their development period and reduces fecundity (Saulich and Musolin, 2009). Similarly, the prey population is lower (Rácz, 1989) and the phenology of pollen providing plants is also delayed. In contrast high temperatures, at a given day length, accelerate the development of Orius species, their prey consumption, mobility, and foraging/oviposition activity on the plants (Cocuzza et al., 1997; Baniameri et al., 2005; Tuda and Shima, 2002). Individuals of the second and third generations appear earlier (Rácz, 1989), more eggs are laid and the landscape support larger populations. Orius niger W. and Orius minutus L., the two most abundant species in Hungary (Rácz, 1989), differ in their responses to climate factors. The seasonal development of *O. minutus*, in contrast to other species, appears to be independent of temperature, being regulated by photoperiod (Saulich and Musolin, 2009; Tuda and Shima, 2002). In addition, *O. niger* has a shorter nymphal development and ovipositioning period when assayed under similar temperatures (Fathi, 2009). It is also considered to be more mobile than *O. minutus*, which moves mostly by short flights at a low height (1–3 m) (Southwood, 1960).

Provided the importance of semi-natural areas for generalist predators overwintering and spillover, together with and the abundance of prey and other sources of food, conservation biological control by *Orius* adults can potentially take advantage of the presence of semi-natural areas in the agricultural landscape. Three years of surveys were conducted in an agricultural landscape in Hungary with the aim of evaluating the *Orius* spatial pattern at landscape scale, and linking aggregation, i.e. higher abundance, to the presence of semi-natural areas. Our two hypotheses are that: (1) the *Orius* abundance spatial pattern is aggregated in the landscape; and, (2) this spatial aggregation can be explained by the arrangement of semi-natural areas.

2. Methods

2.1. Experimental design

A three-year survey was conducted on poison hemlock (Conium maculatum L., Veres, 2010; Veres et al., 2010) in the landscape around 5 villages in the Jászság region of Hungary (Boldog, Jászfényszaru, Jászfelsőszentgyörgy, Pusztamonostor, Szentlőrinckáta, North-East Hungary, N47 36.449 E19 39.929). The climate is continental, annual mean temperature is 9.5 °C, and the mean temperature ranges from -5 °C in winter (with 90 days of frost) to 20 °C in summer; the 1971–2000 average precipitation is 562 mm with 138 days of rain quite uniformly distributed (ca. 11–12 rainy days/month). The sampling was on poison hemlock because (1) it grows only in a typical association of the same plant species (ruderal area), thus in similar local environments; (2) sampling is easy and standard; (3) the flowering period lasts for one month, a period short enough to avoid the bias of cumulated effects; (4) Heteropteran species are abundant on it; (5) the sampling proved to be reliable enough (Veres et al., 2012). The use of a trap plant is recognized in other landscape studies (e.g. nettle, Urtica dioica in Rand and Tscharntke, 2007), as well as the use of the flowering of a plant (i.e. dandelion, Taraxacum officinale in Diekötter et al., 2008) as an indicator to start sampling and so to standardize phenological differences between landscapes.

Land use is dominated by agriculture (85% of the total area, forestry 7%, natural area 5%, urban area 3%), and the cropping system in the region is based on arable crops (maize 40%, cereals 40%, sunflower and oilseed rape 15%, other crops 5%) and greenhouse sweet pepper. Arable fields are managed with low input systems (little investment because of high financial risks, see Vasileiadis et al., 2011). No insecticides are generally applied on cereals, maize or sunflower, and they are only used on oilseed rape during the flowering period.

Poison hemlock was sampled randomly near roads over the entire landscape, keeping a minimum distance of 200 m between sampling points (one plant per sampling point). *Orius* adult abundance in total, and *O. niger* and *O. minutus* abundances in particular, were measured on individual plants as sampling units. The sampling was conducted at the beginning of the poison hemlock flowering period each year, and lasted 3 days. Sampling was timed by the poison hemlock phenology, it therefore started late in 2005 (28th July, 164 samples) and 2006 (4th July, 155 samples), and early in 2007 (18th June, 140 samples). Arthropods were shaken from the flower-umbel of one plant into an adapted sweep-net and

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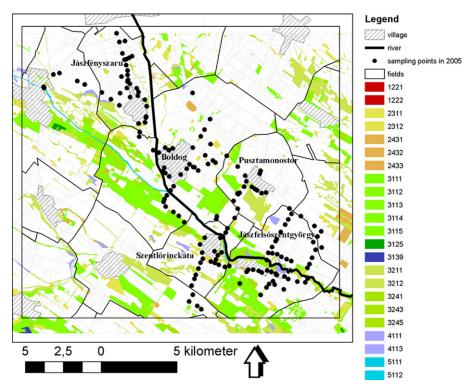


Fig. 1. Experimental design of the *Orius* spp. survey in Hungary. Poison hemlock (*Conium maculatum* L.) sampling points in red, 2005. CORINE LandCover (Büttner et al., 2000, © FÖMI) codes selected in the layer SEMI-NATURAL. Five main categories are indicated: 1 (roads and rails network), 2 (agricultural land), 3 (forests and semi-natural areas), 4 and 5 (water dominated areas). Sub-categories of the main category 2: 2311: intensive pastures, degraded grasslands without trees and shrubs; 2312: intensive pastures, degraded grasslands with trees and shrubs; 2431: agricultural areas with significant share of natural vegetation and with prevalence of arable land; 2432: agricultural areas with significant share of natural vegetation and with prevalence of scattered natural vegetation.

conserved in ethyl-alcohol. *Orius* adult abundance in total and at species level (i.e. *O. niger*, *O. minutus*) was measured. The locations of the sampling points were marked by GPS. The *Orius* habitats were mapped in Esri ArcGIS 9.2. geographical information system. Landscape features were digitized from a 0.5 m resolution color digital orthophoto (acquisition date 2005, FÖMI archive) into CLC 50 categories (FÖMI, Büttner et al., 2000). To create the map of potential habitats, features of CORINE categories (Fig. 1) were selected into a new layer called SEMI-NATURAL. Buffers within a distance of 1000 m were calculated around each sampling point for each year, and intersected with the SEMI-NATURAL layer. The area of each habitat polygon was calculated in the intersected layers and summed up to the points.

2.2. Data analysis

Differences in total abundance between years were tested using one-way ANOVA (StatSoft Inc., 2011). In addition, SADIE (Spatial Analysis by Distance IndicEs) statistical analysis method (Perry, 1995) was applied to describe the spatial distribution of abundance. SADIE "red-blue" analysis allows the identification of the observed counts arranged at random or in clusters of units in two forms: (1) as a patch when there is a high density of counts near one another and (2) as a gap when composed of relatively small or zero counts in nearby sampling points. SADIE measures potential overall aggregation through "distance to regularity" (D), which is a minimum total distance individuals should move to achieve an equal count in each sub-plot. After a number of randomizations, "simulated mean distance to regularity" (E_a) can be calculated. The index of aggregation is defined as $I_a = D/E_a$. A sample is aggregated if $I_a > 1$, randomized if $I_a = 1$, or regular if $I_a < 1$. The test statistic P_a is the probability that observed counts are arranged randomly among the given sample units, and P_a < 0.05 indicates aggregation. Two clustering indexes (v) are also calculated. Each subplot with a higher count than the overall mean is assigned a patch cluster vi (positive), otherwise it is assigned a gap cluster index vj (negative), both with the associated probability. The "red-blue" plots can quantify the degree to which the count for each unit contributes to the overall degree of clustering, either as part of a patch or a gap. Similarly, the pattern of the habitat was characterized by running SADIE "red-blue" analysis on the SEMI-NATURAL area values calculated per point (see above). Spatial association tests were then used to measure associations between the abundance patterns and the semi-natural area pattern each year. The degree of association (χ) of insect abundance pattern to the habitat pattern is calculated by comparing their clustering indices at each sampling unit. The significance of χ is determined through randomization by SADIE taking into account the spatial autocorrelation. Positive values indicate similarity in location of two datasets patches and/or gaps, whereas negative values point out dissociation. A two-tailed test was used with P_{γ} < 0.025 for significant association and P_{γ} > 0.975 for significant dissociation. Spatial patterns were analyzed with SADIEShell v. 1.22 and Surfer 8.04 (Golden-Software Inc., 2004) was used to create "red-blue" plots.

3. Results

3.1. Orius abundance

A total of 4176 *Orius* adults were found on 457 poison hemlock plants during the three study years. The individuals were classified into five *Orius* species: *O. niger* (86%), *O. minutus* (12%), *O. majusculus* (0.1%), *O. vicinus* (4 counts) and *O. horvathi* (12 counts). A total of 758 (sex-ratio = 0.651), 615 (sex-ratio = 0.618), 2228 (sex-ratio = 0.589)

Table 1 Spatial distribution of *Orius* spp. in the landscape, region Jászság, in 2005, 2006 and 2007 (I_a : average distance flow; p_a : associated probability, significant if p < 0.05 (in bold); vi, vj: cluster index; $p_{(mean \, vj)}$, $p_{(mean \, vj)}$: associated probability, significant if p < 0.05 (in bold); NA: no appropriate data).

	2005	2006	2007
O. niger			
I_a	1.353	1.582	2.656
p_a	0.115	0.048	0.003
vi	1.298	1.412	2.453
$p_{(\text{mean } vi)}$	0.144	0.089	0.006
vj	-1.295	-1.597	-3.015
p _(mean vj)	0.121	0.051	0.000
O. minutus			
I_a	1.001	NA	0.573
p_a	0.394	NA	0.881
vi	1.254	NA	0.943
$p_{(\text{mean } vi)}$	1.667	NA	0.548
vj	-0.982	NA	-0.776
$p_{(\mathrm{mean}\ vj)}$	0.419	NA	0.842

adults were identified as *O. niger* in the three study years respectively, compared to 154 (sex-ratio = 0.604), 69 (sex-ratio = 2.136), 275 (sex-ratio = 0.978) adults of *O. minutus*. The diversity of *Orius* species in the study area was low. *O. niger* and *O. minutus* are the two dominant species, however the abundance of *O. minutus* was low.

The total *Orius* abundance was significantly higher in 2007 than in 2005 or 2006 ($F_{(2,456)}$ = 53.9, p < 0.001). The year 2005 was extremely cold, with cold winter and spring (mean T = 9.7 °C, Bihari et al., 2008), and a lower abundance of individuals (5.6 ± 7.3; total count: 918). It was also colder than average in 2006, even if warmer than 2005 (mean T = 10.3 °C), and the observed abundance was again low (4.6 ± 6.1; total count: 712). Contrastingly, 2007 was extremely warm and dry (mean T = 11.7 °C), so that flowering of poison hemlock was earlier (i.e. one month before 2005), and the abundance significantly higher (18.2 ± 19.7; total count: 2456) (all abundances are mean ± sd) (Fig. 2). The relative abundance of O *minutus* decreased in 2006 (9%) and 2007 (10%) compared to 2005 (16%) in favor of O. *niger*.

3.2. Spatial aggregation

Differences between years were detected in population size and distribution pattern. The most abundant species *O. niger* showed no pattern in 2005, but was aggregated across the landscape in 2006 and in 2007 (Table 1, Fig. 2). The level of aggregation also differed between years, being strongest in the warm year 2007. The less abundant *O. minutus* was randomly distributed in 2005 and 2007, while in 2006 there were not enough individuals sampled to complete the tests.

3.3. Landscape characteristics

Regarding the landscape, 50% of the features were categorized as large agricultural fields (2111), 14% as small agricultural fields (2112), 4% as complex cropping system without buildings (2421), 2.8% as complex cropping system with buildings, giving approximately 70% agricultural dominance. Semi-natural areas made up approximately 20% of the land use, with the dominance of forest plantations (8%, 3115), semi-natural grasslands without trees (4%, 3211), intensive degraded grasslands (1.5%, 2311) and young forests (1.6%, 3241). In addition, 2% were family houses with gardens (1122) and 10% other categories with less than 1% dominance. The proportions of semi-natural areas in the 1000 m buffer around the sampling points were balanced between years: 2005 (16 \pm 14%,

Table 2 Association of *Orius* abundance pattern to the pattern of semi-natural areas, region Jászság, in 2005, 2006 and 2007 (χ : association index; P_{χ} : associated probability; significant if $p_{\chi} < 0.025$ or $p_{\chi} > 0.975$ (in bold); NA: no appropriate data).

	2005	2006	2007
O. niger	0.217	0.199	-0.246
X	0.023	0.006	0.997
p	association	association	dissociation
O. minutus	0.107	NA	0.033
X	0.137	NA	0.390
p	Not significant	NA	Not significant

minimum 0%, maximum 72%), 2006 (16 ± 13 %, minimum 0%, maximum 59%), 2007 (15 ± 13 %, minimum 0%, maximum 56%).

3.4. Spatial association

Spatial association between abundance of *O. niger* and seminatural area pattern was significant or marginally significant in all three study years, but the direction of the relationship differed between years (Table 2, Fig. 2). Data on *O. minutus* did not show any evidence of relationship. The *O. niger* abundance was associated with semi-natural areas (χ was positive) in both 2005 and 2006. On the contrary, in 2007 its abundance was dissociated from semi-natural areas (χ was negative), thus *O. niger* is likely to be related to semi-natural areas, but the direction of the relationship differs between the years.

4. Discussion

O. niger populations were larger in warm years, an observation consistent with the fact that its reproduction ability depends on climate factors (Baniameri et al., 2005; Rácz, 1989; Saulich and Musolin, 2009). Besides the direct seasonal effects such as temperature, the differences in the amount of prey might also have indirectly influenced Orius populations (Rácz, 1989) even if this research did not include direct prey-predators study. The carrying capacity of the landscape was shown to be larger in warm years, which might affect conservation biological control. O. niger responded more to differences between years than O. minutus. This result is in accordance with the difference in the biology of the two species, as 0. minutus was shown to respond to photoperiodic changes and to be independent of temperature (Saulich and Musolin, 2009). However, the abundance of O. minutus was lower in the area than might have been expected from the literature (Rácz, 1989), which could be due to the sampling method used. The trap plant poison hemlock provides suitable habitat only during the flowering period (approximately one month), so it may be better colonized by O. niger which has a higher mobility (Southwood,

Our results demonstrate aggregated spatial distribution for *O. niger*, but not for *O. minutus*. *O. minutus* females were shown to be less mobile at large scale (Southwood, 1960), which can explain the lack of clear spatial pattern. *O. niger* is the smallest and most mobile of the indigenous species in Hungary, and it is believed capable of rapidly moving around the landscape with changes in resource availability. The level of its aggregation also differed between years, which could be a result of enhanced population development, the positive effect of temperature on insect activity (Saulich and Musolin, 2009; Tuda and Shima, 2002), and the larger population (our results).

O. niger population was related to semi-natural areas, in accordance with the assumption that abundance of natural enemies and their conservation biological control potential depend on the

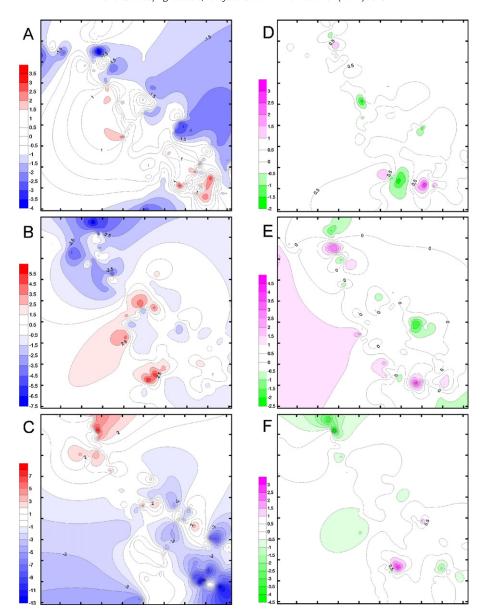


Fig. 2. Spatial aggregation of *O. niger* individuals and their relation to semi-natural areas. Interpolated (Kriging) ν cluster index of SADIE "red-blue" analysis in the year 2005 (A), 2006 (B), 2007 (C). Red filling refers to patch (ν i > 1.5), blue to gap (ν j < -1.5), (p < 0.05). Interpolated (Kriging) χ values of SADIE association test in the year 2005 (D), 2006 (E), 2007 (F). Magenta filling indicates association (χ > 0.5), green dissociation (χ < -0.5), (p < 0.05).

amount of semi-natural areas (Bianchi et al., 2006; Tscharntke et al., 2007; Veres et al., 2011). Orius species can overwinter more successfully in semi-natural areas, which may explain the association in cold years, whereas the dissociation in warm years suggests association to other resources in the landscape. Seasonal dynamics may be particularly relevant for organisms with a relatively short life-span (Orius species have two to three generations per year in the study area) and for temperate agricultural landscapes in which patch composition and qualities are affected by weather conditions, cultivation practices and plant phenology (Brewer et al., 2008; Costamagna et al., 2004; Thies et al., 2005, 2008). Our results suggest that in cold years, O. niger population development is slow and associated with semi-natural areas as main overwintering sites. In warm years however, O. niger may spread out from semi-natural areas and aggregate to other resources in the landscape such as cultivated areas. In the study area, the landscape is dominated by two main feature groups (i.e. semi-natural areas and cultivated areas), which might both be resources for Orius species that are habitat generalists. Agrobiont species, i.e. those that reach high dominance

in agro-ecosystems (Samu and Szinetár, 2002) can take advantage of tolerance to human disturbance and recolonize fields repeatedly (Wissinger, 1997), profiting from the high amount of available resources (Blitzer et al., 2012; Rand et al., 2006) in the form of green plant material (Bàrberi et al., 2010; Lundgren et al., 2009), pollen (Westphal et al., 2003) or honeydew (Vollhardt et al., 2008). *Orius* species are typical agrobionts, being abundant in arable, horticultural and ornamental agro-ecosystems where they feed on various pest species and plant tissues (Bosco and Tavella, 2008; Tommasini, 2004; Perdikis et al., 2011; Rácz, 1989).

A direct consequence of *Orius* being a habitat generalist is that management intensity rather than crop composition of cropping systems at landscape level may impact their population dynamics. Management intensity has been reported to affect landscape level populations in a large range of other taxa (Geiger et al., 2010; Rundlöf et al., 2008; Ricci et al., 2009; Winqvist et al., 2011). The predation rates of Lepidopteran pest eggs by *Orius* were negatively affected by the intensively managed horticultural areas in the surroundings (Bianchi et al., 2005). There is some

evidence that *Orius* abundance in intensive apple orchards depended on the proportion of extensive arable crops over the land-scape (Whalon and Croft, 1986). Differences in *Orius* abundance between regions are often observed, e.g. in Italy (Tommasini, 2004), but not discussed in relation to the cropping system; nonetheless no clear host-plant preference for the dominant species explained these differences in the above study. Our results suggest the relevance of the cropping system of the region as a factor in *Orius* abundance at landscape scale. The cropping systems in Central-Europe, i.e. in our study area, are based on arable crops (i.e. winter wheat, maize, sunflower, oilseed rape), which are managed extensively (Vasileiadis et al., 2011), so they may provide suitable habitat for *Orius* species at various times during the growing season.

Agricultural intensification has many components, such as loss of landscape elements, enlarged farm and field sizes and high fertilizer and pesticide inputs (Geiger et al., 2010). Arthropod richness is higher in areas of less intensive land use, and the decline is greater between native vegetation and agricultural land use than among different agricultural land uses, emphasizing the importance of the conservation of natural and semi-natural habitats (Attwood et al., 2008). These habitats were shown to be important resources for Orius species. However, in highly intensified agricultural landscapes with little remaining native vegetation, the adoption of reduced-input crop management and the provision of relatively low intensity agricultural land uses may prove to be effective in maintaining arthropod diversity and potentially promoting functionally important groups such as predators (Attwood et al., 2008), which was shown to be particularly the case for Orius species in this study. In addition, the population was larger in the year when the abundance was dissociated from semi-natural areas, which could be explained by the higher carrying capacity of cultivated areas (Rand et al.,

Understanding factors driving the spatio-temporal pattern of Orius abundance at landscape scale appears relevant for conservation biological control. Indeed, in a former study, the mean abundance of Orius in greenhouses in 2006 and 2007 followed the same pattern as in the present study and the level of colonization of greenhouses surrounded by arable fields corresponded to the patches and gaps identified in this study (Bán et al., 2009). A specific study and measurement of resources such as pollen and prey would add clarity to results, but this information has not been collected in our study, being a typical "structure detecting" one (Bàrberi et al., 2010) without direct evaluation of the abundance-to-distance link. Even so our result suggests that the presence of semi-natural areas in the landscape is necessary but not sufficient for sustaining conservation biological control, because the mass reproduction of Orius spp. is probably linked to extensively managed arable fields. In conclusion, Orius abundance pattern at landscape scale is shown to be driven by resource patterns and availability of both semi-natural and cultivated areas, which may vary in the season and between years.

Acknowledgments

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