Conservation tillage mitigates the negative effect of landscape simplification on biological control

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Summary

1. Biological pest control is a key ecosystem service, and it depends on multiple factors acting from the local to the landscape scale. However, the effects of soil management on biological control and its potential interaction with landscape are still poorly understood.

2. In a field exclusion experiment, we explored the relative effect of tillage system (conservation vs. conventional tillage) on aphid biological control in 15 pairs of winter cereal fields (barley and wheat) selected along a gradient of landscape complexity. We sampled the abundance of the main natural enemy guilds, and we evaluated their relative contribution to aphid predation and parasitism.

3. Conservation tillage was found to support more abundant predator communities and higher aphid predation (16% higher than in the fields managed under conventional tillage). In particular, both the abundance and the aphid predation of vegetation- and ground-dwelling arthropods were increased under conservation tillage conditions. Conservation tillage also increased the parasitism rate of aphids.

4. A high proportion of semi-natural habitats in the landscape enhanced both aphid parasitism and predation by vegetation-dwelling organisms but only in the fields managed under conventional tillage. The better local habitat quality provided by conservation tillage may compensate for a low-quality landscape.

5. *Synthesis and applications.* Our study stresses the importance of considering both soil management and landscape composition when planning strategies to maximize biological control services in agro-ecosystems, highlighting the role played by conservation tillage in supporting natural enemy communities. In simple landscapes, the adoption of conservation tillage will locally improve biological control provided by both predators and parasitoids mitigating the negative effects of landscape simplification. Moreover, considering the small scale at which both predation and parasitism responded to landscape composition, a successful strategy to improve biological control would be to establish a fine mosaic of crop and non-crop areas such as hedgerows, tree lines and small semi-natural habitat patches.

Key-words: aphid, ecosystem services, landscape complexity, natural enemies, parasitoids, pest control, predation, tillage intensity

Introduction

Biological control of pests is an important ecosystem service shaping yield production. Insect natural enemies have been estimated to be responsible for the 50–90% of the pest control occurring in crop fields (Pimentel 2005) reducing large proportions of yield loss (Losey & Vaughan 2006; Power 2010). A large body of evidence suggests that agricultural intensification is threatening biological control (Kleijn *et al.* 2009; Geiger *et al.* 2010; Winqvist *et al.* 2011; Bommarco, Kleijn & Potts 2013). Moreover, despite the steady increase in chemical pesticide use over the last 50 years, estimated crop losses to insect pests have also significantly increased (Oerke 2006). In a future where agriculture will face severe environmental, economic and social challenges (Foley *et al.* 2005; MEA 2005), improving or maintaining the biological

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control services provided by natural enemies arises as an ecologically and economically promising solution.

Aphids are considered severe pests of crops world-wide (Dedryver, Le Ralec & Fabre 2010). In winter cereal crops, food webs contributing to aphid biological control include specialized aphid suppressors such as parasitoids, lacewing and ladybird larvae and more generalist predators such as carabid beetles, spiders and rove beetles (Diehl *et al.* 2013a). Although birds have been shown to play an important role in controlling pest populations or in constraining biological control by intraguild predation in several systems (Martin *et al.* 2013; Railsback & Johnson 2014), their contribution to aphid biological control in winter cereal crops has never been tested.

Biological control depends on multiple factors acting from the local to the landscape scale (Tscharntke *et al.* 2007; Rusch *et al.* 2010). Various farming practices have been found to affect natural enemy communities and the associated biological control. For instance, organic farming has been often shown to locally support higher biological control compared to more intensively managed farming systems (Winqvist, Ahnström & Bengtsson 2012). However, much less is known about the mechanisms linking soil management (e.g. crop rotation, soil tillage) to above-ground ecosystem services such as biological control (but see Rusch *et al.* 2013). Conservation tillage is a farming practice that includes all the techniques characterized by non-inversion of soil often combined with a permanent vegetation cover. Globally, it has been estimated to be practised on 45 million ha in 2004, mainly in North and South America, but it is increasingly adopted in Europe and other parts of the world (Holland 2004). It has been shown to be a promising soil management system able to minimize negative impacts of farming operations with several beneficial consequences on soil structure, hydrology and biodiversity (Kladivko 2001; Holland 2004; Power 2010; Soane *et al.* 2012; Boscutti *et al.* 2015). The higher tillage intensity typical of conventional management has a stronger impact on ground-dwelling arthropods directly, by mechanically injuring or killing individuals, and indirectly, by degrading habitat quality and availability of alternative prey (e.g. Holland 2004). Populations of several generalist predators have been shown to be favoured under conservation tillage because of reduced soil disturbance, increased surface residues and greater weed diversity that all together provide a more suitable environment (e.g. Thorbek & Bilde 2004; Soane *et al.* 2012). For instance, residues of crops and associated cover crops are important in providing shelter and in maintaining soil climatic conditions suitable for the survival and development of several arthropods throughout the year (Roger-Estrade *et al.* 2010). Whether conservation tillage enhances biological control services remains, however, largely unknown.

Landscape is a further key factor shaping natural enemy communities. Complex landscapes with a large cover of semi-natural habitats provide a more stable environment than landscapes dominated by arable land (e.g. Tscharntke *et al.* 2007). Semi-natural habitats can maintain populations of alternative hosts and prey for parasitoids and predators, protect natural enemies from disturbance, offer additional nectar resources during the vegetative season and shelter during overwintering (Landis, Wratten & Gurr 2000; Bianchi, Booij & Tscharntke 2006). A growing number of studies have shown how complex landscapes support more diverse and abundant communities of natural enemies and, generally, higher biological control (e.g. Gardiner *et al.* 2009a; Letourneau *et al.* 2009; Chaplin-Kramer *et al.* 2011; Chaplin-Kramer & Kremen 2012). Highly mobile organisms in particular have been shown to be strongly affected by landscape composition because, although delivering services locally, their behaviour, biology and dynamics depend on spatial distribution of resources (e.g. Kremen *et al.* 2007). However, soil management has been rarely considered in relation to landscape complexity. In particular, the potential benefits of conservation tillage described above can vary according to the degree of landscape intensification.

Using a design where landscape complexity and tillage system (conservation vs. conventional tillage) were statistical orthogonal factors, our study explores for the first time their relative importance on aphid biological control. In a field exclusion experiment, we first quantified the predation provided by three different guilds of natural enemies in winter cereal crops (i.e. barley and wheat): birds, parasitoids/vegetation-dwelling predators and ground-dwelling predators. Secondly, we sampled the abundance of vegetation- and ground-dwelling predators in the field. Thirdly, along with predation, we also quantified parasitism rate in aphid populations. Assessing the level of biological control provided by different natural enemy guilds might be important if we are to plan sustainable management strategies in agricultural landscapes (Loreau, Mouquet & Gonzalez 2003). We therefore hypothesized that (i) conservation tillage enhances biological control services and in particular predation by ground-dwelling organisms and (ii) the level of biological control increases with landscape complexity in particular for highly mobile organisms such as flying predators and parasitoids. We also tested whether landscape complexity additively or synergistically acted with conservation tillage in enhancing biological control.

Material and methods

STUDY AREA, EXPERIMENTAL DESIGN AND LANDSCAPE ANALYSES

The study was conducted between April and June 2014 in 30 fields located in the agricultural landscape of the Udine Province, north-east Italy (latitude 46°4′0″N, longitude 13°14′0″E). This region is an extensive lowland area (*c.* 950 km^2) characterized by temperate climate with a mean annual precipitation of *c.* 1300 mm and a mean annual temperature of 13 °C.

Our sampling consisted of 15 pairs of neighbouring winter cereal fields. Within each pair, one field was managed under

conservation tillage and the other under conventional tillage (distance range: 0–1·2 km). Field pairs were separated by at least 1 km except for two that were distant by 300 m. Among the 15 pairs, seven were sown with winter wheat and eight with barley in autumn 2013. Crop species was consistent within the pairs. Crop rotation for the selected fields was usually a 3-year rotation (maize, winter wheat or barley, and soya bean). Conservation tillage included all techniques characterized by non-inversion of soil for at least 5 years (10 years on average, ranging from 5 to 20 years), whereas under conventional tillage, the seedbed was prepared by mouldboard ploughing (30 cm depth) followed by one or two tills before sowing. Only in the fields managed under conservation tillage, cover crops such as Italian ryegrass, vetch, sorghum and common melilot were adopted between cash crops. In each field, we identified one 60 × 20 m strip located on one side of the field. Within each pair, the adjoining habitat had similar structure and composition (either a grass margin or a hedgerow) for both fields. Each strip was divided into six 10 × 20 m plots, of which the outer ones were considered as buffer zones. Among the four left, two non-adjacent plots were randomly selected for the exclusion experiment and the natural enemy sampling. Nitrogen fertilizer (ammonium nitrate) was applied to the selected plots following local farming recommendations (80 kg N ha^{-1} in two applications). No chemical pesticides and herbicides were applied on the plots during the experiment.

Field pairs were selected along a gradient of landscape complexity ranging from 1·2 to 22·4% of cover of semi-natural habitats (1060 m radius around each field). Since the increase in the cover of semi-natural habitats was consistent with the increase in landscape complexity (correlation index = 0·62), landscapes with a high cover of semi-natural habitats are hereafter referred to as 'complex' and landscapes with low cover as 'simple' (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer *et al.* 2011). Land cover class 'semi-natural' included forest patches, hedgerows, tree lines, field margins and grasslands. To measure the landscape composition around each field, a total of eight nested spatial scales were considered within windows of varying radii (95, 135, 190, 265, 375, 530, 750 and 1060 m). Each increment in scale doubled the surrounding area from 0·028 (95 m) to 3·5 km^2 (1060 m). ARCGIS 9.3 was used for landscape analyses of regional land use maps, verified and ameliorated with aerial photographs to increase class discrimination accuracy.

PRELIMINARY APHID SURVEY

Natural colonization of crop plants by aphids can be very irregular both in time and in space, and it can affect predator and parasitoid occurrence in the field (e.g. Walde & Murdoch 1988). Different initial aphid density in fields could thus confound the effect of tillage management and landscape complexity on biological control. We therefore conducted a preliminary aphid survey at the stem elongation stage (BBCH35; Zadoks, Chang & Konzak 1974) in order to account for potential factors influencing biological control besides those explicitly explored in the present study. Aphid abundance was assessed visually by inspecting 50 randomly selected plants per field. The total number of aphids per field was analysed with a general linear mixed-effects model where tillage system and landscape complexity were included as fixed factors and the type of crop and the field pair as random factors. Aphid abundance was ln-transformed to achieve normal distribution of model residuals. The density of naturally occurring aphids was not affected by tillage system ($F = 0.81$, $P = 0.386$), whereas it increased together with landscape complexity at the 95-m scale ($F = 4.50$, $P = 0.057$). However, aphid abundance in the fields was considerably low (0·7 aphids per plant on average), always below the economic threshold, that is no outbreak was present in our experimental fields.

PREDATION

The contribution to aphid biological control of the three different guilds of natural enemy mentioned above was quantified by arranging an exclusion experiment. Exclusion treatments consisted of cylindrical cages (height: 1·5 m, diameter: 0·3 m) designed to exclude combinations of three different guilds of natural enemies: ground-dwelling predators – G (carabid beetles, cursorial spiders and rove beetles); vegetation-dwelling predators and parasitoids – V (parasitoids, flying beetles, larvae of ladybirds, hoverflies, lacewings and web spiders); and birds and other vertebrates – B. Vegetation-dwelling predators and parasitoids were excluded using polyester fine mesh (mesh size: 1 mm), and birds and other vertebrates with an anti-bird net (mesh size: 1·5 cm). Nets were supported by poles. In the treatments excluding ground-dwelling predators, a plastic ring (0·3 m in diameter and 0·25 m in height) was dug 10 cm into the soil and an 8-cm-wide band of insect glue was applied along the perimeter. Inside each plastic ring, one live pitfall trap was placed to capture the ground-dwelling predators. These live pitfall traps were checked for the duration of the experiment and predators were eventually removed and released outside the plastic rings. In the other exclusion treatments, access of ground-dwelling predators was guaranteed by fixing nets to the support poles 5 cm above the ground. An opening at the side of the cages sealed with blinder clips was used to examine plant material during the experiment. A total of six exclusion treatments (-G, -B, -V-B, -G-B, one closed treatment -V-G-B and one open treatment O) were installed and randomly located within one of the two selected plots in each field.

To avoid bias due to differences in the initial aphid abundance, we inoculated field plants with aphids reared under laboratory conditions. For each exclusion treatment, seven wheat/barley tillers were selected 10 days before the inoculation to standardize crop density. The selected plants and the ground were cleared from natural enemies and then covered by nonwoven fabric supported by sticks to exclude insect recolonization. Aphids *Sitobion avenae* were provided by Katz Biotech AG$^®$ and directly placed on the plants (*c.* 150 aphids per treatment including both adults and nymphs). Inoculation was done at the heading stage of the cereals (BBCH50-55) under good weather conditions (absence of precipitation and strong wind, minimum air diurnal temperature of 18 °C). After 5 days, established aphids were counted and plants were re-inoculated if needed (i.e. cages with less than 15 aphids). Ten days after the first inoculation, aphids were counted (time 0) and the exclusion treatments started.

Aphids were counted in each treatment on two occasions: five and ten days after the onset of the exclusion experiment. In each plot, for five exclusion treatments (-G, -B, -V-B, -G-B, O), aphid predation was quantified for each 5-day period as the proportion of aphids predated compared with the aphid population growth in the closed treatment (-V-B-G), calculated following the methodology of Gardiner *et al.* (2009a):

$$Predation\ Index = N_{treatment5}/(R_{closed} \times N_{treatment0}),$$

where $N_{treatment5}$ is the number of aphids counted in the exclusion treatment after 5 days, R_{closed} is the aphid population growth in the associated closed treatment, and $N_{treatment0}$ is the number of aphids in the exclusion treatment at the beginning of the 5-day period. This predation index ranges from 0 to 1 (0: no net loss of aphids; 1: 100% of aphids predated). Where the index was found to be negative (more aphids in the exclusion treatment than in the closed one; only 10 cases out of 240), a value of zero was assigned to these cages as this indicates no effective predation (Gardiner *et al.* 2009a; Rusch *et al.* 2013).

Just before the onset of the exclusion experiment, a storm event damaged the cages in two field pairs (four fields) compromising the aphid establishment. Moreover, the tillers in four cages were damaged by rodent activity, three during the first 5-day period and one during the second 5-day period. The analyses regarding the predation were thus based on data from 13 field pairs (26 fields; 152 cages).

PREDATOR SAMPLING

In each field, the second, undisturbed plot was used for the sampling of natural enemies. Ground-dwelling predators were caught with three plastic pitfall traps per field (9·5 cm in diameter and 13-cm deep) placed along a linear transect spaced at 3-m intervals. The pitfall traps were filled with 150 ml of 50% ethylene glycol. Plastic roofs fixed with nails to the soil prevented flooding by rain. The first sampling period coincided with the exclusion experiment (10 days) and a second lasted for the following 10 days in order to improve accuracy in sampling the ground-dwelling predator community (e.g. Niemälä, Halme & Haila 1990). Invertebrates were preserved in 70% ethanol. We considered the abundance of carabid beetles, cursorial spiders and rove beetles as the total number of individuals per field (the total catch of the three pitfall traps per arthropod group, for each sampling period). In one field, during the second sampling period, the pitfall traps were damaged. The analyses regarding the pitfall catches were thus based on data from 30 fields for the first sampling period and from 29 fields for the second. Vegetation-dwelling predators were visually monitored once, 3 days after the onset of the experiment. The sampling was conducted along two 20-m transects inspecting 50 randomly chosen tillers each. Abundance of flying beetles, web spiders, larvae of hoverflies, ladybirds and lacewings was measured as the total number of individuals per 100 tillers.

PARASITISM

In all the exclusion treatments where parasitoids were not excluded (-G, -B, -G-B and O; 120 cages), parasitized aphids (mummies) were visually counted after 10 days from the onset of the exclusion experiment. Parasitism rate was calculated as:

$$Parasitism\ rate = N_{mummies}/(N_{mummies} + N_{non-parasitized\ aphids}).$$

Due to the storm and rodent damage, parasitism analyses were based on data from 13 field pairs (26 fields, 100 cages).

DATA ANALYSIS

The predation index, the predator abundance and the parasitism rate were analysed using general linear mixed-effects models (eight models) and generalized linear mixed-effects models (one model). We first built full models and then we simplified them by removing one-by-one the non-significant interaction terms. Crop type and abundance of aphids naturally occurring in the field were initially included in all the models as fixed effects to test for potential effects of different crop species and aphid density on predation, predator abundance and parasitism. Since both factors did not influence any response variable, they were therefore removed from the models.

Predation index (model 1) was calculated for each 5-day period of the exclusion experiment (from time 0 to the 5th day and from the 5th to the 10th day) for each exclusion treatment. The counting period, the field pair and the plot ID were included in the model as random factors. Predation response to landscape composition was analysed for different predator guilds separately, as the different groups were expected to respond to landscape at different spatial scales. Since bird exclusion did not affect predation (see Results), landscape effect on predation was tested for ground-dwelling predators, vegetation-dwelling predators and the combination of the two groups (model 2, 3 and 4, respectively). The counting period and the field pair were included in the all three models as random factors. Abundance of carabid beetles, cursorial spiders and rove beetles were analysed separately (model 5, 6 and 7, respectively) and ln-transformed to achieve normal distribution of model residuals. The sampling period and the field pair were set as random factors. Abundance of ladybirds, hoverflies and web spiders, due to the large amount of zeros in the data, was pooled together and analysed as one group (vegetation-dwelling predators) with a generalized mixed linear model with a Poisson distribution (model 8). The field pair was included in the model as a random factor. Parasitism rate (model 9) was ln-transformed to meet the normality assumptions of the model, with the field pair and the plot ID as random factors.

When the landscape variable was included in the models, analyses were performed at all spatial scales between 95 and 1060 m around the fields. Only scales that gave significant main effects and interactions were presented in the results. The analyses were performed using the 'nlme' and 'lme4' packages (Pinheiro *et al.* 2015) implemented in R STATISTICAL Software 3.1.1 (R Development Core Team 2014).

Results

In the exclusion experiment, an average of 55 (SE = 3·9) aphids successfully colonized the plants. The predation index was on average 0·68 (SE = 0·05) in fields managed under conservation tillage and 0·57 (SE = 0·05) in the fields managed under conventional tillage. The natural enemy guilds considered in the study differently contributed to aphid predation (Table 1) and their effect on predation was found to be influenced by tillage system (interaction treatment × tillage, Fig. 1). The exclusion of birds and other vertebrates did not lead to differences in predation compared to the same treatments in which they were not excluded (-G, O). In the exclusion treatments where only one predator guild had access to aphids, the differences in predation between tillage systems were more evident. The predation provided by ground-dwelling predators (-V-B, model 2) differed between tillage systems, being 39·8% higher in fields managed under conservation tillage, while it

Table 1. Results of (generalized) linear mixed-effects models relating the predation index, parasitism rate and predator abundance to explanatory variables. Only significant interactions were reported

| Explanatory variables	nDF	dDF	Test	P	Figures
Predation					
Predation index (model 1)			F		Fig. 1
Treatment	4	193	15·79	<0·001	
Tillage	1	25	11·33	0·002	
Treatment × tillage	4	193	2·23	0·067	
Predation by ground dwellers (model 2)					
Tillage	1	25	8·76	0·007	
% Semi-natural (any scales)	–	–	–	NS	
Predation by vegetation dwellers (model 3)					
Tillage	1	21	12·86	0·002	Fig. 2
% Semi-natural (256 m)	1	21	2·40	0·136	
Tillage × % semi-natural (256 m)	1	21	8·14	0·009	
Predation by vegetation + ground dwellers (model 4)					
Tillage	1	23	1·96	0·1743	
% Semi-natural (any scales)	–	–	–	NS	
Predator abundance					
Ground-dwelling predator abundance			F		Fig. 3
Carabid beetles (model 5)					
Tillage	1	28	5·07	0·032	
% Semi-natural (any scales)	–	–	–	NS	
Cursorial spiders (model 6)					
Tillage	1	28	11·34	0·002	
% Semi-natural (any scales)	–	–	–	NS	
Rove beetles (model 7)					
Tillage	1	28	0·14	0·7116	
% Semi-natural (any scales)	–	–	–	NS	
Vegetation-dwelling predator abundance (model 8)			χ^2		Fig. 3
Tillage	1	–	−2·57	0·010	
% Semi-natural (any scales)	–	–	–	NS	
Parasitism					
Parasitism rate (model 9)			F		Fig. 4
Tillage	1	10	5·38	0·043	
% Semi-natural (375 m)	1	10	4·67	0·056	
Tillage × % semi-natural (375 m)	1	10	6·00	0·034	

Explanatory variables are treatment (exclusion treatment, five levels of natural enemy exclusion), tillage (tillage system, conservation vs. conventional), % semi-natural (landscape complexity measured as the proportion of semi-natural habitats in a 256 m or 375 m radius around plots) and their interactions. nDF = numerator degrees of freedom; dDF = denominator degrees of freedom.

did not respond to landscape complexity at any scale. Vegetation-dwelling predators (-G-B) showed higher predation in conservation-tilled fields compared with conventional managed ones (25% higher, model 3). Moreover, we found an interaction between tillage system and landscape complexity (256-m scale), that is the effect of landscape complexity was evident in the fields managed under conventional tillage, while in the fields managed under conservation tillage, the predation index remained stable along the landscape complexity gradient (Fig. 2). These effects were maintained from 95 to 375 m around fields. The combination of vegetation- and ground-dwelling predators (-B, model 4), on the contrary, did not show any variation in response to both tillage system and landscape complexity.

With pitfall traps, a total of 14 136 carabid beetles, 654 cursorial spiders and 1910 rove beetles were caught during the two sampling periods. The abundance of both carabid beetles and cursorial spiders was increased by conservation tillage (Fig. 3), while rove beetle abundance did not differ between tillage systems. The abundance of vegetation-dwelling predators was found to be higher under conservation tillage with respect to conventional tillage. The most abundant groups were web spiders (86·2%), ladybirds (8·6%) and hoverfly larvae (5·2%). The abundance of both ground- and vegetation-dwelling predators did not respond to landscape complexity at any scales.

Parasitism rate was higher in fields managed under conservation tillage (an average of 10% parasitized aphids) with respect to conventional tillage (6%) and was positively influenced by high landscape complexity (375-m scale). However, we found an interaction between tillage system and landscape: parasitism rate increased together with landscape complexity only in the fields managed under conventional tillage, while in the fields managed under conservation tillage, the proportion of parasitized aphids remained stable along the landscape complexity gradient (Fig. 4). These effects were maintained from 265 to 750 m around the fields.
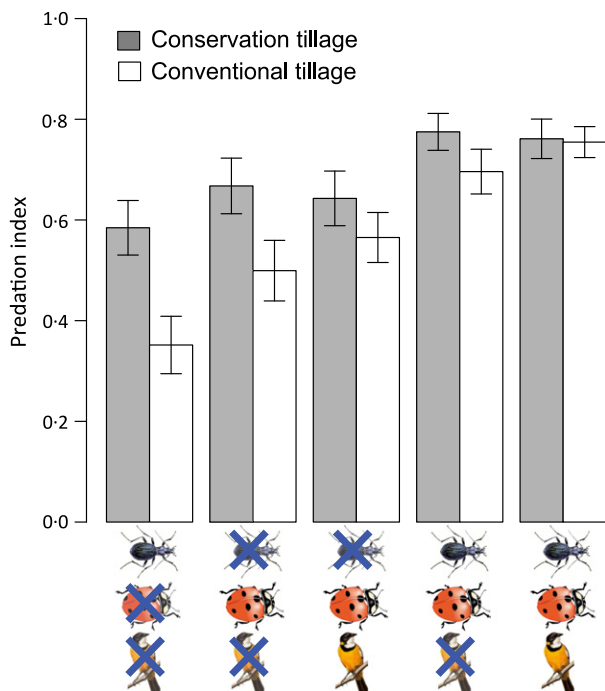
Fig. 1. Effect of natural enemy exclusion on mean (± SE) predation index per exclusion treatment and tillage system (grey bars = conservation tillage; white bars = conventional tillage). Crossed-out symbols signify exclusion of corresponding natural enemy guilds. Guilds of natural enemies are as follows: ground-dwelling predators (beetle symbol); vegetation-dwelling predators (ladybird symbol); birds and other vertebrates larger than 1·5 cm (bird symbol).
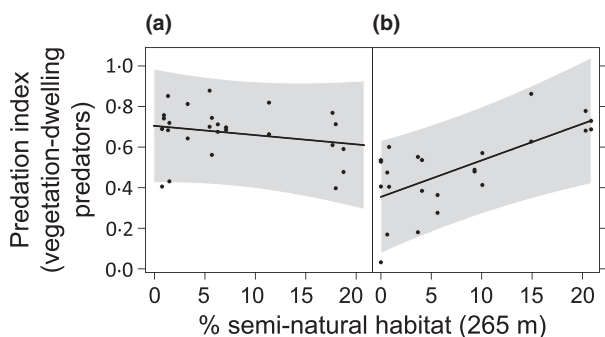
Fig. 2. Effect of landscape complexity (% of semi-natural habitats in a 265 m radius) on the predation provided by only vegetation-dwelling predators in fields managed under (a) conservation and (b) conventional tillage. Points correspond to model predictions. Confidence intervals (95%) are also shown.

Discussion

Our study explored the combined effect of soil management and landscape complexity on the biological control of aphids in winter cereal crops. The combination of an exclusion experiment with the sampling of natural enemies enabled us to directly link the abundance of natural enemies in the field to biological control and to reveal how conservation tillage and the proportion of semi-natural

habitats in the landscape shape biological control. We found a consistent positive effect of conservation tillage on abundance of predators (except rove beetles), predation rate and parasitism of aphids, while contrasting landscape effects on biological control by vegetation-dwelling predators and parasitoids under conventional tillage. We found that complex landscapes enhanced both aphid parasitism and predation by vegetation-dwelling organisms only in fields under conventional tillage showing for the first time an interaction between soil management and landscape composition for two pivotal components of the biological control service.

Conservation tillage supported more abundant ground- and vegetation-dwelling arthropod communities and, in line with our first hypothesis, higher predation by these groups, with a stronger effect on ground-dwelling organisms. However, small populations of aphids were equally well controlled under both conservation and conventional tillage systems when aphids were accessible by all natural enemy guilds. Our findings confirm previous studies showing a response of both ground- and vegetation-dwelling natural enemies to within-field habitat quality and, specifically, to lower disturbance of conservation tillage (Stinner & House 1990). For instance, more abundant ground beetle communities were often found in conservation-tilled fields compared with conventional ones (Kromp 1999; Holland 2004; Soane *et al.* 2012). Holland & Reynolds (2003) showed that spiders are affected by tillage systems as well: conservation tillage promotes a more stable soil environment that, together with the often associated higher weed density, creates a deeper layer of litter and a more structurally complex vegetation ideal for spider colonization and establishment (Holland 2004; Diehl *et al.* 2013b). Conservation tillage can also positively affect generalist predators indirectly, by sustaining more abundant populations of detritus feeding organisms, such as Collembola, that serve as an important alternative food source when crop pests are not present (Kladivko 2001; Roger-Estrade *et al.* 2010). Not all the natural enemy guilds contributed to aphid population control: the exclusion of birds and other vertebrates did not lead to any significant differences in predation index. Birds can play an important role in tropical agro-ecosystems (Martin *et al.* 2013; Railsback & Johnson 2014), whereas, in European environments, only few species can feed on polyphagus predators and consume aphids as alternative prey (e.g. Eeva, Ahola & Lehikoinen 2009). Our study suggests that they may not be important in winter cereal fields; probably, the simplified structure of the crop stands did not allow birds to easily locate and hunt their prey.

Parasitism rate was also increased by conservation tillage. Several studies reported non-conventional tillage systems (conservation, reduced or no-tillage) to increase weed abundance and diversity (Soane *et al.* 2012). Floral nectar resources have been shown to be an important component of the diet of adult parasitoids (Rusch *et al.* 2010; Araj *et al.* 2011). This, along with limited distur-
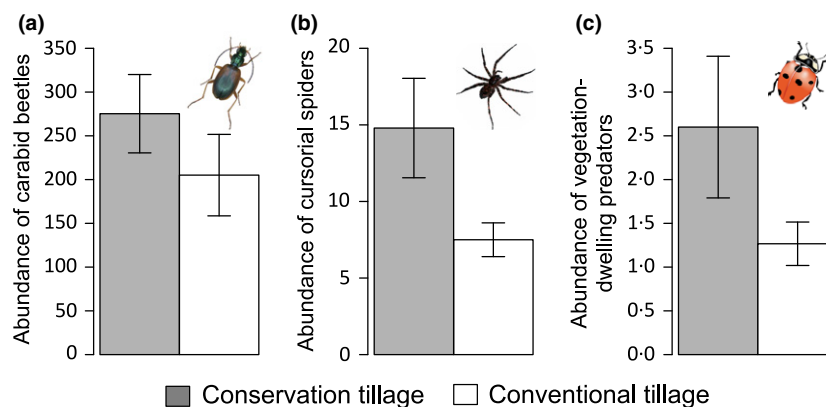
Fig. 3. Abundance (mean ± SE) of (a) carabid beetles, (b) cursorial spiders and (c) vegetation-dwelling predators in response to tillage system (grey bars = conservation tillage; white bars = conventional tillage). Abundance of ground-dwelling predators refers to the two periods of pitfall trap sampling (10 days each). Abundance of vegetation-dwelling predators was calculated as the total number of individuals per 100 tillers (web spiders, larvae of hoverflies and ladybirds).
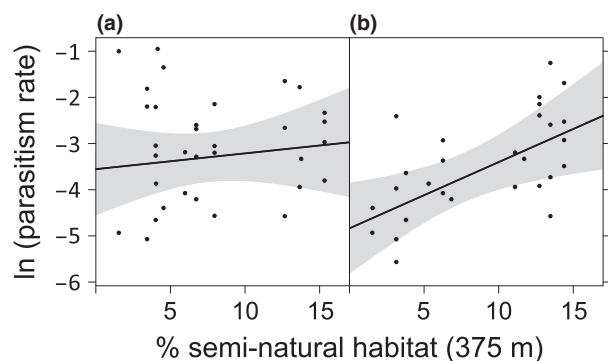
Fig. 4. Effect of landscape complexity (% of semi-natural habitats in a 375 m radius) on ln-transformed parasitism rate in fields managed under (a) conservation and (b) conventional tillage. Points correspond to model predictions. Parasitism varied between 0 and 37%. Confidence intervals (95%) are also shown.

bance by farming practices, might have contributed to sustaining and enhancing parasitoid populations both in complex and simple landscapes.

Predation provided by vegetation-dwelling organisms and parasitism showed similar patterns in response to landscape complexity interaction with the tillage system. In both cases, aphid biological control increased with landscape complexity in the fields managed under conventional tillage, whereas under conservation tillage, neither predation nor parasitism depended on landscape complexity. These results suggest that conservation tillage may improve within-field habitat quality, locally supporting predator and parasitoid communities and therefore providing higher aphid biological control in simple landscapes as well. Fields under conventional tillage may instead offer a less favourable habitat for natural enemy persistence. The control of aphid populations in these fields may hence depend more on the spillover of mobile antagonist organisms from the surrounding semi-natural habitats, rather than on the predation and the parasitism

provided by those established in the crop fields. Both vegetation-dwelling predators and parasitoids are in fact known to benefit from complex landscapes due to the higher availability of overwintering sites, refuges from disturbances and more diverse and abundant food sources (e.g. Thies, Roschewitz & Tscharntke 2005; Tscharntke *et al*. 2007; Rusch *et al*. 2010; Thies *et al*. 2011). However, the importance of landscape complexity in enhancing biological control may be predominant when within-field habitat quality is poor. Both predation by vegetation-dwelling organisms and parasitism best responded to landscape complexity at small spatial scales (265-m and 375-m scale for predation and parasitism, respectively). Our findings are in line with previous studies showing landscape composition affects more specialized enemies, mainly at small scales (Chaplin-Kramer *et al*. 2011). The different scale at which parasitoids and vegetation-dwelling predators responded to landscape complexity can probably be ascribed to different dispersal abilities and movements across habitats of the two groups (Perović *et al*. 2010).

We hypothesized that the level of biological control increases with landscape complexity in particular for highly mobile organisms, and this was only partially sustained by our results. Surprisingly, we did not find any effect of landscape composition on the abundance of vegetation-dwelling predators, although ladybirds, for example, have been demonstrated to strongly respond to landscape composition (Bianchi & Werf 2004; Gardiner *et al*. 2009b). Neither the abundance nor the biological control provided by ground-dwelling predators was influenced by landscape composition at any scale. Although several studies highlighted the importance of landscape in building the population of natural enemies, some authors showed that it is not always possible to find a general positive effect of landscape complexity on overall abundance because different functional groups or species may respond differently to the landscape (Purtauf, Dauber & Wolters 2005; Schmidt &

Tscharntke 2005; Shackelford *et al.* 2013). The effect of the landscape may also have been mediated by other factors known to have a strong impact on ground-dwelling communities, such as seasonality or prey abundance (Östman, Ekbom & Bengtsson 2001).

SYNTHESIS AND APPLICATIONS

Our results emphasize the importance of considering both local management and landscape composition when planning strategies for maximizing biological control services in agro-ecosystems, highlighting the role played by soil management in shaping natural enemy communities. The differences between predator and parasitoid response to landscape complexity and to soil management entail relevant management implications. While in complex landscapes, the biological control of aphids is supported by abundant suitable habitats for natural enemies, in simple landscapes, the biological control provided by vegetation-dwelling predators and parasitoids is limited. In these systems, the adoption of conservation tillage may locally improve the biological control provided by the natural enemy guilds involved in the control of aphid populations, mitigating the negative effects of landscape simplification. Moreover, considering the small scale at which both predation and parasitism responded to landscape composition, a successful strategy to improve biological control would be to establish a fine mosaic of crop and non-crop areas such as hedgerows, tree lines and small semi-natural habitat patches.

For several crops, conservation tillage has been already proposed as a win–win practice able to support environmental health and to achieve production profits comparable to conventional systems (Soane *et al.* 2012). Besides the expected positive effects on soil due to the reduced mechanical disturbance and compaction (Holland 2004), decreased tillage intensity may also reduce production costs (e.g. fuel, machinery, human labour) decreasing time and energy required for seedbed preparation (Tabatabaeefar *et al.* 2009). The enhancement of generalist natural enemy populations also might lead to higher biological control for the crops following cereals in the crop rotation (e.g. soya bean), resulting in a lower dependence on insecticide applications and therefore limiting negative environmental impacts (Thomas 1999). However, the benefits of reducing tillage intensity may change depending on soil type and climate (Ogle, Swan & Paustian 2012; Soane *et al.* 2012), and sometimes, these positive effects can be counteracted by several downsides such as increased weed abundance (Streit *et al.* 2003; Holland 2004). Additional studies considering the effect of soil management and landscape composition on multiple ecosystem services (e.g. soil fertility, carbon sequestration, pollination, productivity, weed control) for different crops and different climatic conditions are needed to examine the actual environmental and economical sustainability of reduced tillage practices in modern cropping systems.

Data accessibility

Data available from the Dryad Digital Repository: doi:10.5061/dryad.-gr020 (Tamburini *et al.* 2015).

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