

High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields

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Summary

1. Field-margin diversification through conservation and restoration of hedgerows is becoming a prominent intervention for promoting biodiversity and associated ecosystem services in intensive agricultural landscapes. However, how increasing cover of hedgerows in the landscape can affect ecosystem services has rarely been considered.

2. Here, we assessed the effect of increased field-margin complexity at the local scale and increasing cover of hedgerows in the landscape on the provision of pest control, weed control and potential pollination. Locally, three types of field margin were compared as follows: (i) standard grass margin, (ii) simple hedgerow and (iii) complex hedgerow, along two independent gradients of hedgerow cover and arable land cover in the landscape. We performed an exclusion experiment to measure biological control of cereal aphids and assessed natural enemy and pest abundance in the field. We sampled plant weed communities and performed a phytometer experiment to test the effects of pollinators on plant reproductive success.

3. At the local scale, planting a new hedgerow or improving its structural complexity and vegetation diversity did not enhance the delivery of ecosystem services in the neighbouring field.

4. However, high cover of hedgerows in the landscape enhanced aphid parasitism (from 12 to 18%) and potential pollination (visitation rate and seed set increased up to 70%) irrespective of local margin quality. The cover of arable land in the landscape reduced the abundance of plant-dwelling predators and weed diversity, but did not affect the delivery of the investigated ecosystem services.

5. *Synthesis and applications.* Our results highlight the key importance of the surrounding landscape context, rather than local factors, to the delivery of ecosystem services. This suggests a need for new policies that pay particular attention to the conservation of hedgerows at large scales for promoting multiple ecosystem services in agroecosystems. Specifically, hedgerows can serve to develop a network of ecological corridors that can facilitate the movement of beneficial organisms, such as pollinators and natural enemies in the agricultural matrix. Such interventions may be a 'low cost–high benefit solution', since farmers can create or conserve high-quality habitats taking little or no land from crop production and without the need to change their crop management.

Key-words: aphid, biological control, ecosystem services, field-margin diversification, hedgerows, landscape complexity, natural enemies, off-field interventions, pollination, weed control

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Introduction

Over the past half-century, agricultural intensification has dramatically increased, transforming agricultural landscapes into simplified monocultures with a low cover of semi-natural habitats (Tscharntke *et al.* 2005). This trend has led to severe biodiversity loss and the deterioration of key ecosystem services to agriculture (Tilman *et al.* 2001). Among ecosystem services, pest and weed control and pollination have been demonstrated to have a substantial impact on crop production world-wide (Bommarco, Kleijn & Potts 2013). However, these ecosystem services are also those most at risk from agricultural intensification (Tscharntke *et al.* 2005; Biesmeijer *et al.* 2006). Their deterioration can make farming systems highly dependent on external inputs contributing to significant environmental harm. For instance, the overuse of chemical pesticides can lead to secondary pests and pest resurgence (Ekström & Ekblom 2011), as well as population decline of pollinators (Klein *et al.* 2007) and natural enemies (Furlong & Zalucki 2010). Such decline is often compensated by using honeybees as an agricultural input to ensure crop pollination (Aizen & Harder 2009; Garibaldi *et al.* 2013). The global degradation of ecosystem services may undermine the capacity of agriculture to support increasing food demands (Foley *et al.* 2005; Godfray *et al.* 2010). Therefore, there is an increasing interest in approaches that reconcile agricultural production with the conservation and sustainable use of biodiversity and associated ecosystem services (Kremen & Miles 2012; Bommarco, Kleijn & Potts 2013; Pywell *et al.* 2015).

To reverse the degradation of ecosystem services, several interventions have been suggested (Pretty 2008; Bommarco, Kleijn & Potts 2013; Garibaldi *et al.* 2014). Field-margin diversification through the conservation and restoration of hedgerows is becoming a prominent intervention for promoting biodiversity and ecosystem services in intensive agricultural landscapes. Recent studies have shown that hedgerows can help mitigate the negative effects of agricultural intensification on biodiversity (Batáry, Matthiesen & Tscharntke 2010; Merckx *et al.* 2012; Haenke *et al.* 2014; Dainese *et al.* 2015; M'Gonigle *et al.* 2015; Ponisio, M'Gonigle & Kremen 2016). In particular, hedgerows can promote pollinator populations and export wild bees to adjacent fields (Hannon & Sisk 2009; Morandin & Kremen 2013), as well as enhance natural enemies (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer & Kremen 2012; Morandin, Long & Kremen 2014; Dainese *et al.* 2015; Inclán *et al.* 2016). Also, hedgerows can be an effective practice to improve regulating ecosystem services such as soil erosion control (Forman & Baudry 1984; Sitzia *et al.* 2014b). Increasing environmental heterogeneity through hedgerow planting can be an effective way of decreasing the abundance of problematic weeds by shifting the species abundance distribution (Dornelas *et al.* 2009; Fox *et al.* 2013).

However, hedgerows may also be reservoirs of weeds and pests, which can spread into the fields (Forman & Baudry 1984). Hence, more research is needed to elucidate the role of hedgerow quality in supporting multiple ecosystem services.

Despite the increasing interest in the effects of landscape on the provision of ecosystem services (Tscharntke *et al.* 2005, 2012), it remains less clear whether the effectiveness of off-field interventions may depend on the wider landscape context. Landscape context can play a relevant role in shaping plant and invertebrate assemblages in agroecosystems (Gonthier *et al.* 2014). Communities of natural enemies and pollinators are often found to be more abundant in complex landscapes where semi-natural habitats are better conserved (Chaplin-Kramer *et al.* 2011; Garibaldi *et al.* 2011; Kennedy *et al.* 2013). **These habitats can provide larger and more stable availability of food resources for natural enemies and pollinators, as well as refuge sites during overwintering** (Bianchi, Booij & Tscharntke 2006; Winfree, Bartomeus & Cariveau 2011). Likewise, weed diversity seems to increase with increasing landscape complexity (Gabriel, Thies & Tscharntke 2005; Gaba *et al.* 2010). Despite this evidence, it is not known whether increasing density of hedgerows in the landscape can affect these ecosystem services. In addition, studies addressing the impact of such interventions have mostly focused on one particular ecosystem services, while there are no studies that use multiple experiments to capture the impacts of hedgerows on multiple ecosystem services, simultaneously.

In this study, we assessed the effects of field-margin diversification at the local scale and hedgerow cover at the landscape scale on multiple ecosystem services. The impact of field-margin diversification was tested by comparing three types of field margin with different levels of structural complexity along two independent gradients of hedgerow cover and arable land cover in the landscape. We conducted a field exclusion experiment to measure the biological control of cereal aphids and assessed natural enemy and pest abundance in the field. We examined weed abundance and species richness, as well as the effects of pollinators on plant reproductive success using a phytometer experiment. We hypothesized that (i) natural enemies and pollinators are more abundant in complex field margins with subsequent benefits for natural pest control and plant reproductive success, (ii) increasing hedgerow cover in the landscape will amplify these positive benefits, and (iii) landscape simplification (quantified as the cover of arable land in the landscape) diminishes pest control and pollination services while increases weed control. We also tested whether the effectiveness of margin diversification can depend on the surrounding landscape. We discuss to what extent our findings are relevant to farm policy designed to maintain and enhance multiple ecosystem services in agroecosystems.

Materials and methods

STUDY DESIGN

The study was conducted in 2014 in the Venetian–Friulian Plain (north-eastern Italy: 46°09′–45°16′ N, 11°45′–13°22′ E). The area is dominated by intensive agriculture (~65%) with maize, wheat, and soybean, interspersed with fragments of semi-natural habitats such as forests, grasslands and hedgerows. In recent years, planting of oilseed rape and sunflower have increased in this region.

Our study design consisted of 26 field margins adjacent to winter wheat fields. Field margins were separated by at least 400 m – with the majority ($n = 19$) separated by more than 1 km (mean minimum distance = 4 km). Three types of field margins were chosen to represent different levels of structural complexity (Fig. 1; see Appendix S1 in Supporting Information): (i) grass margin ($n = 10$), (ii) simple hedgerow ($n = 8$) and (iii) complex hedgerow ($n = 8$). A perennial herbaceous strip without any nearby tree characterized the grass margins. Hedgerows consisted of a herbaceous strip adjacent to a single-storied hedge formed by a few dominant tree species in the case of simple hedgerows or a multi-storied hedge composed of different shrubs and tree species in the case of complex hedgerows (Sitzia *et al.* 2013). In the study region, hedgerows were mainly established for their barrier or fence effect and the provision of wood for fuel. Each field margin was characterized by sampling plant species composition (see Appendix S1).

The three types of field margin were selected along two independent gradients of hedgerow cover and arable land cover in the landscape. First, a large number of field margins were selected ($n = 50$) along a gradient of arable land cover ranging from 38 to 100% (1-km buffer around each field margin). Information on the arable land cover was derived from a detailed vector-based land-cover map and quantified using QUANTUM GIS 1.7 (Open Source Geospatial Foundation Project, <http://qgis.osgeo.org>). Secondly, around each margin selected in the previous step, hedgerow cover was quantified within a 1-km buffer. Hedgerow patches were manually digitized from a visual inspection of satellite images (Google Earth®). By satellite images, it was not possible to distinguish the structure of the hedgerows. Therefore, hedgerow cover at the landscape scale included both simple and complex hedgerows. Although we did not have detailed regional data on hedgerow vegetation, the large majority of hedgerows in the study area were composed of simple, single-storied hedgerows (Sitzia *et al.* 2014a). The cover of hedgerow in the landscape was strongly correlated with several configuration metrics, such as number of hedgerows ($r = 0.87$, $t = 8.52$, $df = 24$, $P < 0.01$), edge density ($r = 0.95$, $t = 14.55$, $df = 24$, $P < 0.01$) and patch shape ($r = 0.77$, $t = 6.05$, $df = 24$, $P < 0.01$). To ensure that the local and landscape variables were uncorrelated, we replicated the three types of field

margins to cover as far as possible the gradient of both arable land and hedgerow network maintaining the two factors uncorrelated (see Appendix S3, Fig. S1). Collinearity among local and landscape factors was also controlled for, and the factors at the two spatial scales were kept independent (see Appendix S2, Tables S1–S2). Cover of arable land and hedgerows was also measured in a 0.5-km buffer to test for potential scale dependence.

NATURAL PEST CONTROL

In the selected fields, a crop strip (3 m wide) adjacent to the field margin was excluded from any fungicide treatments while insecticides were not applied in the whole investigated fields. Natural pest control of cereal aphids was measured using an exclusion experiment (see Appendix S1). The exclusion experiment consisted of two treatments placed at the field margin (2 m into the field): (i) a cage treatment, in which all natural enemies (ground-dwelling and flying predators and parasitoids) were excluded, and (ii) an open treatment, in which all natural enemies had access to the plants. For each treatment, one pot containing five winter wheat plants was inoculated with 10 English grain aphid (*Sitobion avenae* F.) in the laboratory to establish aphid colonies. Two weeks after inoculation, the pots were placed in the field. To ensure similar aphid abundance between treatments in each field, the pots were paired according to the number of aphids counted just before the placement in the field. In each field, aphid predation was quantified after 5 days as the proportion of aphids predated in the open treatment compared with the aphid population growth in the cage treatment, calculated following the methodology of Gardiner *et al.* (2009). The resulting aphid predation index varied from 0 to 1, with 0 representing no aphid suppression and 1 representing total aphid suppression.

In 26 farmers' fields, natural enemies were counted by inspecting plant tillers and by pitfall traps. Vegetation-dwelling predators (web spiders, ladybirds, lacewings and larvae and eggs of hoverflies) were visually quantified inspecting 50 tillers per visit along a 20-m transect parallel to the field margin (2 m apart from the first drill row). Observations were repeated three times: once during the stem elongation, once in the heading period and once during ripening of wheat. For each sampling round, abundance of vegetation-dwelling predators was quantified as the total number of individuals per 50 tillers. Aphids and parasitized aphids ('mummies') were also counted. Parasitism rate was calculated as the ratio between the number of mummies and the total number of aphids (mummies + non-parasitized aphids).

Ground-dwelling predators (carabid beetles, rove beetles and cursorial spiders) were caught with three plastic pitfall traps per field (9.5 cm in diameter and 13 cm deep). The three pitfall traps were placed along a perpendicular transect at three increasing distances from the margin, that is at 0, 1 and 3 m into the adjacent



Fig. 1. Contrasting field margins used in the study: (a) grass margin, (b) simple hedgerow and (c) complex hedgerow.

wheat field. The pitfall traps were left out for 10 days concurrently with the exclusion experiment. For each sampling distance, abundance (i.e. activity density) of ground-dwelling predators was quantified as the total number of individuals per pitfall trap.

WEED CONTROL

The diversity and abundance of weeds were recorded once in the second half of May (during the ripening stage of winter wheat). Sampling was conducted on a plot of 10 × 10 m within the crop adjacent to the selected field margins (one side of the plot bordered by a field margin). As preliminary observations indicated that weed distribution was rather homogeneous in the field, we opted to use only one large plot. In each plot, species cover (%) was recorded. All the plant species other than the crop observed in the plot were considered as weeds. Weed cover was quantified by summing the cover of each species in the plot. In the investigated winter wheat fields, no herbicides were usually not sprayed (Boscutti *et al.* 2015), as the current rotation practice maintains weed population at economically acceptable levels.

POTENTIAL POLLINATION

Pollinator activity and their effects on plant reproductive success were quantified using a **phytometer experiment** (see Appendix S1). Although the results of phytometer experiment have no direct link with our focal crop, the experiment was set up with the aim of determining the effect of field-margin diversification on potential pollination service. The experiment consisted of two treatments: (i) a 'bagged' treatment, in which all pollinators were excluded by covering the potted plants with a fine transparent polyethylene mesh bag (mesh 1 × 1 mm), and (ii) an 'open' treatment, in which all natural pollinator species had free access to the plants. The two treatments were replicated three times for each site. Radish, *Raphanus sativus* L. (Brassicaceae), was selected as phytometer due to its quick germination and fast growth. Moreover, this species has been used as phytometer to study the effects of pollinator activity on plant reproductive success (Albrecht *et al.* 2007, 2012). Within each site, six plants were placed in three blocks with both treatments.

Plants were placed on the grass strip, c. 30 cm far from the wheat field edge, and among unmown vegetation composed of grasses and flowering herbs. In this way, we reduced a possible concentration effect due to the use of an attractive plants (radish) in an unattractive matrix (wheat). For each site, insect visitation rate was quantified three times between 28th May and 11th June. The experiment started when the oilseed rape blooming was already past. The three observations covered the entire flowering period. Each open plant was observed for 5 min (15 min per site). All insects that made contact with the reproductive organs of the flower were considered as visitors and identified to the following taxonomic groups: *Apis mellifera* L., wild bees (Apoidea excluding *Apis* and *Bombus*), bumblebees (*Bombus*), hoverflies (Syrphidae), other Diptera, butterflies (Lepidoptera) and other families. The cumulative number of visits per plant observed during the three sampling rounds was used as a measure of visitation rate. The potted plants were taken back to a screen house at the end of the flowering period (on the 19th of June 2014) to complete fruit maturation. For each plant, seed set was determined as the average number of seeds per fruit. To test the effect of insect pollinators on plant reproductive success, we calculated the average difference in seed set between the open and bagged plants. Due to storm, agricultural

operations or vandalism damage, seed set analysis was based on data from 21 field margins (68 potted plants).

STATISTICAL ANALYSES

Analysis of variance (ANOVA) was used to test whether plant species richness differed among field-margin types. Paired *t*-test was used to analyse the effects of cage treatment on aphid populations at the beginning and the end of the experiment. Aphid abundance was $\log(x + 1)$ -transformed to meet the assumptions of linear models.

To test the effect of local and landscape factors on pest control, weed control and potential pollination, we built statistical models accounting for the different sampling design and data distribution (see Appendix S2, Table S3). In all the models, field-margin type was entered as categorical fixed factor, while the cover of arable land and hedgerow at the landscape scale, as continuous fixed factors. Interactions between field-margin type and landscape variables were tested. We included aphid abundance (at each sampling round) as a covariate in the model of parasitism rate and vegetation- and ground-dwelling predators since we expected a positive effect of local host/prey density. To account for possible weed exchange between field margin and the adjacent field, we included the number of annual plant species that occurred in the field margins as a covariate in weed models. We also entered the number of nectar plants found in the field margins as a covariate in parasitism, predation and potential pollination models since we expected a positive effect on natural enemies and pollinators. For each model, we tested the effect of the landscape (cover of arable land and hedgerows) using two scales (0.5 or 1 km), separately. The radius with the highest explanatory power was selected based on minimized AICc values (see Appendix S2, Table S4). Model residuals approximated a normal distribution and exhibited homogeneity of variance. Spatial autocorrelation in the residuals of the models was examined using Moran's *I* statistic. No spatial autocorrelation was found in any models.

In all the models, we applied an information-theoretic model selection procedure to evaluate alternative competing models (Burnham & Anderson 2002). We compared the fit of all possible candidate models obtained by the combination of the predictors using second-order Akaike Information Criterion (AICc). Then, we ranked the models according to their AICc, identified top models (i.e. $\Delta AICc$ from the best model < 7) for each hypothesis and calculated associated Akaike weights (w_i) (Burnham, Anderson & Huyvaert 2011). For each parameter, we used model averaging based on the 95% confidence set to incorporate model selection uncertainty into our parameter estimates (Burnham & Anderson 2002). We used 95% confidence intervals (CIs) around model-averaged partial slope coefficients to detect a significant effect, that is CIs did not overlap zero. In all the models, the interactions between local and landscape variables had no support ($\Sigma w_i < 0.20$). The interactions were then removed from the analyses, and only the main effects are presented. Model comparison was performed using the R package 'MuMIn'. All statistical analyses were conducted in R version 3.0.2 (R Development Core Team 2013).

Results

FIELD-MARGIN CHARACTERISTICS

The three margin types did not differ in plant species richness (ANOVA: $F_{2,23} = 1.05$, $P = 0.365$). The average number

\pm SD of vascular plant species was 16.1 ± 5.6 in grass margins, 20.0 ± 6.7 in simple hedgerows and 17.3 ± 6.0 in complex hedgerows. Woody species richness was significantly different between simple (2.6 ± 1.0) and complex hedgerows (7.7 ± 2.3 ; t -test: $t = 5.46$, $P < 0.001$).

NATURAL PEST CONTROL

In the exclusion experiment, there was no difference in the number of inoculated aphids between the cage and the open treatment at the beginning of the experiment (paired t -test: $t = 1.66$, $P = 0.108$) (see Appendix S3, Fig. S2). In each pot, an average of 58 ± 13 aphids was initially established for each treatment. After 5 days, a significant effect of the exclusion treatment (paired t -test: $t = 11.93$, $P < 0.001$) was detected with more aphids in the cage (98 ± 39 SE) than in the open treatment (7 ± 6 SE). Predation by natural enemies was high in all the sites and was unrelated to field-margin complexity and landscape factors (all the predictors with $\Sigma w_i < 0.50$ and 95% CIs including zero) (Table 1; Fig. 2a; see Appendix S2, Table S5). The predation index was on average 0.91 ± 0.03 SE in grass margins, 0.93 ± 0.03 SE in simple hedgerows and 0.93 ± 0.02 SE in complex hedgerows.

During visual inspections of wheat tillers in the 26 fields, a total of 1105 aphids (parasitized and non-parasitized), 176 mummies and 603 vegetation-dwelling predators were observed. Aphid abundance in the fields was on average 0.3 aphids per plant. Among vegetation-dwelling predators, ladybirds were the most abundant (79%), followed by web spiders (18%), and lacewings (3%). No larvae and eggs of hoverflies were found during visual inspections of wheat tillers. Parasitism rate was best predicted by the cover of hedgerows at the landscape scale ($\Sigma w_i = 0.80$), while other factors had low Σw_i (Table 1; see Appendix S2, Table S5). The cover of hedgerows had a positive effect on parasitism rate (Fig. 2b). Vegetation-dwelling predators were positively affected by aphid abundance (Table 1) and negatively by the cover of arable land

(Fig. 2c). Among vegetation-dwelling predators, ladybirds showed the same effects found in the overall model, while spiders were only positively affected by aphid abundance (see Appendix S2, Table S6). The abundance of lacewings was not analysed due to their low occurrence.

A total of 1697 ground-dwelling predators were caught in the pitfall traps. Carabid beetles were the most abundant (77%), followed by rove beetles (14%) and cursorial spiders (9%). Total abundance of ground-dwelling predators was best predicted by the cover of arable land ($\Sigma w_i = 0.71$), while other factors had low Σw_i (< 0.40) (Table 1; see Appendix S2, Table S5). The cover of arable land had a positive effect on ground-dwelling predators (Fig. 2d). Among ground-dwelling predators, the abundance of carabid beetles was best predicted by the cover of arable land showing a positive effect (see Appendix S2, Table S6). Abundance of both the rove beetles and cursorial spiders was unrelated to field-margin complexity and landscape factors (see Appendix S2, Table S6).

WEED CONTROL

Overall, 60 weed species were recorded in the plots. The average species richness \pm SD per field was 6.0 ± 3.24 with a range between 1 and 13. Weed species richness was best predicted by the cover of arable land ($\Sigma w_i = 0.77$) (Table 1; see Appendix S2, Table S5) showing a negative effect (Fig. 2e). Weed cover was not explained by any examined variables (all the predictors with $\Sigma w_i < 0.50$) (Table 1).

POTENTIAL POLLINATION

In the phytometer experiment, a total of 420 flower-visiting insects were counted during the three visits. Wild pollinators represented the great majority of pollinators (97%), while *A. mellifera* visits were rare (3%). Hoverflies were the most abundant group (46%), followed by wild bees (21%), butterflies (11%), other Diptera (9%), other species (mainly coleopterans 8%) and bumblebees (1%)

Table 1. The sum of model weights (Σw_i) for each variable included in the multimodel inference procedure for (a) natural pest control, (b) weed control and (c) potential pollination models

	Field-margin type	Aphid abundance	Annual plant species richness	Visitation rate	Nectar plant species richness	Hedgerow cover	Arable land cover
(a) Natural pest control							
Predation index	0.08				0.22	0.28	0.47
Parasitism rate	0.15	0.32			0.35	0.82 (+)	0.40
Vegetation-dwelling predators	0.09	0.99 (+)			0.40	0.25	0.99 (-)
Ground-dwelling predators	0.22	0.27			0.26	0.35	0.71 (+)
(b) Weed control							
Species richness	0.10		0.25			0.26	0.77 (-)
Cover	0.09		0.22			0.22	0.52
(c) Potential pollination							
Visitation rate	0.51				0.25	1.00 (+)	0.23
Δ Seed set	0.11			0.36	0.29	0.79 (+)	0.24

In bold are reported the Akaike weights (Σw_i across the entire model set) of the significant explanatory variables (CIs did not overlap zero). The direction of the relationship is indicated by (+) or (-) for the significant explanatory variables.

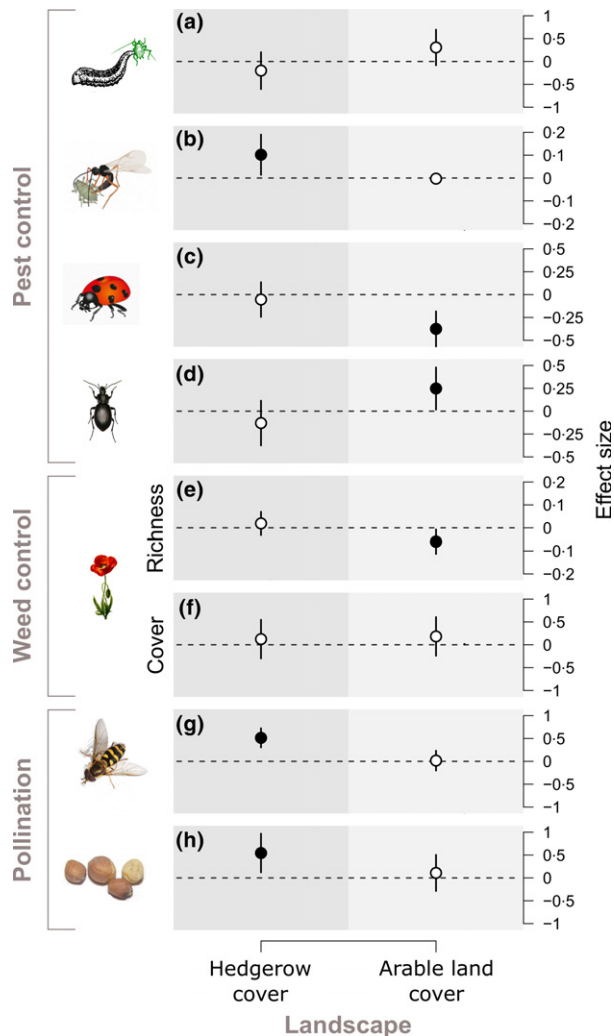


Fig. 2. Model-averaged effect sizes and 95% confidence intervals for the landscape parameters included in the models with $\Delta AIC_c \leq 7$ explaining (a) predation index, (b) parasitism rate, (c) abundance of vegetation-dwelling predators, (d) abundance of ground-dwelling predators, (e) weed species richness, (f) weed cover, (g) visitation rate and (h) Δ seed set. Open and closed symbols reflect estimated model-averaged confidence intervals that include (open symbols) and did not include 0 (closed symbols).

(see Appendix S3, Fig. S3). Considering the whole pollinator community, visitation rate was best explained by the cover of hedgerows at the landscape scale ($\Sigma w_i = 1.00$), while the effect of field-margin type and nectar plant species richness was not supported (Table 1; see Appendix S2, Table S5). The cover of hedgerows had a positive effect on the whole pollinator community, as well as on the single pollinator groups (Fig. 2g; see Appendix S3, Fig. S4). Hoverfly visitation rate was best explained by the cover of hedgerows ($\Sigma w_i = 0.72$), while the effect of the other predictors had no support (see Appendix S2, Table S7). Visitation rate of wild bees and butterflies was best predicted by the cover of hedgerows ($\Sigma w_i = 0.71$ and 0.74) and by field-margin type ($\Sigma w_i = 0.90$ and 0.58 ; 95% CIs did not overlap 0 in both cases). Simple hedgerows had a positive effect on wild bees, while

both simple and complex hedgerows had a positive effect for butterflies (see Appendix S3, Fig. S5). The visitation rate of the other groups was not explained by the investigated factors (all $\Sigma w_i < 0.50$). Because the visitation rate of bumblebees and *A. mellifera* was low, these two groups were not analysed. Seed set was best predicted by the cover of hedgerows ($\Sigma w_i = 0.79$) (Table 1; see Appendix S2, Table S5), showing a positive effect (Fig. 2h).

Discussion

Although local field-margin diversification did not enhance the delivery of pollination and pest and weed control in the neighbouring winter wheat fields, it contributed to overall landscape complexity, thereby benefiting the ecosystem service providers. Indeed, increasing the cover of hedgerows in the surrounding landscape enhanced aphid parasitism and potential pollination irrespective of local margin quality. Our results highlight the key importance of the surrounding landscape context, rather than local factors, to the delivery of ecosystem services.

LOCAL FIELD-MARGIN DIVERSIFICATION

Concerning aphid control, our results confirm previous studies showing a strong reduction in aphid populations in cereal fields due to natural enemies (Schmidt *et al.* 2003; Rusch *et al.* 2013; Tamburini *et al.* 2016). However, we observed high pest control in all fields irrespective of the local margin complexity (i.e. the average reduction in aphids in open plants was $92 \pm 8\%$). Previous research using the same methodology found an average reduction in aphids by *c.* 60% in the middle of cereal fields (Rusch *et al.* 2013). In our case, the likely higher abundance and diversity of natural enemies close to the field margin could explain the stronger aphid suppression. Therefore, in such environmental conditions, a shorter interval for measuring aphid predation could be worthwhile in future studies. Surprisingly, we did not find any effect of field-margin complexity on either parasitism rate or abundance of vegetation- and ground-dwelling predators. Aphid occurrence in the field was rather low (0.3 aphids per plant on average), always below the economic threshold (>5 –7 aphids/tiller; Larsson 2005), suggesting that no outbreak was present in our experimental fields. A positive effect of local field-margin diversification was detected by Morandin, Long & Kremen (2014) who found more predatory lady beetles and higher parasitism rate in fields adjacent to restored hedgerows than to unimproved field edges. The better performance was probably due to the fact that the restored hedgerows were planted using flowering plants known for providing key food resources for natural enemies.

Likewise, weed control and potential pollination did not differ among the three types of field margins. Considering pollination service, our findings are in line with a

previous study by Sardiñas & Kremen (2015) who found that neither hedgerow presence nor distance from the field edge impacted sunflower seed set even though hedgerows supported richer and more diverse pollinator communities. Thus, local field-margin diversification alone may not be sufficient to enhance the provision of ecosystem services in farmland, even if significant benefits for service provider organisms are observed.

HEDGEROWS IN THE LANDSCAPE

Despite no apparent effect of local field-margin diversification on the delivery of ecosystem services, margins located in landscapes with high cover of hedgerows supported more abundant communities of beneficial arthropods improving both natural pest control by parasitoids and potential pollination. In particular, parasitism rate increased from 12 to 18%, while visitation rate and seed set increased up 70%, as the cover of hedgerows at the landscape scales increased from 1 to 6%. For natural enemies, parasitoid populations should benefit from high density of hedgerow due to better nectar resources and larger availability of alternative hosts (Bianchi, Booij & Tscharntke 2006; Gagic *et al.* 2011; Alignier *et al.* 2014; Puech *et al.* 2014). Although we found increased parasitism, it would be interesting to verify whether such interventions can be sufficient to maintain aphid populations below economic thresholds also during outbreak years.

For pollinators, large cover of hedgerows in the landscape should provide suitable nesting sites and larger availability of pollen and nectar resources throughout the seasons (Garibaldi *et al.* 2014; Schüepp, Herzog & Entling 2014). The observed covariation between seed set and visitation rate indicates that hoverflies were probably the major service providers in our study area. Further studies are needed to better explore whether the benefits from high cover of hedgerows on pollination can be scaled up to whole fields (Birkhofer *et al.* 2015). Future studies should address the possible negative effects of hedgerows on pollinator services as these corridors can facilitate pollen flow along the hedgerow but impede dispersal across (Klaus *et al.* 2015).

LANDSCAPE INTENSIFICATION

Although landscape simplification, quantified as the cover of arable land in the landscape, did not affect the delivery of ecosystem services, the abundance of vegetation- and ground-dwelling predators responded to this factor. The two groups showed, however, an opposite response to landscape simplification. In agreement with previous studies (Elliott, Kieckhefer & Beck 2002; Gardiner *et al.* 2009; Woltz & Landis 2014), vegetation-dwelling predators were more abundant in complex landscapes, while ground-dwelling predators preferred simple landscapes. The conservation of nonlinear semi-natural habitats is, therefore,

of key importance for several vegetation-dwelling predators, such as ladybirds, due to their role as overwintering habitats (Elliott, Kieckhefer & Beck 2002; Woltz, Isaacs & Landis 2012). This consequently leads to larger populations emerging in spring. Conversely, ground-dwelling predators, such as carabid beetles, seem to be better adapted to agriculturally dominated landscapes (Schmidt *et al.* 2008), where they can benefit from a greater availability of prey resources within the crop fields (Rand & Tscharntke 2007).

A positive effect of landscape simplification was also found for weeds. According to our expectations, weed control increased in simplified landscapes with a reduction in weed diversity and cover. This is probably because in landscapes dominated by arable fields the larger use of herbicides can have greater efficacy in suppressing weed populations. Further explanations can be due to the loss of semi-natural habitats which can provide refugia for weed species that are most sensitive to intensive agricultural practices (Gabriel, Thies & Tscharntke 2005; Roschewitz *et al.* 2005; Gaba *et al.* 2010). However, the decline of weeds could also have a negative impact on other ecosystem services such as pest biocontrol and pollination given that weeds can serve as food sources for several beneficial insects (Norris & Kogan 2005). In this context, specific studies considering potential synergies or trade-offs between ecosystem services or management options targeting different ecosystem services are urgently needed.

CONCLUSIONS AND IMPLICATIONS

Ecosystem service delivery depended on the total cover of hedgerows in the surrounding landscape but not on the quality of the neighbouring field margins. However, until now, hedgerow-related interventions have mainly focused on the local scale. While increasing the structural complexity and vegetation diversity of single hedgerows are certainly beneficial for conserving farmland biodiversity (Dainese *et al.* 2015), our results suggest that, for supporting multiple ecosystem services, there is a need to promote the conservation of hedgerows at larger spatial scales. Specifically, hedgerows can serve to develop ecological corridor networks that can support larger populations of beneficial organisms and facilitate their movement between crop and non-crop areas (Forman & Baudry 1984). As we found no interactions between the cover of hedgerows and the degree of landscape intensification, increasing hedgerow cover can enhance the provision of multiple ecosystem services in landscapes dominated by arable land, as well as in landscapes with a large proportion of other semi-natural habitats (i.e. forest and grassland patches). Such large-scale conservation interventions, however, require coordinated joined-up actions to form an ecological network over large geographical areas involving the participation of a large number of farmers. Locally, such interventions may be a 'low cost-high benefit solution', since farmers can create or conserve

high-quality habitats taking little or no land from crop production and without the need to change their crop management (Garibaldi *et al.* 2014). As the benefits to ecosystem service delivery of planting a hedgerow spread beyond the borders of individual farms, any assessment of hedgerow cost-effectiveness should incorporate these positive externalities. The implementation of these measures at the landscape scale could translate into economic returns for farmers that would require, for example, fewer pesticide applications (Morandin, Long & Kremen 2014). However, these off-field interventions cannot be considered a unique solution to enhance the provision of ecosystem services in farmland and other off- and on-field management options (e.g. conservation tillage, diversified crop rotation, wildflower strips) may be necessary to achieve the desired level of pest control or pollination service (Garibaldi *et al.* 2014; Schneider *et al.* 2015; Tschumi *et al.* 2015; Tamburini *et al.* 2016). The integration of different management strategies for the delivery of multiple ecosystem services in modern farming systems will represent a major challenge for future policy strategies.

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sp70m> (Dainese *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplemental methods.

Appendix S2. Supplemental tables.

Appendix S3. Supplemental figures.