



Increasing amount and quality of green infrastructures at different scales promotes biological control in agricultural landscapes

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ABSTRACT

Green infrastructures are key elements for the delivery of ecosystem services in agricultural landscapes. However, how to combine quality and quantity of green infrastructures at multiple spatial scales to optimize the delivery of ecosystem services remains largely unknown. In this study, we investigated how hedgerow amount in the landscape modulated the local effect of grassland quality (plant species richness) on the spillover of biological pest control services in adjacent sunflower fields. We quantified biological pest control and predator communities in 23 adjacent sunflower-grassland field couples selected along two uncorrelated gradients: a gradient of plant species richness in grassland and a gradient of hedge length in the landscape. Our study shows that increasing the amount or the quality of green infrastructures can enhance biological pest control in adjacent crops but that the effects depend on the pest considered. We found that weed seed predation depends only on hedge length in the large scale landscape, while aphid predation depends on plant species richness in the adjacent grassland and on the hedge length in the immediate landscape. Also, the abundance of spiders affects aphid predation suggesting a key role of this functional group for controlling aphids in sunflower fields. This study suggests that management options based on increasing local plant species richness should be prioritized in landscapes with low amount of hedgerows, and confirms the fact that increasing hedgerow networks should promote pest control services.

1. Introduction

Biological control of crop pests is a key regulating service delivered by natural enemies that can significantly increase crop production while contributing to the reduction of pesticide use (Naranjo et al., 2015). Biological control by predatory arthropods depends on multiple factors operating at different spatial scales from the plant and the field, up to the whole landscape level (Tscharntke et al., 2007; Rusch et al., 2010). Green infrastructures, such as grasslands or hedgerows, can increase the abundance and the diversity of natural enemies which may in turn increase local pest regulation (Rand et al., 2006; Chaplin-Kramer et al., 2011). The effects of green infrastructures on biological control have been either examined at the local or landscape scales, e.g. by testing the effect of an adjacent green infrastructure, such as flower

strips or fallows (Albrecht et al., 2010; Tschumi et al., 2015), or by quantifying the effect of large-scale proportion of green infrastructures, such as grasslands or hedgerows in the landscape (Chaplin-Kramer et al., 2011; Rusch et al., 2016). However, a limited number of studies have investigated how broad-scale landscape context modulates the effect of local green infrastructure on biological pest control and have yielded contrasting results (Werling and Gratton, 2010; Tschumi et al., 2015). For instance, it has been hypothesized that landscape complexity may modulate the local effect of green infrastructure on biodiversity and ecosystem services (Tscharntke et al., 2012). Minimal effect of local green infrastructure is predicted in extremely simplified landscapes or in complex landscapes with a high proportion of non-crop habitat (> 20%) whereas maximal effect is predicted in simple or intermediate landscapes. The reason is that extremely simplified landscapes do not

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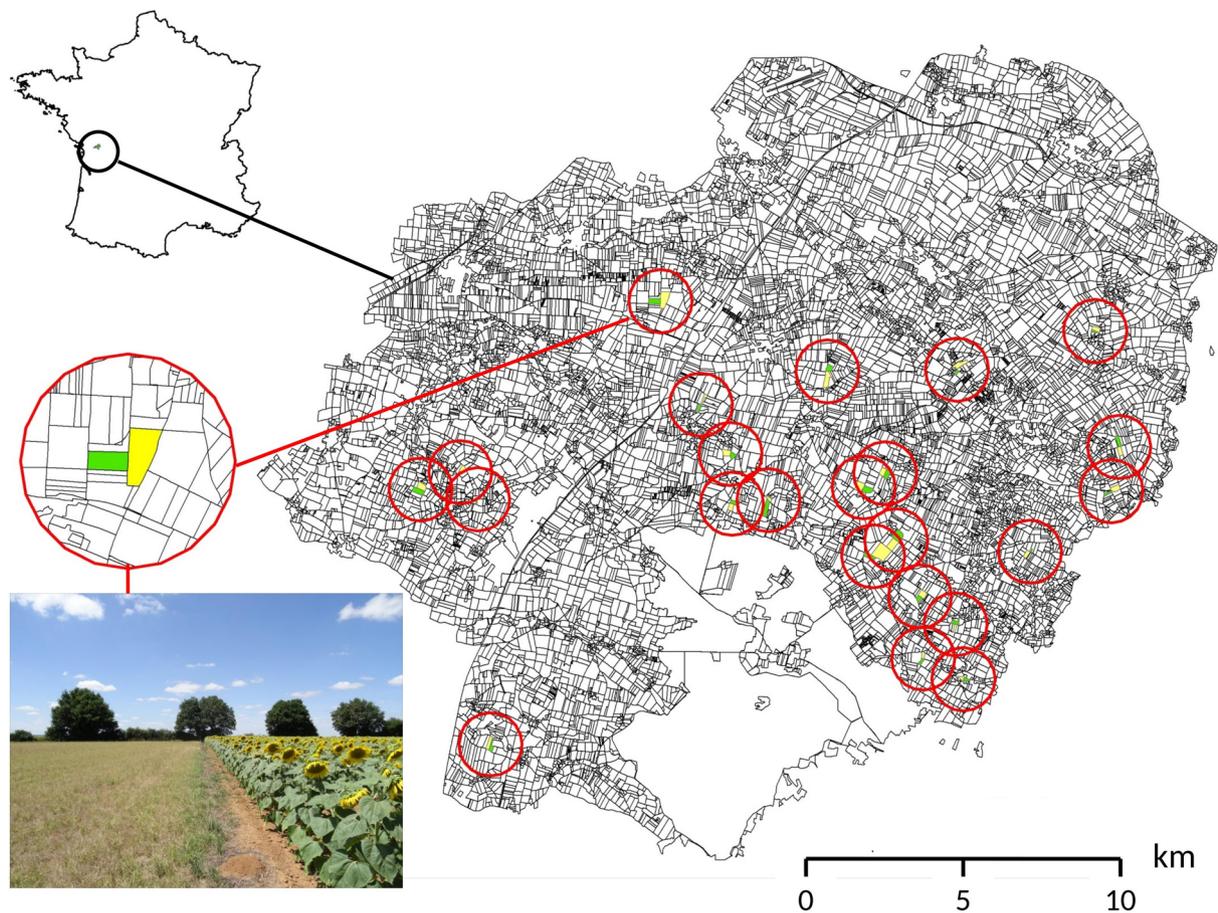


Fig. 1. Map of the study area showing its location in France, the 1 km radius landscapes around each of the 23 sampled sunflower-grassland fields and the paired design: a sunflower field (in yellow) adjacent to a grassland field (in green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

provide sufficient resources to maintain efficient natural enemy communities whereas complex landscapes already support abundant and diverse communities already providing high level of biological pest control. Producing operational knowledge about multi-scale effects of green infrastructures on biodiversity and ecosystem services is urgently needed to promote farming systems less dependent on agrochemical inputs.

Beside the importance of landscape context potentially shaping biological pest control services in agricultural landscapes, the quality of green infrastructures is expected to affect population dynamics, spillover of beneficial organisms as well as the function they provide (Riolo et al., 2015). An important parameter of green infrastructure quality is the diversity of organisms they host. For instance, plant species richness – used as a surrogate of quality – can enhance diversity (Hertzog et al., 2017) as well as organism abundance (Scherber et al., 2010; Garrat et al., 2017) at multiple trophic levels, and increase the level of ecosystem functioning such as primary productivity, soil fertility, biological pest control or pollination (Scherber et al., 2010; Garrat et al., 2017; Isbell et al., 2017). In addition, we do not know how green infrastructure quality may interact with the landscape context. Indeed most studies conducted at the landscape scale usually assume similar levels of quality across green infrastructures while investigating landscape composition or configuration (e.g. Aviron et al., 2005; Olimpi and Phipott, 2018). Considering explicitly the quality of green infrastructure may provide major insights into how landscape context influences predator-prey interactions and pest regulation service (Sarhou et al., 2014; Garrat et al., 2017; Bengtsson et al., 2019).

Grasslands are key green infrastructures for biodiversity conservation and provision of multiple ecological functions in agricultural

landscapes (Werling et al., 2014; Newbold et al., 2015). The level of contribution of grasslands to the maintenance of such ecological functions depends on habitat characteristics related to plant communities, management intensity as well as the surrounding landscapes (Joern and Laws, 2013). Enhancing grassland plant species richness may be a way to improve the potential contribution of grassland towards pest control in agricultural landscapes. To develop this management opportunity, it is important to evaluate its effectiveness within landscapes which provide contrasted amounts of green infrastructures, i.e. resources for natural enemies. Among green infrastructures, hedgerows may be particularly appropriate to maintain biodiversity and ecosystem services in intensive agricultural landscapes that are generally poor in grasslands and other semi-natural habitats (Dainese et al., 2017). Hedgerows are shown to benefit many invertebrate natural enemies, such as carabid beetles or spiders (Pywell et al., 2005), and vertebrate natural enemies, such as birds (Vickery et al., 2009) or rodents (Michel et al., 2007).

In this study, we examined the role of local grassland quality and hedge length at different scales in the landscape in shaping pest control in sunflower fields. We tested 1) whether higher plant species richness of focal grassland (a local factor) increases weed and aphid predation in adjacent sunflower field; 2) whether higher amount of hedgerows at different spatial scales (a landscape factor) enhances weed and aphid predation in sunflower field; and, 3) how local and landscape variable interactions affect natural pest control services. We hypothesized that an increase in plant species richness has a global positive effect on diversity and abundance of predatory arthropods in the focal grassland, which in turn should lead to higher predation rates of weeds and aphids in sunflower field due to natural enemy spillover. We hypothesized that

the amount of hedges has also a positive effect on pest predation rates in sunflower field. Lastly, we expected that hedge amount in the landscape modulates the positive effect of local grassland plant diversity on biological pest control.

2. Material and methods

2.1. Study area and experimental design

The study was conducted in 2015 in the French Long-Term Socio-Ecological Research site (LTSER) “Zone Atelier Plaine et Val de Sèvre” located in western France (46.11°N, 0.28°W) (Fig. 1) (Bretagnolle et al., 2018). The study area covered 450 km² of an intensively managed agricultural plain, mostly dedicated to cereal production. Historically, it was a typical rural area characterized by the presence of mixed crop-livestock systems, grassland being the dominant land-use fifty years ago (> 60 % of the total area) (Bretagnolle et al., 2018). Since that time, the conversion from grazing livestock to annual crop production has resulted in a strong decline in grassland cover which represented in 2015 about 10 % of the total surface. Other permanent green infrastructures in the study area were mainly composed of hedgerows and in a lesser extent of forest fragments (3 % of the area) (Bretagnolle et al., 2018). Since 1994, land use has been monitored yearly at the field scale (15 000 fields approximately) and mapped onto a Geographical Information System (QUANTUMGIS 2.18) (QGIS Development Team, 2017). Around 34 categories of crop types were recorded as well as roads, paths, forests, towns and hedgerows.

The study design consisted in the selection of 23 sunflower fields, each of them being adjacent to a grassland field. The 23 pairs of fields were located along two uncorrelated gradients ($r = 0.38$) (Appendix A in supplementary material, Fig. A.1): one gradient of plant species richness in the adjacent grassland and one gradient of hedgerow length within a 1 km radius around each pair of fields (Table 1). The gradient of hedge length was calculated at this scale as it falls within the range of the most explaining scales for invertebrate diversity and abundance (Chaplin-Kramer et al., 2011; Marrec et al., 2017). We selected the fields in 1 km landscapes representative of the average composition of the study area in other green infrastructures, i.e., grasslands and woodlands (Table 1), excluding extremely simplified or complex landscapes. Therefore, grassland or woodland covers were not correlated with the gradient of hedgerow amount (Appendix A in supplementary material, Table. A.1). This design allows us to disentangle the effects of local grassland plant species richness and hedge length from other potentially confounding variables known to affect predator communities (Chaplin-Kramer et al., 2011; Karp et al., 2018). In addition, we calculated hedge length within 0.25 km radius and used it as an explanatory variable (see below) to explore its effect at a local scale. We

Table 1

Characteristics of the 23 selected pairs of fields (a grassland field adjacent a sunflower field) at the local scale and in 1 km radius buffers around each pair of fields.

Scale	Descriptor	Mean ± SE	Range
Local	Grassland field area (ha)	3.4 ± 0.4	0.7 – 8.5
	Sunflower field area (ha)	5.2 ± 0.7	1.1 – 11.8
	Grassland age (yr)	7.2 ± 1.6	1 – 38
	Between field distance within each pair (m)	8.8 ± 2.8	0 – 40
	Grassland plant species richness	11.8 ± 1.6	3 – 28
Landscape (1 km radius)	% grassland cover	10.0 ± 0.6	5.2 – 16.7
	% woodland cover	2.9 ± 0.7	0 – 13.0
	Hedge length (km)	10.1 ± 0.8	4.4 – 17.5
	Minimal distance between pairs (km)	1.8 ± 0.2	0.9 – 4.0

checked that it was not correlated with grassland plant species richness ($r = 0.19$) (Appendix A in supplementary material, Fig. A.1). Selected field pairs were separated from one another by at least around 1 km to avoid spatial autocorrelation and fields within each pair were adjacent or in close proximity (Table 1).

2.2. Estimating grassland plant species richness and predator communities in grasslands and sunflower fields

We conducted a botanical survey in July 2015 on the 23 selected grasslands. To estimate plant species diversity, we randomly located 10 quadrats of 50 cm x 50 cm per grassland. The total number of species recorded over the 10 quadrats was calculated as our measurement of plant species richness.

In each grassland and sunflower field, we established ten sampling points, evenly spaced every 5 m along a 45 m transect. The transects were established from the field boundary to 45 m inside the field, the starting points being where the two fields of each pair were at the smallest distance from each other. Weed seed and aphid predation rates in sunflower fields were assessed at the 10 points using sentinel prey cards. While cards were accessible to both vertebrates and invertebrates, we only tested the potential effects of invertebrate community features. We sampled carabid beetles and spiders in grassland and sunflower fields at 4 of the 10 points (i.e., inside the field at 1 m from field boundary, 16 m, 31 m and 46 m). Carabid beetles and spiders were sampled using one pitfall trap (Thiele, 1977) at each of the 4 sampling points. The traps were plastic cups of 8.5 cm diameter filled with a mixture of salted water and a drop of soap. Traps were established between 17th and 27th July. The content of traps was collected four days after. We identified carabid beetles and adult spiders at the species level, while juvenile spiders were identified at the genus or at the family level. We considered carabid beetles to test their effect on seed and aphid predation. For seed predation, we tested the effects of individual seed-eating (granivorous and omnivorous) abundant species, or a functional subset of seed-eating species, or all species pooled. For aphid predation, we tested the effects of a functional subset of potentially aphid-eating species (carnivorous and omnivorous) or all species pooled. Carabid beetle diets were obtained from Laroche (1990) and the online database ‘carabids.org’ (Homburg et al., 2014). In addition, spiders were also considered as potential predators of aphids. We calculated the species richness (number of recorded species per field based on adult carabid beetles and adult spiders) and Shannon index of carabid beetles and spiders, and their activity-densities as the numbers of trapped individuals (juveniles and adults) per field (cumulated over the 4 pitfall traps whatever their location in the field).

2.3. Estimating weed seed and aphid predation rates

Weed seed and aphid predation rates were quantified using sentinel preys (Chisholm et al., 2014; Birkhofer et al., 2017). Sentinel preys consist in exposing seeds and aphids glued on cards to predation to measure prey removal. We used methods adapted from Westerman et al. (2003) and from Winqvist et al. (2011). We specify here that such approach makes it possible to quantify biological pest control potential and not actual biological pest control services but is extensively used in the literature. Weed seed predation was assessed using the very common weed in the study area, *Viola arvensis* Murray. Ten seeds were glued on one side of pieces (5 cm x 5 cm) of red sand paper (grain 120) using repositionable spray glue. These cards were put top surface up on the ground and bound with a pin. Aphid predation was assessed using three live pea aphid (*Acyrtosiphon pisum* Harris) adults or nymphs at the third or fourth instar, which were glued with repositionable spray glue on one side of pieces (5 cm x 6 cm) of black sand paper (grain 400) which were folded in half. These cards were bound on the ground with a pin, top surface down. We placed one seed card and one aphid card at each of the 10 points per sunflower field so that there was a total of 10

seed cards and 100 seeds, and 10 aphid cards and 30 aphids in each sunflower field. All cards were set on 30th July and left in place during 4 effective-days for seed cards and 1 effective-day for aphid cards. At that time, the number of consumed seeds or aphids per card was noted and allowed us to calculate seed and aphid predation rates per field as i/ the number of seeds (ranging from 0 to 100) or aphids (ranging from 0 to 30) consumed and as ii/ the number of cards (ranging from 0 to 10) with a predation event, i.e., with at least 1 consumed seed or aphid.

2.4. Data analysis

The number of cards with at least one event of seed or aphid predation was highly correlated with respectively the number of consumed seeds ($r = 0.93$) or aphids ($r = 0.89$). We thus analysed the proportion of preyed cards, i.e. with at least one event of seed or aphid predation, as it provided smaller dispersion parameters than the proportion of preyed seeds or aphids. Seed predation rates were analysed using the proportion of preyed cards with generalized linear models (GLM) with a binomial error distribution. Aphid predation rates were analysed using binary response variable (status of each individual aphid card: 0 if no aphid has been preyed or 1 if at least one aphid has been preyed) with generalized linear mixed effects models (GLMM) and a binomial error distribution to take into account overdispersion. Sunflower field identity was set as random effect. We run two sets of competing models to respectively analyze seed and aphid predation. In each set of models we examined whether the response variable was related to: plant species richness in the adjacent grassland (all models), predator species richness (Models 1, 4 and 7, 10), Shannon Index (Models 2, 5 and 8, 11) and activity-density (Models 3, 6 and 9, 12) in the sunflower field, hedge length in the landscape within 0.25 km radius (Models 1, 2, 3 and 7, 8, 9) and within 1 km radius (Models 4, 5, 6 and 10, 11, 12) (Table 2). An interaction term between grassland plant species richness and hedge length was included to test for potential modulation of local quality effects by landscape context at the two scales. The effects of distance from field margin and of its interactions with grassland quality and hedge length were tested. As they were not significant (Appendix B in supplementary material, Table B.1) they were not discussed further. Model simplification (within each of the competing models) was done using a backward stepwise procedure based on chi-squared statistics (Fox and Weisberg, 2011). Then, we used an information-theoretic approach (AIC-based approach corrected for small sample size; AICc;

Burnham and Anderson, 2002) to select the best model among the competing simplified models for seed and aphid predation (i.e., the model with the smallest AICc and delta AICc < 2 among competing simplified models).

If predators (species richness, Shannon Index or activity-density) in the sunflower fields impacted significantly pest predation, then additional analyses were carried out to determine whether predator communities were driven by: plant species richness in the adjacent grassland, hedge length in the landscape within 0.25 km radius and 1 km radius and predators (species richness, Shannon Index or activity-density) in the adjacent grassland. An interaction term between grassland plant species richness and hedge length in the landscape was included in the models. We also tested for the effect of grassland plant species richness and hedge length in the landscape within 0.25 km radius and 1 km radius on predators in the grassland fields. Predator response variables were only those which were retained in the selected predation models and they were analysed with generalized linear models (GLM) using adequate distributions. We checked for spatial autocorrelation in the residuals of the final models using bubble plots and no spatial autocorrelation was detected (Appendix C in supplementary material).

We performed statistical analyses in R 3.5.0 (R Development Core Team, 2018), using the ‘lme4’ (Bates et al., 2015), ‘car’ (Fox and Weisberg, 2011), ‘ggplot2’ (Wickham, 2016) and ‘MuMIn’ (Barton, 2018) packages.

3. Results

We recorded 81 plant species in the focal grasslands including *Medicago sativa* L., *Lolium perenne* sp., *Dactylis glomerata* L., *Festuca arundinacea* Scherb. and *Trifolium pratense* L., *Picris hieracioides* L., *Plantago lanceolata* L., *Daucus carota* L., *Arrhenatherum elatius* L. and *Convolvulus arvensis* L. (Appendix D in supplementary material, Table D.1). Grassland plant species richness ranged from 3 to 28 species (mean ± SE = 11.8 ± 1.6) per field and was significantly positively correlated with grassland age ($r = 0.59$; $p = 0.002$) (Appendix D in supplementary material, Fig. D.1).

In total, 22 carabid beetle species were trapped. Mean species richness per field was 2.2 ± 0.2 (mean ± SE) in sunflower fields and 1.5 ± 0.4 in grassland fields. Mean cumulated carabid beetle activity-density over the 4 pitfall traps per field was 13.4 ± 4.3 in sunflower fields and 11.3 ± 7.8 in grasslands. Carabid beetle communities in

Table 2
Fitted GLMs with binomial error distribution for seed (*Viola arvensis*) predation (proportion of preyed cards) and GLMMs with binomial error distribution for aphid (*Acyrtosiphon pisum*) predation (proportion of preyed cards). Filled cells = explanatory variables included in the models.

	Model	Grassland quality		Predators in sunflower fields:				Landscape : hedge length	
		Plant_SPR	Carab_SPR	Carabid beetles		Spiders		H_0.25km	H_1km
				Carab_Sh	Carab_AD	Spider_SPR	Spider_Sh		
Seed predation	1	■	■	■	■			■	
	2	■	■	■	■			■	
	3	■	■	■	■			■	
	4	■	■	■	■	■			■
	5	■	■	■	■	■			■
	6	■	■	■	■	■			■
Aphid predation	7	■	■	■	■	■			■
	8	■	■	■	■	■			■
	9	■	■	■	■	■	■		■
	10	■	■	■	■	■	■		■
	11	■	■	■	■	■	■		■
	12	■	■	■	■	■	■	■	

Plant_SPR is grassland plant species richness, Carab_SPR, Carab_Sh and Carab_AD are respectively carabid beetle species richness, Shannon Index and activity-density (log-transformed) in sunflower field, Spider_SPR, Spider_Sh and Spider_AD are respectively spider adult species richness, spider adult Shannon Index and activity-density (adults + juveniles) (log-transformed) in sunflower field, H_0.25 km and H_1km are the lengths of hedges in respectively 0.25 km and 1 km radius landscapes centred on each field pair. In all models, an interaction term between grassland plant species richness and hedge length in the landscapes was included.

sunflower fields were dominated by three species, i.e., *Pseudoophonus rufipes* De Geer, *Poecilus cupreus* L. and *Amara consularis* Duftschmid which were trapped respectively in 87 %, 39 % and 22 % of the fields. Numerically, these species represented more than 92 % of the trapped carabid beetles (*P. rufipes*: 73.5 %, *P. cupreus*: 12.0 %, *A. consularis*: 6.8 %). In grassland fields, *P. rufipes* and *P. cupreus* were also the most frequent species, being trapped in respectively 43 % and 26 % of the fields while *A. consularis* was not observed. Numerically, these species encountered for 90 % of the counts (*P. rufipes*: 16.9 %, *P. cupreus*: 73.2 % mainly due to one grassland field).

For spiders, we recorded 40 species and 29 genera. Mean species richness was 2.9 ± 0.3 (mean \pm SE) in sunflower fields and 3.7 ± 0.5 in grasslands. Mean cumulated spider activity-density over the 4 pitfall traps per field was 12.5 ± 2.1 (juveniles and adults) in sunflower fields and 25.1 ± 7.1 in grasslands. Lycosidae family was trapped in 95 % of the sunflower fields and 78 % of the grasslands. Numerically, this family encountered for 68 % of the counts in the sunflower fields and 85 % in the grasslands. Linyphiidae family was also well represented in sunflower fields with 20 % of the counts while in grasslands they only represented 4 % of the counts. *Pardosa agrestis* Westring and *Oedothorax apicatus* Blackwall were the main species in sunflower fields, being trapped in respectively 74 % and 43 % of the fields, while *O. apicatus* was rarely trapped in grasslands where the main species were *Pardosa proxima* C.L. Koch, *P. agrestis*, *Pardosa vittata* Keyserling and *Xysticus ninnii* Thorell trapped respectively in 48 %, 43 %, 39 % and 35 % of the grasslands.

The complete list of species and their activity-density are provided in Appendix E in supplementary material (Table E.1).

3.1. Weed seed predation

Seed predation rates of *V. arvensis* estimated at the end of July in sunflower fields ranged from 0 to 60 % of preyed seed cards, i.e. with at least one predation event, and averaged 23 ± 3 % (mean \pm SE) per field. The proportion of seeds which were consumed per field was quite low ranging from 0 to 28 % of preyed seeds and averaged 7 ± 2 % per field.

The proportion of preyed cards increased with the amount of hedges in the landscape within 0.25 km (Models 1, 2, 3: AICc = 82.7) and within 1 km (Models 4, 5, 6: AICc = 74.9) (Appendix F in supplementary material, Table F.1). The plant species richness in grasslands and the various metrics describing carabid beetle communities in the sunflower fields (species richness, Shannon Index or the activity-density of individual species, granivorous and omnivorous functional group, or all species pooled) had no effect on the proportion of preyed cards (Appendix F in supplementary material, Table F.1). The model with the lowest AICc (i.e. amount of hedges within 1 km) was then selected as

Table 3

Results of GLM with binomial error distribution fitted for seed predation (proportion of preyed cards) and GLMM with binomial error distribution fitted for aphid predation (proportion of preyed cards).

	Term	Est. \pm SE	P
Seed predation	Intercept	-2.78 \pm 0.50	< 0.001
	H_1km	0.15 \pm 0.04	< 0.001
Aphid predation	Intercept	-4.19 \pm 0.85	< 0.001
	Spider_AD_Sun	0.74 \pm 0.22	0.001
	Plant_SPR	0.11 \pm 0.04	0.008
	H_0.25 km	4.24 \pm 1.10	< 0.001
	I(Plant_SPR: H_0.25 km)	-0.21 \pm 0.06	0.001

Parameter estimates (Est.), standard errors (SE) and P of the fixed-effects terms in GLM and GLMM with the proportion of cards with a predation event as response variable. Plant_SPR is grassland plant species richness, Spider_AD_Sun is spider activity-density in sunflower field, H_0.25 km and H_1km are the lengths of hedges (km) in respectively 0.25 km and 1 km radius landscapes centred on each field pair. Spider_AD_Sun is log-transformed in the models.

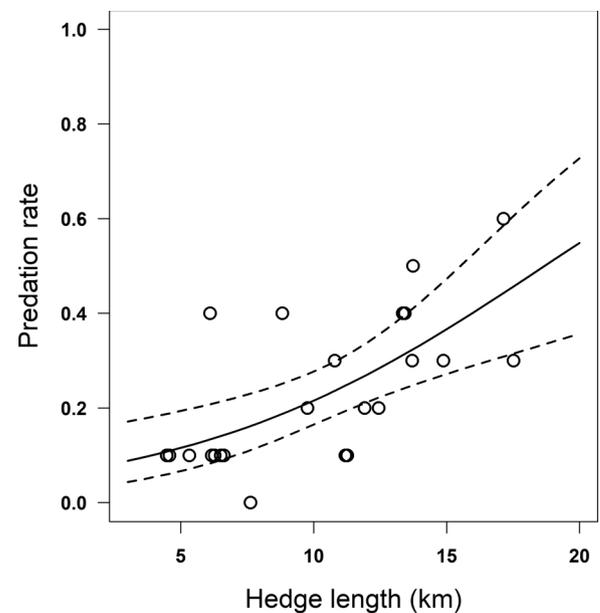


Fig. 2. Effect of the length of hedges within 1 km radius landscapes on seed predation (proportion of preyed cards) in sunflower fields (See model parameters in Table 3). Black dots represent the observed proportion of preyed cards in each sampled sunflower field.

the best model (Table 3 and Fig. 2). We obtained the exact same results when using the proportion of preyed seeds instead of the proportion of preyed cards as response variable (Appendix F in supplementary material, Table F.3).

3.2. Aphid predation

The proportion of preyed aphid cards, i.e. with a predation event, ranged from 0 to 90 % and averaged 43 ± 5 % (mean \pm SE) per field. Regarding the proportion of consumed aphids per field, predation was high ranging from 0 to 86 % and averaged 32 ± 5 %.

Predator communities in sunflower fields, plant species richness in grasslands and hedge length in the landscape had positive effects on aphid predation rates. Model 9 (Table 2) was selected among competing models (Δ AICc > 2 with the other competing models: AICc = 289.8, 290.0, 282.5, 294.6, 295.0, and 290.2 respectively for Models 7, 8, 9, 10, 11 and 12) (Appendix F in supplementary material, Table F.2). The length of hedges within 0.25 km radius and grassland plant species richness had an interactive effect on the proportion of preyed cards. Increasing either plant species richness in the adjacent grassland or hedge length within 0.25 km resulted in an increase in aphid predation rates in sunflower fields. However, the positive effect of grassland plant species richness on aphid predation rates vanished when hedge length within 0.25 km was high, and the positive effect of hedge length on aphid predation rates vanished when grassland plant species richness was high (Fig. 3). Aphid predation was also explained by predator communities in sunflower fields, namely by spider activity-density which had a positive effect on predation (Table 3). Carabid beetles metrics (species richness, Shannon Index or the activity-density of carnivorous and omnivorous functional group or all species pooled) had no effect on aphid predation (Appendix F in supplementary material, Table F.2). We obtained the same results when using the proportion of preyed aphids instead of the proportion of preyed cards (Appendix F in supplementary material, Table F.4).

3.3. Spider activity-density

We only analysed spider activity-density since it was the only

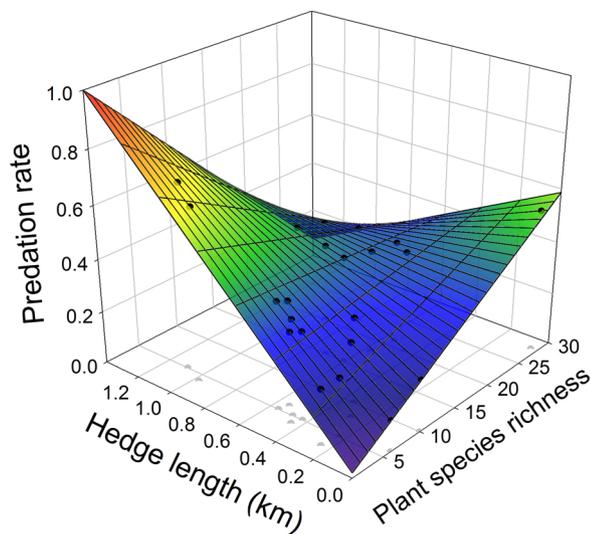


Fig. 3. Predicted effects of the length of hedges within 0.25 km radius landscapes and of grassland quality (plant species richness) on aphid predation rate (proportion of preyed cards) in sunflower fields (See model parameters in Table 3). Black dots represent the predicted proportion of preyed cards in each sampled sunflower field.

Table 4

Results of GLMs with binomial negative distribution fitted for spider activity-density in sunflower fields and in grassland fields.

	Term	Est. \pm SE	P
Spider_AD_Sun	Intercept	1.74 \pm 0.39	< 0.001
	Spider_AD_Grass	0.29 \pm 0.13	0.03
Spider_AD_Grass	Intercept	0.32 \pm 1.10	0.77
	Plant_SPR	0.11 \pm 0.08	0.22
	H_1km	0.37 \pm 0.11	0.001
	I(Plant_SPR:H_1km)	-0.02 \pm 0.01	0.02

Parameter estimates (Est.), standard errors (SE) and *P* of the fixed-effects terms in generalized linear models with spider activity-density in sunflower fields (Spider_AD_Sun) and in grassland fields (Spider_AD_Grass) as response variables. Plant_SPR is grassland plant species richness, H_1km is the length of hedges (km) within 1 km radius landscapes centred on each field pair. Spider_AD_Grass as an explanatory variable is log-transformed in the models.

variable characterizing ground-dwelling predator communities which had an effect on biological control in our study.

Spider activity-density in sunflower fields ranged from 0 to 35 spiders (mean \pm SE: 12.5 \pm 2.1) while it ranged from 0 to 116 spiders (mean \pm SE: 25.1 \pm 7.1) in grassland fields.

Grassland plant species richness and hedge length in the landscape within 0.25 km or 1 km radius landscapes had no effect on spider activity-density in sunflower fields. Spider activity-density in sunflower field increased only with spider activity-density in the adjacent grassland (Table 4).

Hedge length in the landscape within 1 km had a positive effect on spider activity-density in grasslands (Table 4) while grassland plant species richness had a null or adverse effect on spider activity-density in the grasslands depending on the amount of hedges in the landscapes within 1 km (Fig. 4).

4. Discussion

In this study, we sampled arthropod predator communities (carabids and spiders) and measured pest predation rates in crop fields along two independent environmental gradients: a gradient of local green infrastructure quality and a gradient of green infrastructure amount in the landscape. We show that increasing the amount or the

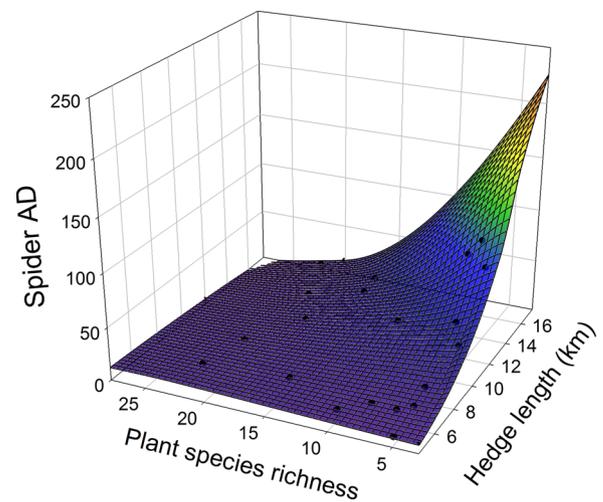


Fig. 4. Predicted effects of the length of hedges within 1 km radius landscapes and of grassland quality (plant species diversity) on spider activity-density in the local grassland (See model parameters in Table 4). Black dots represent the predicted spider activity-density in each sampled grassland field.

quality of green infrastructures can enhance pest predation rates in adjacent crops. Both weed seed and aphid predation rates in the sunflower fields increased with the length of hedges but at different spatial scales. As hypothesized, pest predation in the sunflower fields increased with plant species richness in the adjacent grassland field, but this effect was observed only for aphid predation, and was positive only when hedge length in the immediate landscape was low. In addition, we highlight the key role of spider abundance in aphid pest control in our system.

4.1. Effects of local grassland plant species richness and hedge amount in the landscape on pest predation rates in sunflower fields

We show that aphid predation rates depended on an interaction between the quality and the quantity of green infrastructures in the immediate field surroundings. Therefore, our results on aphid predation partly validate our hypothesis about a modulation of the local effect of green infrastructure quality on biological control by the landscape context (Tschamtko et al., 2012) which acted however at a very local scale in our study. Aphid predation rates were the weakest when sunflower field was adjacent to plant species poor grassland and when there were few hedgerows in the 0.25 km radius landscape. From that point, increasing either plant species richness in grassland or hedge length increased aphid predation rates. On one side, increasing plant species richness in grasslands may increase the local pool of natural enemies that could spillover in adjacent crops by local diffusion (Rand et al., 2006). On the other side, increasing hedge length may increase the abundance and diversity of natural enemies thereby increasing the flow of individuals towards crop habitats due to mass effect (i.e., immigration of individuals from different patches in the immediate landscape). When grassland species richness and hedge length were simultaneously high, aphid predation rates reached a plateau. Such saturating effect may be explained because greater abundance and diversity of natural enemies in crop habitats may result in higher competition and intra guild predation. This could limit their efficiency in preying aphids thereby resulting in a slowdown or a decrease in predation rates at some levels of natural enemy abundance and diversity (Caballero-Lopez et al., 2012).

In contrast to aphid predation, weed seed predation only depended on the length of hedges in the landscape at 1 km scale. This result is in line with previous studies (Trichard et al., 2013) and suggests that weed seed predation in sunflower fields is mainly affected by mass effects resulting in immigration of beneficial organisms mainly coming from

hedgerows at this scale and that characteristic of adjacent grassland is not a major factor explaining the level of weed seed predation. This result does not validate our hypothesis about the positive effects of local grassland plant species richness on weed seed predation.

4.2. Which predators are in play?

Our results clearly show that spiders were an important functional group involved in aphid biological control as the activity-density of spiders in sunflower fields positively affected aphid predation rates. This was also observed in wheat fields surrounded by hedgerows (Garraat et al., 2017). Spider communities in our sunflower fields were largely dominated by Lycosidae (68 % of the total spider abundance) and by Linyphiidae (20 % of the total spider abundance). Our results are therefore in line with what is known about the diet of these two spider families. Several studies involving field or laboratory observations as well as molecular analyses of predator gut contents have shown that aphids can represent a significant part of Lycosidae's diet (Nyffeler and Benz, 1988; Roubinet et al., 2018).

However, our results also suggest that other groups of natural enemies may be important for both aphid and weed seed predation. First of all, our results on aphid predation indicate that spiders alone did not explain all the variability in aphid predation rates but that carabid beetles did not affect aphid predation rates whatever the groups we considered (all species pooled or carnivorous and omnivorous functional group). Our data support the hypothesis that aphid predation rates partly depended on the spillover of spiders from grassland to sunflower fields (i.e., there is a positive relationship between the activity-density of spider in sunflower fields and the activity-density of spiders in grasslands). However, our analyses about the environmental drivers of both the activity-density of spiders in grasslands and the predation rates in sunflower fields indicate a positive effect of plant species richness on aphid predation rates in 0.25 km radius landscapes with low amount of hedgerows despite very low spider densities in the adjacent grassland (Fig. 4). These results suggest that other taxa may be involved in the spillover between habitats and that plant species richness in the adjacent grassland can benefit aphid predation rates via other natural enemies. We particularly suggest that ants, staphylinid beetles, true bugs or lacewings can be important groups to consider that could contribute to the observed spillover effects on aphid predation rates (Symondson et al., 2002; Thies et al., 2011; Garraat et al., 2017).

Secondly, our analyses indicate that no variables describing natural enemy communities in the sunflower fields were important predictors of weed seed predation. We initially hypothesized that carabids were the main group of natural enemies explaining weed seed predation variability (Bohan et al., 2011; Trichard et al., 2013). In our study, carabid communities were mainly dominated by *P. rufipes*, *P. cupreus* and *A. consularis*. Knowledge about the diet of these species is variable but indicates that it ranges from omnivorous to granivorous (Laroche, 1990; Honek et al., 2003; Homburg et al., 2014). In particular, *P. rufipes* which has strong preferences for seeds of *V. arvensis* in laboratory diet assessment is a good candidate for *V. arvensis* predation (Petit et al., 2014). However, activity-density of both pooled, granivorous and omnivorous functional group and individual carabid species did not significantly explain the level of weed seed predation in our experiment at that time. This may be explained by the quite low activity-densities that we observed compared to other studies establishing a positive effect of carabids on *V. arvensis* seed predation in field conditions using a similar methodology (Petit et al., 2014). Recent studies have revealed that vertebrates (including rodents or birds), much more than invertebrates, are responsible for seed predation in agroecosystems (Tschumi et al., 2018). The fact that the only important predictor for seed predation was the length of hedges at the 1 km scale is in line with the scale at which rodents and birds operate in agricultural landscape and with other studies about seed predation in agricultural landscapes (Baker et al., 2012; Trichard et al., 2013). Our results on

weed seed predation therefore highlight that dispersal abilities of species in play strongly determine the scale of response of biological control services to green infrastructures.

4.3. What is the optimal spatial scale to enhance biological control potential in sunflower fields?

Our study indicates that management options to enhance biological control potential in agricultural landscapes depend on the type of pest considered. We found that management options to enhance biological control of aphids in sunflower fields are more local than management options to increase biological control of weed seeds. Several studies have shown that aphid predation rates respond to the proportion of green infrastructures at large scales such as in a 1 or 1.5 km radius (Roschewitz et al., 2005; Rusch et al., 2013, 2016). However, these studies did not explicitly examine the effects of both green infrastructure quality and quantity at multiple scales on aphid predation rates. Here, we demonstrate that taking into account both quality and quantity of green infrastructures at different scales, i.e., adjacent habitats and immediate landscape, can help in explaining the context-dependency of green infrastructure effects on aphid biological control. Our results about the most important spatial scale to explain biological control of weed seed (i.e. 1 km) are in line with other studies (Baker et al., 2012; Trichard et al., 2013). We demonstrate that building functional landscape to optimize the delivery of ecosystem services in agricultural landscapes needs a multi-spatial scale and a multi-taxa approach that takes into account species traits, landscape structure as well as potential trade-offs in the delivery of multiple ecosystem services (Nelson et al., 2009; Ekroos et al., 2016).

5. Conclusions and applications

Our study clearly highlights that both quality and quantity of green infrastructures in the landscape are major drivers of spillover of beneficial organisms and biological control services in agricultural landscapes. Our study highlights the benefit of having grassland fields and hedgerow networks in the landscape mosaic which act as biodiversity reservoirs for neighboring crop fields. We also show that increasing grassland quality through management options may counteract in some extent the negative effect of landscape simplification on aphid biological control. Our study therefore provides practical guidelines to help the development of agri-environmental schemes aiming at maximising the flow of ecosystem services in farmland. Indeed, our results suggest that efforts of local plant diversification to enhance pest control services should be prioritized in landscapes with low amount of hedgerows. Also, our results extend previous findings suggesting that the conservation or the restoration of hedgerow networks in agricultural landscapes is a promising way to promote pest control services without taking much land out of production.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2019.106735>.

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