



# Proportion of Grassland at Landscape Scale Drives Natural Pest Control Services in Agricultural Landscapes

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Managing regulating ecosystem services delivered by biodiversity in farmland is a way to maintain crop yields while reducing the use of agrochemicals. Because semi-natural habitats provide shelter and food for pest enemies, a higher proportion of semi-natural habitats in the landscape or their proximity to crops may enhance pest control in arable fields. However, the ways in which the spatial arrangement of these habitats affects the delivery of this beneficial ecosystem service to crops remains poorly known. Here, we investigated the relative effects of the amount of grassland in the landscape versus the distance to the nearest grassland on the predation rates of weed seeds and aphids into 52 cereal fields. We found that both seed and aphid predation levels increased with the proportion of grassland in a 500 m radius buffer while the distance to the nearest grassland displayed no effect. We show that increasing from 0 to 50% the proportion of grasslands in a 500 m radius, respectively, increased seed and aphid predation by 38 and 20%. In addition to the strong effect of the proportion of grassland, we found that seed predation increased with the proportion of forest fragments while aphid predation increased with the proportion of organic farming in the landscape. Overall, our results reveal that natural pest control in cereal crops is not related to the distance to the nearest grassland, suggesting that natural enemies are not limited by their dispersal ability. Our study indicates that maintaining key semi-natural habitats, such as grasslands, is needed to ensure natural pest control and support food production in agricultural landscapes.

**Keywords:** ecosystem services, agricultural intensification, predation, agroecology, natural enemy, aphid, weed

## INTRODUCTION

Agricultural intensification, which manifests through a massive use of pesticides, low crop diversity or landscape simplification, has major impacts on biodiversity (Beketov et al., 2013; Maxwell et al., 2016). Since biodiversity is one of the main determinants of ecosystem productivity (Tilman et al., 2014), this decline may threaten the long-term sustainability of food production

(Cardinale et al., 2012). A paradigm shift is therefore needed to meet the double challenge of maintaining – and in some cases, enhancing – food production and minimizing negative environmental impacts (Godfray et al., 2010; Garibaldi et al., 2017). One possible way forward is to increase regulating and supporting ecosystem services in agricultural fields to replace agrochemical inputs (Bommarco et al., 2013).

Among key functions supported by biodiversity, natural pest control, i.e., the suppression of pest species by their predators, is a major one. Natural pest control can benefit farmers by limiting crop yield loss (Maas et al., 2013; Bengtsson, 2015; Schneider et al., 2015; Ali et al., 2018) and pesticide use (Naranjo et al., 2015; Huang et al., 2018). High diversity in natural enemy communities is often associated with high levels of pest suppression (Letourneau et al., 2009). Indeed, a large body of research has focused on understanding the mechanisms operating at multiple spatial scales, from the plant to the landscape, driving the presence of natural enemies and the level of pest suppression in agroecosystems (Bianchi et al., 2006; Rusch et al., 2010, 2016; Chaplin-Kramer et al., 2011). While these studies have demonstrated that landscape heterogeneity is a major predictor of the level of natural pest control, the relative importance of landscape composition (i.e., amount of habitats) and of its configuration (i.e., spatial arrangement of habitats) on this key function remains poorly explored (but see Martin et al., 2019).

Population and community dynamics at the landscape scale can be viewed as a “source-sink” dynamic between habitats, under which both landscape configuration (e.g., fragmentation) and composition (e.g., amount of habitat) are strong drivers of biodiversity dynamics and ecosystem functioning (Haddad et al., 2017). These effects act in concert over multiple spatial scales and are mediated by dispersal abilities of species, rates of colonization and local extinction (Haddad et al., 2015, 2017; Hanski, 2015; Watling et al., 2020). In agricultural landscapes, semi-natural habitats such as woodlands, hedgerows, or grasslands are important sources of natural enemies because they provide alternative sources of food or hosts, refuges from disturbances and overwintering and breeding sites for a large range of species (Landis et al., 2000; Veres et al., 2013; Sarthou et al., 2014). Natural enemies disperse from semi-natural habitats to crops, and their spatial dynamics can be explained by the distribution of source habitats in the landscape through complementation or supplementation processes (Dunning et al., 1992; Rand et al., 2006; Blitzer et al., 2012). The importance of semi-natural habitats for natural pest control mainly comes from studies exploring how the amount of semi-natural habitats in the landscape enhances the activity of natural enemies or the amount of pest control in arable fields (Rusch et al., 2013, 2016; Veres et al., 2013; Haan et al., 2020). However, how the spatial arrangement of semi-natural habitats affects natural pest control remains poorly explored and the few studies investigating the effect of the distance of semi-natural habitats on natural pest control show idiosyncratic effects (Farwig et al., 2009; Thomson and Hoffmann, 2013; González et al., 2017; Lindgren et al., 2018; Aristizabal and Metzger, 2019). In addition, due to their strong correlation in the landscape (Fahrig et al., 2011), the relative

importance of composition and configuration of semi-natural habitats on natural enemies and pest control services remains largely unknown (Haan et al., 2020).

Distance of arable crops to semi-natural habitats is expected to be a critical driver of the spillover of natural enemies. The distances are highly species-dependent because dispersal abilities vary from poor dispersal abilities (<1,000 m) for ground-dwelling species such as carabids or spiders, to high dispersal abilities for flying predators, such as ladybirds or syrphids (Schmidt et al., 2005; Saska et al., 2008; Jauker et al., 2009; Maes et al., 2014). Dispersal capacities further interact with the spatial distribution of semi-natural elements: natural enemies with “passive” dispersal (*sensu* Holt, 1985) forage near their semi-natural habitat source, and natural pest control increases with the proximity to the source habitat (Holzschuh et al., 2010; Haenke et al., 2014). Conversely, natural enemies with “active” dispersion depend less on adjacent natural habitats. As such, identifying the scale of effects of habitat sources for natural enemy communities involved in the delivery of pest control services is of major importance to understand the functioning of agricultural landscapes.

Among semi-natural habitats, grasslands are key habitats for many species, including natural enemy species (Bengtsson et al., 2019) and contribute to many ecosystem services in agricultural landscapes (Habel et al., 2013; Bengtsson et al., 2019). Grasslands shelter more natural enemies in early spring than any other type of semi-natural habitats and are therefore a major source of predators in agricultural landscapes (Albrecht et al., 2010; Sarthou et al., 2014; Werling et al., 2014). However, in most studies, grasslands are aggregated with other types of semi-natural habitats, thus their individual effect on pest control services remains poorly understood (Holland et al., 2017). In the few cases where the effect of grasslands was specifically considered, grassland proportion was shown to increase natural enemy abundance or pest predation, and reduce pest abundance in crops (Rusch et al., 2011; Trichard et al., 2013; Alignier et al., 2014; Koh and Holland, 2015; Petit et al., 2017). The distance effect of grasslands on natural pest control services is even less informed, but proximity to grasslands increases pest predation or pest abundance in adjacent crops (French et al., 2001; Badenhauer et al., 2020). However, to our knowledge, the relative importance of grassland proportion in landscape versus distance-decay effects on pest control has never been studied simultaneously in a single study.

The aim of this study is to disentangle the relative effects of the amount of grassland from the effect of distance to the nearest grassland on natural pest control in focal cereal fields. We used predation sentinel cards, and focused on predation rates of two different types of prey, i.e., aphids and weed seeds, which are known to incur cereal yield loss (Ali et al., 2018; Adeux et al., 2019). Both aphids and seeds are preyed by a large number of predators, with highly variable dispersal abilities and diets. These include carabid beetles, birds and small rodents for seeds (Bohan et al., 2011; Eraud et al., 2015; Tschumi et al., 2018a,b); ladybirds, carnivorous ground beetles, spiders or syrphid larvae for aphids (Schmidt et al., 2005; Saska et al., 2008; Jauker et al., 2009; Maes et al., 2014). However, in most cases,

the identity of natural enemies responsible for pest suppression remain unknown (Furlong and Zalucki, 2010). We hypothesized that if natural pest control services are driven by local and passive diffusion, then the level of pest control should be more affected by the distance to the nearest grassland than by its proportion in the landscape. On the contrary, if natural pest control services are mainly driven by complementation processes mediated by active dispersal from sources habitats to crops, then grassland proportion is more important than the distance to the nearest grassland.

## MATERIALS AND METHODS

### Study Area

The study took place in 2016 in the Long Term Social-Ecological Research site “Zone Atelier Plaine & Val de Sèvre” (ZAPVS), an agricultural landscape located in central western France (Bretagnolle et al., 2018), in the Nouvelle Aquitaine Region (46.23°N, 0.41°W). Land use is surveyed annually in each of the c. 13,000 fields of the study site (435 km<sup>2</sup> managed by c. 450 farms), and is stored in a GIS database (Bretagnolle et al., 2018). The area is mainly used for intensive cereal farming. Grasslands (including meadows and long-term set-a-sides, but excluding alfalfa) represent only 7.1% of the ZAPVS, while cereals, mainly winter wheat varieties, are the dominant crop (37.1% cover). The other main crops consist of oilseed rape (7.1%), sunflower (7.4%) and maize (8.9%). Forests cover about 13.7% of the ZAPVS (including the large Chizé forest, **Figure 1**). The remaining area is comprised of other crops such as alfalfa, pea, linseed or ryegrass, and urbanized surfaces. Crop fields have an average size of 5.7 ha, ranging from 0.4 to 35.2 ha.

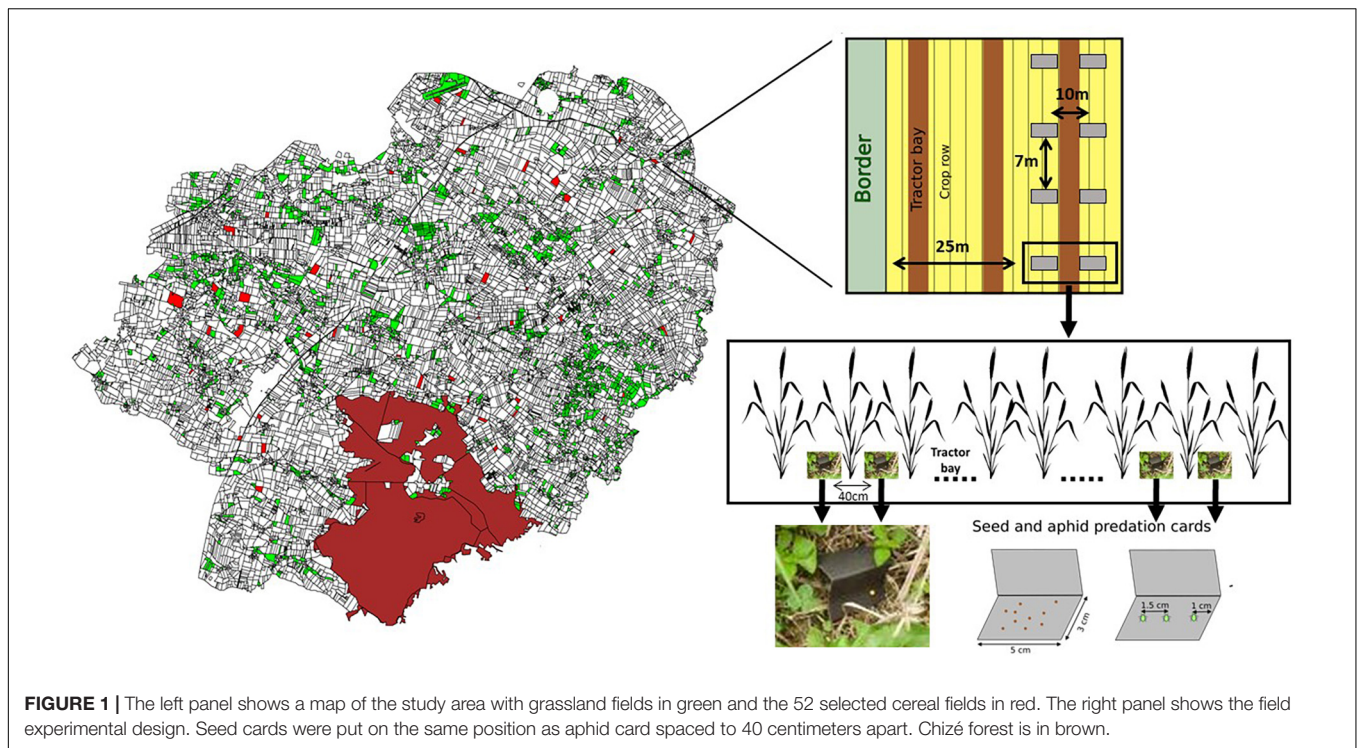
### Site Selection and Landscape Metrics

Two landscape gradients of interest were particularly studied: the first gradient, related to landscape configuration, was the distance between the barycentre of sentinel card position and the nearest grassland field (represented by its border), while the second gradient was the proportion of grassland in the landscape at a given buffer size (radius). We selected 52 cereal focal fields (45 winter wheat and 7 winter barley fields) along these two landscape gradients which could influence the predation rates of aphids and weed seeds in these fields (Rusch et al., 2010, 2013). The fields were randomly selected with a moving window aiming at lowering the correlation between two landscape gradients of interest and making them independent (see Fahrig et al., 2011; Sirami et al., 2019). Correlation between the distance to the nearest grassland and the proportion grassland never exceeded 0.52 whatever the radius (**Supplementary Figure 1** shows correlations between distance to the nearest grassland and proportion of grassland for the different buffer scales). Distance to closest grassland varied from 25 to 972 m (average: 289.9 m, see **Figure 1**), while the area of the nearest grassland varied from 0.26 to 7.6 ha (average: 2 ha). In addition to these two landscape metrics, we also calculated the proportions of crops organically farmed, forests and hedgerows, since these landscape metrics are known to affect natural pest control as well as natural

enemies presence and abundance (Farwig et al., 2009; Rusch et al., 2010; Muneret et al., 2019). All these landscape metrics were calculated at six different radii ranging from 250 to 1,500 m around the barycentre of sentinel prey card position (see below, Martin et al., 2015; Rusch et al., 2016; Tschumi et al., 2018a). **Table 1** shows habitat proportions in the six different buffer sizes. Correlations between organic farming, hedgerow, forest and grassland metric were lower than 0.6 (see **Supplementary Figure 2** for all correlations between landscape metrics).

### Experimental Design

We used sentinel preys to estimate natural pest control potential as it is a standard and efficient method related to predator activity (Lövei and Ferrante, 2017; Boetzl et al., 2020a) and pest regulation (Perez-Alvarez et al., 2019). In each cereal field, we measured natural pest control as the realized predation rate on two common pests: the aphid *Acyrtosiphon pisum* (Ximenez-Embun et al., 2014) which is commonly used to estimate aphid predation in cereal fields (Winqvist et al., 2011; Ricci et al., 2019), and the weed *Viola arvensis* (Petit et al., 2017) which is relatively common in cereal fields (Bourgeois et al., 2020). Weed seeds were bought at Herbiseed (Reading, United Kingdom). Aphids colonies were bought at Monster-Souris (Nantes, France) and raised on peas (*Pisum sativum*) in the laboratory from the beginning to the end of the sentinel card experiment under ambient temperature and natural day-night cycle. Predation rates were quantified using sentinel cards, on which either three dead aphids or 10 weed seeds were glued (Aero'Colle, Cléopâtre) on the rough side of 5 cm × 6 cm sandpaper cards (Boetzl et al., 2020a; McHugh et al., 2020, **Figure 1**). Cards were placed 24 h in the freezer at −20°C before the experiment to avoid attractive or deterrent effect of predator due to glue evaporation (Boetzl et al., 2020a). Two parallel transects of 21 m were selected per field, distant by at least 10 m from each other to ensure independence between transects. To limit potentially confounding field margin effects, we set up transects at least two tractor bays (i.e., approximately 25–35 m) away from the field border, (**Figure 1**). On each transect, four cards of each prey type were set on the ground, held a pin (Winqvist et al., 2011; Boetzl et al., 2020a), from the 7th April to 30th June (i.e., from heading to grain ripening of cereals), each being 7 m apart (**Figure 1**; Ricci et al., 2019; Boetzl et al., 2020b). Seed and aphid cards were put on the same position on the transect and spaced 40 cm apart. Cards were folded in half to provide a tent-like with aphids facing to the ground to limit the deterioration of the aphid or seed gluing by climatic conditions (rain, sun, wind...) as advised by Winqvist et al. (2011). The position of cards in the fields was recorded with a GPS. The barycentre of global card positions in a given focal field was used as the center of buffer and to measure the distance to the nearest grassland. Each field was sampled twice over the spring and summer seasons to account for temporal variation of predation rates throughout the season (Ximenez-Embun et al., 2014). A total 832 cards per prey type were set up (i.e., 8 cards per field and per session). On average, 44.1 days (range: 28–56 days) separated the two sampling sessions for a given field. Seed cards were left 4 days in the field whereas aphid ones were collected after 1 day (24 h) because of much higher predation rates (see



**TABLE 1** | Habitat proportions calculated in different buffer radii.

Buffer size	Grassland	Hedgerow	Forest	Organic farming
250 m	5.7 (0 – 48.4)	1.2 (0 – 6.6)	2.9 (0 – 49.9)	5.8 (0 – 47)
500 m	7.3 (0 – 50.7)	1.2 (0 – 5.4)	2.8 (0 – 33)	7.2 (0 – 58.8)
750 m	7.1 (0 – 46.0)	1.2 (0 – 4.6)	3.1 (0 – 27.3)	7.3 (0 – 49.8)
1,000 m	7.4 (0 – 39.3)	1.3 (0.1 – 4.1)	3.5 (0 – 28.5)	7.7 (0 – 39.8)
1,250 m	7.4 (0.5 – 33.6)	1.3 (0.2 – 3.9)	4 (0 – 29.1)	7.7 (0 – 36)
1,500 m	7.6 (1.2 – 30.6)	1.3 (0.2 – 3.7)	4.4 (0 – 26.7)	7.6 (0.1 – 35.2)

Mean (min and max) are given.

results, Ximenez-Embun et al., 2014). This period is standard in studies using predation sentinel cards (Lövei and Ferrante, 2017; Perez-Alvarez et al., 2019; Boetzel et al., 2020a). A total of 817 seeds cards and 818 aphid cards were recovered from the 832 initially installed, 15 and 14 were lost, respectively. In one field, one session was lost for both seed and aphid cards. We counted the number of aphids or seeds remaining on the cards to estimate predation rates, and then removed cards from fields.

## Statistical Analyses

To disentangle the importance of proportion of grassland in the landscape from the importance of the distance to the nearest grassland on aphid and seed predation rates in cereal fields, we used Generalised Linear Models (GLM). For weed seed predation, we used the ratio of the number of weed seed predated on the total number of seeds placed in the fields as response variable and used a Gaussian error distribution. For aphid predation, we used 1- the number of aphids predated on the total number of aphids placed in the fields (i.e., the number of non-predated aphids) due to the very high predation rates

of aphids (49% fields have more of 90% aphids predated) and used a Poisson-Gamma distribution from the family Tweedie (Dunn and Smyth, 2018). This distribution handles zero values uniformly with positive and continuous values thanks to a power variance function and a log-link function (Lecomte et al., 2013). This distribution performed better than models such as hurdle or negative-binomial models with zero-inflated data (Lecomte et al., 2013; Saha et al., 2020).

First, we investigated how predation rate (seed or aphid and response variable) was explained by the distance to the nearest grassland or the proportion of grasslands. As the correlation of predation rates between the two sessions was very weak (Pearson correlation test between the two sessions,  $\rho = 0.09$ ,  $t = 0.62$ ,  $df = 49$ ,  $p$ -value = 0.54 for seeds, and  $\rho = 0.15$ ,  $t = 1.06$ ,  $df = 49$ ,  $p$ -value = 0.29 for aphids), we used the two sessions as independent observations and included the Julian date in the model as a co-variate to account for season. Six models per pest type were fitted using the two landscape variables calculated in six-buffer radius size (Table 1). The six models were compared using the Akaike Information Criterion (AIC;

Burnham and Anderson, 2002) and we retained the best model for each response variable, i.e., the model with the lowest AIC. The effect of the interaction between grassland proportion and the distance to the nearest grassland was also tested by adding an interaction term to the best model, and was removed in next models if it was not significant.

Since predator activity may depend on weather, e.g., rainfall potentially modifies predator activity (Zaller et al., 2014), we included weather variables in the models. We added average rainfall per day during the experiment as co-variables to these models, calculated over 4 days for seed predation measures (average 1.76 mm per day, range: 0–8.26 mm) and over 2 days for aphid predation measures (average 1.73 mm per day, range: 0–6 mm), to consider rainfalls from the first day where cards were deposited in the fields to the day when they were retrieved. We did not consider average temperature as an explanatory variable in our models as temperature was strongly correlated to Julian days (Pearson correlation test between Julian days and average temperature on 4 days,  $\rho = 0.8$ ,  $t = 13.32$ ,  $df = 102$ ,  $p$ -value  $< 0.001$ , Pearson correlation test between Julian days and average temperature over 2 days,  $\rho = 0.76$ ,  $t = 11.65$ ,  $df = 102$ ,  $p$ -value  $< 0.001$ ). All weather metrics were obtained from a weather station located in the city of Niort, within the study zone, and data were downloaded from United States National Oceanic and Atmospheric Administration.

We further tested whether a grassland that is small in surface but close to the focal crop could be equivalent – in terms of source habitat for natural enemies – to a grassland that is large but distant. Thus, in a separate analysis, we incorporated the area of the nearest grassland by replacing the distance to the nearest grassland by the distance to the nearest grassland divided by its area. Finally, because the proportions of hedgerows, forests and organic farming in the landscape are known to affect natural pest control, we explored their potential effects (Farwig et al., 2009; Rusch et al., 2010; Muneret et al., 2019) in additional models. We added these three metrics as co-variables in the best models for aphid and seed predation. Adding these landscape metrics variables allows quantifying their individual effect on predation rates but also their additional effect with grassland effects (both proportion and distance).

All analyses were performed using the software R (R Core Team, 2015), version 3.6.2 with “stats” package for GLMs and AIC estimation, “tweedie” and “statmod” for GLM models with Tweedie distribution (Giner and Smyth, 2016; Dunn, 2017). All explanatory variables were centered and reduced to facilitate the interpretation of coefficients.

## RESULTS

Overall, 1998 (of 2454) aphids and 3446 (of 8170) seeds were removed across the two sessions in the 52 focal cereal fields. Seed predation rate was in average of  $0.42 \pm 0.29$  (median: 0.42) while aphid predation rate was  $0.81 \pm 0.24$  (median = 0.88). Seed and aphid predation rates were positively correlated (Pearson correlation,  $\rho = 0.2$ ,  $t = 2$ ,  $df = 100$ ,  $p$ -value = 0.048).

The best-fit models were models including explanatory variables calculated in the 500 and 750 m radius ( $\Delta AIC < 2$ ) both for seed and aphid predation rates (Supplementary Figures 3A,B). Effect of grassland was similar between models with landscape variables estimated at 500 and 750 m (Table 2 and Supplementary Table 1), but models with landscape variables calculated at 500 m had lowest AIC for both aphid and seed, thus were chosen. Best models, respectively, explained 15.9 and 15.5% of the variance in seed and aphid predation rates. The proportion of grassland had a positive effect on seed and aphid predation rates, contrasting with the distance to the nearest grassland which had no effect on the predation rates of either prey species (Table 2 and Figures 2A,B,E,F). Predation rates of seeds and aphids, respectively, increased by 42 and 21% along the gradient of grassland proportion (proportion of grassland ranged from 0 to 50% in the 500 m radius). No significant interaction was detected between distance to the nearest grassland and grassland proportion (seeds: *Estimate* =  $-0.082$ ,  $p$ -value = 0.49, and aphids: *Estimate* =  $-0.31$ ,  $p$ -value = 0.6; Supplementary Table 2). Including the area of the nearest grassland in the models did not affect the influence of its distance on predation rates for either preys (seeds : *Estimate* =  $-0.012$ ,  $p$ -value = 0.7, and aphids: *Estimate* =  $-0.19$ ,  $p$ -value = 0.2; Supplementary Table 3).

Adding the proportion of forest, hedgerow and organic farming in the landscape additionally explained 8–10% of the variance in predation rates of seeds and aphids ( $R^2 = 24\%$  for seeds and  $R^2 = 22.3\%$  for aphids). The proportion of forests increased seed predation rates (Table 2 and Figures 2C,G), while the proportion of organic farming increased aphid predation rates (Table 2 and Figures 2D,H). The effect of grassland proportion was partially reduced with the inclusion of other landscape metrics compared with the simpler models (Table 2). In such models, predation rates of seeds and aphids, respectively, increased by 38 and 20% along the gradient of grassland proportion (from 0 to 50% in a 500 m radius, Figures 2B,F). Finally, predation rates of seeds and aphids increased with Julian days and marginally with rainfall (Table 2).

## DISCUSSION

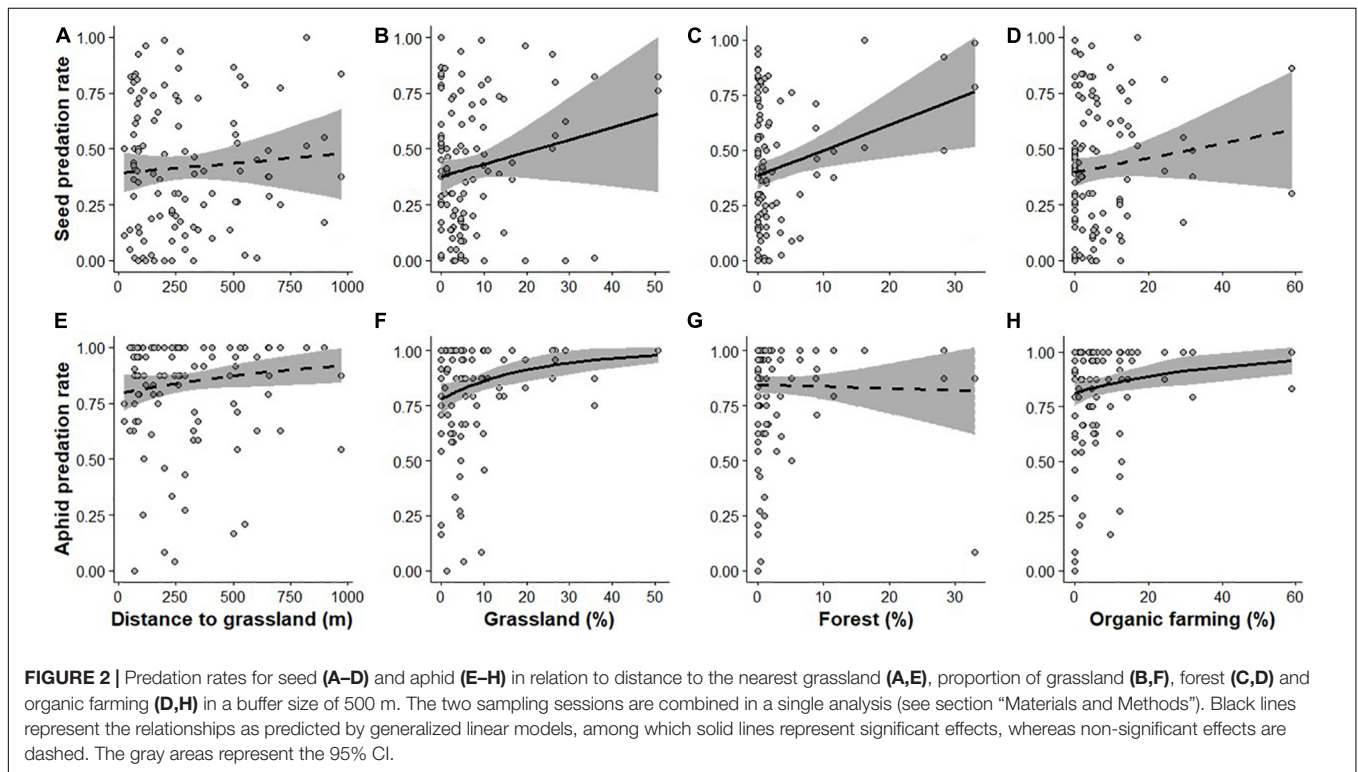
Our study explores the interactive effects of the amount and spatial configuration of grasslands on the predation rates of two types of cereal prey in agricultural landscapes. Our analyses indicate that the proportion of grassland rather than the distance to the nearest grassland increased both seed and aphid predation rates in cereal fields with, respectively, an increase of 38 and 20% from 0 to 50% of grassland in a 500 m-radius buffer. In addition, seed predation increased with the proportion of forests while aphid predation increased with the proportion of organic farming in the surrounding landscape.

The relative importance of habitat composition and configuration at the landscape scale to maintain biodiversity and ecosystem functions is highly debated although few studies examined their relative effects on ecosystem functions and services (Watling and Donnelly, 2006; Haddad et al., 2017;

**TABLE 2** | Summary of generalized linear models for seed and aphid predation rates explained by date (Julian day), average rainfall, and landscape metrics.

	Seed predation rate						Aphid predation rate					
	Only grassland			All landscape metrics			Only grassland			All landscape metrics		
	Estimate	$\chi^2$	p-val	Estimate	$\chi^2$	p-val	Estimate	$\chi^2$	p-val	Estimate	$\chi^2$	p-val
Julian days	<b>0.070</b>	<b>6.970</b>	<b>0.008</b>	<b>0.072</b>	<b>7.951</b>	<b>0.005</b>	<b>0.321</b>	<b>7.907</b>	<b>0.005</b>	<b>0.305</b>	<b>7.303</b>	<b>0.007</b>
Rainfall (mm)	0.048	3.258	0.071	0.044	2.976	0.085	<b>0.256</b>	<b>4.291</b>	<b>0.038</b>	0.232	3.545	0.060
Distance to grassland (m)	0.052	2.800	0.094	0.028	0.769	0.380	0.242	2.979	0.084	0.227	2.299	0.129
Grassland (% at 500 m)	<b>0.083</b>	<b>7.162</b>	<b>0.007</b>	<b>0.077</b>	<b>6.205</b>	<b>0.013</b>	<b>0.495</b>	<b>7.623</b>	<b>0.006</b>	<b>0.483</b>	<b>6.978</b>	<b>0.008</b>
Forest (% at 500 m)	–	–	–	<b>0.071</b>	<b>7.412</b>	<b>0.006</b>	–	–	–	–0.034	0.096	0.757
Hedgerow (% at 500 m)	–	–	–	–0.028	0.873	0.350	–	–	–	0.076	0.268	0.605
Organic farming (% at 500 m)	–	–	–	0.033	1.579	0.209	–	–	–	<b>0.275</b>	<b>4.002</b>	<b>0.04</b>
R-squared			0.159			0.24			0.155			0.23

In a first set of analyses (first and third columns), landscape metrics only include distance to the nearest grassland and proportion of grassland. In the second and fourth columns, other landscape metrics (hedgerow, forest, and organic farming cover) are added to the model. All landscape metrics are estimated in a buffer of radius 500 m. Significant effects ( $P < 0.05$ ) are in bold. For the sake of understanding, we inversed coefficients of aphid models in reported results to have the ratio of predated aphids as for seed model rather of coefficient for 1-ratio of predated aphids.



**FIGURE 2** | Predation rates for seed (A–D) and aphid (E–H) in relation to distance to the nearest grassland (A,E), proportion of grassland (B,F), forest (C,D) and organic farming (D,H) in a buffer size of 500 m. The two sampling sessions are combined in a single analysis (see section “Materials and Methods”). Black lines represent the relationships as predicted by generalized linear models, among which solid lines represent significant effects, whereas non-significant effects are dashed. The gray areas represent the 95% CI.

Bueno and Peres, 2019; Watling et al., 2020). A recent meta-analysis regrouping 35 study sites from different biomes showed that in most cases, composition (in the form of proportion) was more important than configuration to maintain species richness whatever the taxon identity (Watling et al., 2020). Indeed, both the composition and the configuration of agricultural landscapes shape natural enemy communities and pest damage (Martin et al., 2019; Haan et al., 2020), and more specifically the amount of semi-natural habitats enhances the activity of natural enemies or amount of pest control (Rusch et al., 2013, 2016; Veres et al., 2013; Haan et al., 2020). In most cases, the spatial arrangement

had no effect on natural enemies or pest control (Farwig et al., 2009; Thomson and Hoffmann, 2013; González et al., 2017; Lindgren et al., 2018). However, only few studies included both composition and configuration in their analyses (González et al., 2017) as they are strongly correlated in most ecosystems (Fahrig, 2013). Our landscape selection method allowed to disentangle the effect of grassland proportion from the effect of distance to the nearest grassland. Our results suggest that grassland proportion is more important than their distance to crops to increase aphid and seed predation in cereal fields, indicating that the effect of landscape composition on communities also holds

for ecosystem functions (Lamy et al., 2016; Duarte et al., 2018). Our results are consistent with previous studies which showed that aphid and seed predation in cereal fields increase with surrounding grassland proportion (Trichard et al., 2013; Alignier et al., 2014; Petit et al., 2017). Similarly, seed and aphid predation in midfield islets did not decrease with distance to grassland (Lindgren et al., 2018). However, none of these studies accounted for both the configuration and the amount of grassland in their experiments, and grasslands were usually aggregated with other types of semi-natural habitats in a large majority of studies (Holland et al., 2017). Only González et al. (2017) integrated both aspects and showed comparable results with stinkbug egg-predation on soybean crops which increases with forest proportion rather than their distance to crops. The landscape context of our study region may, however, limit the extrapolation of our results to other farmland landscapes. It should be noted that only three cereal fields were more than 750 m away from a grassland (**Supplementary Figure 1**), stressing that additional experiments may be needed with cereal fields more than 1 km from closest grassland to confirm our results. In landscape contexts with few grasslands, and therefore higher distances to the nearest grassland, one may expect a higher effect of distance. Moreover, landscapes with high amount of grassland (>15%) were scarce in our study (7 fields on 52), therefore limiting the scope of our conclusions. Conducting this study with the same experimental design over a large range of landscape gradients and in different pedoclimatic contexts would certainly help to consolidate our conclusions. In addition to the effect of grassland proportion, we found that forest proportion increased seed predation rates while organic farming proportion enhanced aphid predation rates, which suggests a complementation effect of habitat for natural enemies. Diverse semi-natural habitats in agricultural landscape provide alternative prey or additional shelter, hence maintain higher diversity of natural enemies (Tscharntke et al., 2007) and pest predation (Letourneau et al., 2009).

The dispersal and behavioral capacity of natural enemies likely determine the relative importance of composition and configuration of semi-natural habitats for natural pest control (Keinath et al., 2017). We found that the scale of effect of grassland proportion on pest control is at spatial extent ranging from 500 to 750 m radius, rather than small spatial extent. This spatial extent is larger than the one found in a previous meta-analysis which showed that pest predation is best explained by landscapes metrics estimated at small scales (250 m, Karp et al., 2018). High dispersal capacity had been predicted as a key trait of natural enemies effectiveness to remove pests (Bianchi et al., 2010). Natural enemies with high dispersal capacity are less susceptible to landscape heterogeneity (Bianchi et al., 2010). Among seed predators, small mammals, ants and carabids have dispersal capacities ranging from 500 to 750 m (Wegner and Merriam, 1990; Holland et al., 2004; Zumeaga et al., 2021). Moreover, small mammals, ants and carabids can benefit from grasslands (Fischer and Schröder, 2014; Petit et al., 2017; Assis et al., 2018) as well as forest patches (Wegner and Merriam, 1990; Holland and Fahrig, 2000; Assis et al., 2018) to maintain their population and may explain why seed predation rates increase with forest proportion. For aphids, spiders and carabids

are natural enemies with dispersal capacities that match the 500 – 750 m spatial extent (Holland et al., 2004; Schmidt and Tscharntke, 2005; Maes et al., 2014) and appear as potential candidates involved in aphid predation rates here. Abundances of these species were previously found to increase with grassland proportion in agricultural landscapes (Koh and Holland, 2015; Petit et al., 2017; Badenhassner et al., 2020). There is also some evidence that carabids and aphids control by their natural enemies in cereal crops benefit from the proportion of organic farming in surrounding landscape (Caro et al., 2016; Diekötter et al., 2016; Djoudi et al., 2018; Muneret et al., 2019) which may explain why aphid predation rates increased with amount of fields under organic farming. A camera-trap experiment may help to identify the natural enemies responsible for aphid and seed predation (Petersen and Woltz, 2015); especially because the ground position of aphid cards in our study may have excluded predation from aerial predators such as birds or ladybirds. Including such predators might change the spatial extent of the landscape effects detected in our study.

Finally, we found that meteorological conditions modified predation rates. Predation rates of both preys increased with Julian days, but only aphid predation rates increased with rainfall, though we could not disentangle the respective effects of Julian days and average temperature which were strongly correlated. There is clear evidence that both variables affect predator activity: predator dynamics increase with Julian days (Caro et al., 2016), and predator activity and pest predation increase with average temperature (Korenko et al., 2010). It is therefore likely that the increase of predation rates observed in our study resulted from seasonal effect such as increase in average temperature. Predator activity or abundance was also found to be higher with rainfall (Irmiler, 2003; Lundgren et al., 2006; Zaller et al., 2014; Wróbel and Bogdziewicz, 2015), confirming our results on aphid predation rates. However, the absence of relationship between seed predation rate and rainfall may suggest that different natural enemies may contribute to seed and aphid predation and/or that the effect of rainfall is less pronounced on a 4-day (seed predation) than on a 2-day (aphid predation) period. Further studies are now needed to determine how natural enemies of each prey behave under contrasted weather conditions. Similarly, it would be interesting to consider prey abundance or pesticide applications as covariables in our models because these factors can affect natural pest control potential. A high prey abundance can dilute natural pest control by distracting predators from sentinel cards (Lövei and Ferrante, 2017) while pesticide applications can buffer landscape effects (Ricci et al., 2019). These effects need further investigations to fully understand the mechanisms driving natural pest control in agricultural landscapes.

## CONCLUSION

In this study, increasing grassland proportion at landscape scale (500 m buffer radius) by 50% resulted in 38 and 20% increase in seed and aphid predation rates. Conversely, the nearest grassland, whatever its area, displayed no statistical effect on predation

rates. These results highlight the importance of maintaining sufficient amount of grassland habitats in agricultural landscapes to enhance natural pest control services, which might help reducing pest pressure and pesticides applications in agricultural landscapes (Naranjo et al., 2015; Huang et al., 2018). However, a more mechanistic understanding of the effect of landscape context on the delivery of natural pest control and its impact on yield and farmers' income is crucially needed (Schneider et al., 2015; Ali et al., 2018). Pest abundance can also vary with landscape structure, and higher predation rates of pests may not lead to lower abundance and damage (Tscharrntke et al., 2016). Consequently, the study of the relationships between pest control potential, as measured in our study, and actual pest abundance deserves more attention. In addition, increasing grassland area at the landscape scale will result in reducing arable crop area; and this might affect farmers' income. Except for livestock farmers, grasslands have no direct economic benefits, at least under the current European common agriculture policy. Such key topic should now be explored to determine the optimal landscape configuration reducing pest infestation and damage, while maintaining crop yield and farmer profitability (Zhang and Swinton, 2009).

## DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: 10.5281/zenodo.4555503.

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## AUTHOR CONTRIBUTIONS

AR, SG, and VB designed the study. TP and CC prepared the data and conducted the statistical analysis and wrote the first draft of the manuscript. All authors substantially contributed to revisions.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.607023/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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