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Abstract

1. Biological pest control is known to depend on landscape heterogeneity. However, such relationship shows irregular pattern and seems influenced by local farming practices and natural enemies that overwinter within crop fields. The objective of this study was to assess the contribution of emerging natural enemies in spring to biological control, and their response to the interaction between landscape heterogeneity and farming intensity.

2. We monitored the overwintering insect community using emergence traps and measured the local potential pest predation using prey cards in 30 cereal fields, in spring in France. Study fields were selected along a landscape heterogeneity gradient and farming practices were recorded.

3. None of the ten emerging taxa influenced predation of lepidopteran eggs or weed seeds. On the ground, aphid predation was positively correlated with emerging carabid beetles. In foliage, aphid predation was negatively correlated with emerging parasitoids. Overall, the community of natural enemies that overwinter within crop fields seemed to benefit from lower crop diversity and higher edge density in combination with higher farming intensities. This suggest that they represent a subset of species adapted to. This study highlights a large broad taxonomic panel of emerging natural enemies and their potential local pest predation.

KEYWORDS
airborne compartment, beneficial insects, ground compartment, landscape heterogeneity, overwintering, pesticide, potential predation, soil management

INTRODUCTION

The environmental problems caused by modern agriculture calls existing farm production systems into question, particularly their dependence on pesticides and soil management. One of the worldwide agricultural challenges is to reduce the use of chemical inputs while maintaining adequate crop production levels. In addition, farmland biodiversity is decreasing substantially due to the homogenization and intensification of farming practices (Benton et al., 2003; Fahrig et al., 2011). Farmland biodiversity supports many ecosystem services, including pollination, nutrient cycling and pest control (Garibaldi et al., 2018; Tscharntke et al., 2012). In particular, biological control of agricultural pests by their natural enemies could contribute to agricultural production while enabling reduced pesticide use. Many taxonomic groups, including carabid beetles, hoverflies or wasps, and functional groups, such as generalist predators, specialist seed eaters, or parasitoids, contribute to natural pest control (Labruyere et al., 2018; Raymond et al., 2014, 2015; Schmidt et al., 2003; Sigsgaard & Jacobsen, 2017).

Conservation biological control (CBC) relies on fostering naturally-occurring enemies, usually arthropod predators and parasitoids (Tscharntke, Klein, et al., 2005), that are already present in both crops and semi-natural habitats (SNH) (Barbosa, 1998; Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Landis et al., 2000). Most natural enemies require different resources to complete their life

cycle, including food, shelter, nesting and overwintering sites. Various landscape elements may provide these resources at different time of the year (seasonality, Bertrand et al., 2016; Schellhorn et al., 2015). Such distribution of resources in space and time generates species movements between complementary landscape elements, the so-called spill over, which allow natural enemies to find non-substitutable resources they need (Aviron et al., 2018; Blitzer et al., 2012; Duflot et al., 2017; Dunning et al., 1992). It is now widely accepted that landscape heterogeneity is a strong driver of multitrophic diversity, abundance and species composition of natural enemies and, therefore, of CBC (Benton et al., 2003; Dainese et al., 2019; Sirami et al., 2019; Tscharntke et al., 2012). Hence, effects of landscape heterogeneity are to be considered according to multiple trophic levels, which may lead to trade-offs between phytophagous pests, natural enemies and CBC (e.g., Botzas-Coluni et al., 2021).

The role of SNH in the landscape complementation process, where species use complementary resources from different landscape elements, is well known (Fahrig et al., 2011). SNH, or non-crop habitats, include hedgerows and other field boundary habitats, woodlands and permanent grasslands. Increased proportion of SNH in a landscape is usually associated with higher species richness and abundance of natural enemies in crop fields due to their seasonal spill over between SNH, where many species overwinter, and crop fields, where many species find abundant food (Blitzer et al., 2012; Dainese et al., 2019; Tscharntke, Rand, & Bianchi, 2005). For instance, grassy strips near large arable fields provide perennial vegetation and overwintering sites for natural enemies such as beetles, that is, beetle banks (MacLeod et al., 2004; Thomas, 2000). Thus, predators disperse more or less far into the crop, depending on the species, and participate in biological control (Anjum-Zubair et al., 2010; Collins et al., 2002; Thomas, 2000). Moreover, complex landscape configuration leading to high density edges between SNH and crop (indicating a relative small field size) promote natural enemies diversity and enhance pest control (Martin et al., 2019).

Not only SNH but also crop fields can contribute to maintain natural enemies and CBC. On the one hand, the complexity of crop mosaics resulting from the diversity of crop types and field sizes can influence ecological processes such as complementation and spill over (Aviron et al., 2018; Duflot et al., 2016; Vasseur et al., 2013; Vialatte et al., 2017). Populations of natural enemies may be better supported over the course of a year by a continuous flow of crop-based resources rather than by maintaining nearby semi-natural habitat (Bertrand et al., 2016; Schellhorn et al., 2015; Vasseur et al., 2013). By contrast, crops provide almost unlimited resources for pest populations (Root, 1973) and their continuous presence can support the abundance of specialist pests (Nesme et al., 2016; Root, 1973). On the other hand, some species are able to overwinter in crop fields, which is usually assumed to happen in SNH. For instance, crop fields shelter hoverflies during winter, which significantly contribute to biological control of aphids in autumn (Raymond et al., 2014). In addition, most adults of some species of predatory beetles such as cantharids and carabids, which are generalist predators, emerge from larvae that overwinter in crop fields (Noordhuis et al., 2001). The abundance of these populations varies with field-level characteristics, such as crop type and management, including tillage, fertilization and pesticide use

(Herzog et al., 2006; Labruyere et al., 2016). For instance, spring tillage of corn fields has negative effects on carabid beetle communities (Purvis & Fadl, 2002), and pesticides have lethal or sub-lethal consequences for populations of parasitoids (Roubos et al., 2014; Stapel et al., 2000). Although not fully established, it seems that low-intensity farming practices, in terms of pesticide use and of soil management, may offer better within-field overwintering conditions for different taxa of natural enemies (Vasseur et al., 2013).

In sum, crop fields may provide more resources for natural enemies than do SNH (Rusch, Binet, et al., 2016; Rusch, Chaplin-Kramer, et al., 2016), and local farming practices may control the positive effect of SNH on biological control (Labruyere et al., 2016; Ricci et al., 2019). These are two hypotheses that may partly explain the reported irregular response of CBC to landscape heterogeneity (Karp et al., 2018; Tscharntke et al., 2016). However, how the properties of the fields themselves influence CBC and interact with landscape context remains poorly quantified. This study investigates for the first time the contribution of a large range of taxa and of the within-field overwintering community to CBC.

The aims of this study were to evaluate (i) the contribution of locally overwintering natural enemies on local CBC in spring and (ii) the effects of farming practices and the landscape context on the emergence of natural enemies and their own parasitoids or predators in crop fields. We hypothesized that: (i) overwintering natural enemies contribute to biological control early (in spring) because they emerge directly in the fields; (ii) crop fields provide overwintering sites for natural enemies and their parasitoids and predators; (iii) local farming practices interact with the landscape context and influence the abundance of overwintering populations.

MATERIAL AND METHODS

The study was conducted in "*Vallées et Coteaux de Gascogne*", which is part of the Long-Term Socio-Ecological Research site LTSER ZA PYGAR, a 370 km² hilly area located in south-western France (43°17′N, 0°54′E). The region is dominated by mixed crop-livestock farming systems and is therefore characterized by a fine mosaic of woodlands, grasslands and crop fields. Thirty conventional winter cereal fields were selected along a gradient of density of the surrounding woodlands (0%–30% in a buffer zone with a 563-m radius from the sampling location). Wheat is traditionally grown in this region in a wheat–barley–alfalfa or wheat–wheat–sunflower rotations. After overwintering, emergent arthropods were collected in spring 2017, and at the same time, prey sentinel cards were placed in crop fields to evaluate potential biological control. All the variables calculated and surveyed during this study are presented in Supporting Information Appendix A.

Field sampling of overwintering arthropods

Emerging arthropods were caught using emergence traps from the end of winter until the end of spring, covering most of the emergence period of diverse predators and parasitoids. The operating principle of emergence traps is that a specific area of soil is hermetically sealed to

collect all the insects that emerge within the area. Traps (surface area: 0.36 m², Soil Emergence trap 96 × 26 mesh, Black, MegaView Science Co., Ltd. Taichung, Taiwan) were placed in agricultural fields at a distance of 50 metres from the field edge. The collection bottle placed on top of the trap collects all the flying insects that emerge from the ground. A pitfall trap was also placed inside the emergence trap to collect emerging ground-dwelling insects. The bottles were filled two-thirds full with 70% ethanol and the pitfall traps were filled with a solution of soapy water. The traps were set up in the first half of March and collected every other week from March 15 until the last week in May, that is, a total of six sampling periods.

The collected insects were manually sorted: those trapped at the top of the emergence trap were separated from those trapped in the pitfall traps at ground level. The insects were identified to family level and classified into two main functional groups: parasitoids (including hyperparasitoids) and predators. Arthropod families were further classified according to their life history traits into two trophic levels, natural enemies, or hyperparasitoids or parasitoids of natural enemies, and into two compartments of predation/parasitism activity, that is, ground or airborne (Table 1). The total abundance of each family was determined in each field.

Estimation of potential pest biocontrol with sentinel prey cards

Biological control of pests and weeds was evaluated using a standardized protocol based on sentinel prey cards with different types of prey. This method has shown sufficient sensitivity to detect variations in the levels of biological control and the influence of the landscape context (McHugh et al., 2020). The main reason for the massive adoption of monitoring potential predation by sentinel prey cards for 15 years now is that monitoring pest populations is time-consuming. Such methodology has known limitations (McHugh et al., 2020; Meyer et al., 2017) but allows collecting standardized data.

Four complementary types of sentinel preys were placed to monitor diverse predation potential at the ground and crop level. The prey species were selected according to those used in international devices (e.g., Ricci et al., 2019). The three prey species were selected according to their diversity, their similarity to winter cereal pests and the diversity of targeted natural enemies, while considering the constraints of rearing (McHugh et al., 2020; Ricci et al., 2019).

Preys were glued to 5 × 5 cm sandpaper cards. Seed predation was measured using 10 *Viola arvensis* seeds exposed on the ground (glue: SADER® WOOD PRO D3 diluted with two-thirds of water). Insect predation was assessed using predation cards on which three adult pea aphids *Acyrthosiphon pisum* were glued (glue: UHU® Twist&Glue solvent-free). The cards were positioned both on the ground and to the top of a crop plant, as is commonly done to estimate potential CBC (Karp et al., 2018; Östman, 2004; Ricci et al., 2019). In addition to aphids, predation cards containing clusters of *Ephestia kuehniella* (Lepidoptera) eggs were placed at the top of a crop plant. *Ephestia* eggs are too small to allow precise enumeration, so a 5 mm-wide cluster was glued to the card (glue: SADER® all-purpose solvent-free). The glues used were chosen among a set of low toxic glues after practical tests to ensure the prey were just fixed but not mired and that they would not come unstuck during the period of exposure.

TABLE 1 Life history traits of overwintering arthropods sampled in the study

Taxonomic group	Life history traits	Functional group	Compartment of predation/parasitism activity	Mean abundance per field [min;max]
Carabidae	Generalist predator: feeds on eggs, larvae, adults of aphids, slugs, snails and lepidoptera. Some species are also seed predators.	Predator	Ground	9.0 [0; 59.0]
Staphylinidae	Generalist predator: larvae and adults are carnivorous or scavengers. They feed on slugs, underground pests, mites or diptera eggs.	Predator	Ground	202.9 [43.0; 547]
Proctotrupidae	Coleoptera parasite: rove beetles, wireworms, carabid beetles.	Parasitoid of natural enemies	Ground	0.53 [0; 3.0]
Chalcidoidea	Parasitoid of diptera and hemipteran (aphids, for instance).	Parasitoid	Airborne	9.7 [1; 31.0]
	Hyperparasitoid: parasites of parasitoids.	Hyperparasitoid of natural enemies	Airborne	2.3 [0; 11.0]
Braconidae	Parasitoid of diptera and aphids.	Parasitoid	Airborne	2.4 [0; 17.0]
Platygasteridae	Parasitoid of diptera (midges).	Parasitoid	Airborne	0.41 [0; 5.0]
Cantharidae	Generalist predator: feed on aphids, caterpillars. Species are polyphagous.	Predator	Airborne	3.5 [0; 19.0]
Diapriidae	Diptera parasite.	Parasitoid of natural enemies	Airborne	2.3 [0; 11.0]

Note: Each taxon sampled was categorized as predator or parasitoid, and as belonging to the ground or airborne compartment according to its potential predation activity.

Sentinel prey cards were either nailed to the ground ("ground level") or stapled to the top of a crop plant ("crop level"). Aphids were exposed for 24 h to avoid necrophagia, and other sentinel preys were exposed for 96 h.

In each field, we positioned the four sentinel prey cards in 10 plots evenly distributed along two parallel transects separated by a distance of 10 m. The transects were perpendicular to the field border, with the first card placed 50 m away from the border and the last 100 m away. The transects were also about 20 m away from the emergence trap. The number of preys that remains on the cards at the end of the period of exposure was counted in the field, except for *Ephestia*, which, because of their small size, were counted using a magnifying binocular in the laboratory. Two classes were used for *Ephestia* predation: unconsumed (less than 5% of the eggs missing) or consumed (more than 5%). The predation rate of each type of prey in each field was calculated. Two periods of exposure were used during the crop vegetative growth period: from 24 to 28 April and from 29 May to 2 June 2017. The total size of the dataset was 60 predation rates (30 fields, 2 sessions).

Landscape metrics and farming practices

Using ArcGIS Desktop 10.5.1 software, annual land use maps were drawn for the study sites based on direct field observations. Land cover was digitized from aerial orthophotos (50 cm spatial resolution, BDOrtho®) produced by the French national mapping agency. Landscape metrics were then calculated for a 1 km² circle (i.e., inside a circular buffer with a radius of 563 m, centred on the middle of ecological measurements). The heterogeneity of the SNH and the crop mosaic are described using 13 landscape metrics. First, woodlands, hedgerows and permanent grasslands were grouped to calculate the proportion of SNH, their mean patch size, the length of their edges and the length of edges at the interface of SNH and crop fields. Second, land-cover categories were used to characterize the heterogeneity of the SNH: the proportion of wooded habitats, permanent grasslands and the total length of hedgerows. To describe crop heterogeneity, land cover was categorized in spring crops, winter crops

and temporary grasslands; and the proportion of each cover was calculated. Winter crops are sown in autumn and harvested in early summer, and spring crops are sown in spring and harvested at the end of the summer. Finally, the Shannon diversity index (SHDI) was calculated for the whole landscape based on the proportion of each land cover, and the total length of edges, that is, edge density (all types of edges considered), was calculated to evaluate landscape configuration. The SHDI was also calculated specifically for the crop mosaic (SHDI crop), using detailed crop categories (spring crops and winter crops).

Farmers were interviewed during the winter 2017–2018 to collect data on the farming practices used in the sampled fields since the sowing of winter cereal, that is, since the month of October preceding the studied spring. The cumulated tillage depth was used to describe soil management intensity. The quantity of nitrogen provided to the fields was used to describe the fertilization intensity. The treatment frequency index (TFI) was used to characterize the intensity of pesticide use (Lechenet et al., 2014). The TFI was calculated for each type of pesticides separately (insecticides, fungicides and herbicides) and all together (TFI total). The total number of operations, that is, the number of times the crop has been visited, was recorded as an overall proxy of farming intensity.

Correlations between variables were investigated to identify a limited number of noncorrelated variables representative of the landscape context and farming practices, using Pearson's coefficients (Supporting Information Appendices B1, B2). After considering correlations between variables, five landscape metrics and three farming intensity variables were kept for further analyses (Table 2; Supporting Information Appendix C1).

Statistical analysis

First, Pearson's coefficients were calculated between the four types of prey cards to identify possible redundancies in what they measure, that is, the fact the different types of cards may characterize the same predation activity.

Second, statistical analysis was performed on two sets of pooled data from emergent traps (i) all six emergence sampling periods, and

TABLE 2 Definition of the noncorrelated landscape metrics and farming intensity measures used in the study. See Supporting Information Appendix A for the full set of variables

	Name of variable	Meaning	Mean [min; max]
Landscape metrics	SHDI	Shannon diversity of the landscape in 1 km² buffer zone	1.59 [1.31; 1.83]
	SHDI crop	Shannon diversity of crops	1.37 [0.90; 1.93]
	pSNH	Proportion of semi-natural habitats (%)	38.6 [11.2; 68.8]
	pWinterCrop	Proportion of winter crops (%)	21.0 [5.9; 45.1]
	Edge density	Total length of all types of edges (km/ha)	23.2 [13.9; 32.5]
Farming practices	Cumul depth	Cumulated tillage depth (cm)	22.2 [0; 63.0]
	Nqty	Quantity of nitrogen provided in liquid form (kg/ha)	162.4 [46.0; 257.9]
	TFItot	Total treatment frequency index – all types of treatments	4.9 [1; 15.2]

(ii) the first four sampling periods corresponding to the beginning of the spring season and that took place before the first session of predation measurements. In both cases, we modelled the ground and airborne compartments separately, which correspond to the ground and crop level of the sentinel card exposure, and to the ground and airborne traps of the emergence sampling set-up. These compartments relate to predation and parasitism activity of different arthropod families (Table 1). A generalized linear model (GLM) with a Gaussian distribution was built for each type of prey card, either by considering the whole season using the average of the two predation sessions with all six emergence sampling periods, or by considering only the beginning of the season using the first predation session with the first four emergence sampling periods. To reduce the need for further selection of explanatory variables, following the procedure by Ricci et al. (2019), we included only one landscape variable and one farming intensity variable at a time, and their interaction. This method was appropriate as the pre-selected variables had relatively small covariance. Sixteen models were built for each predation rate to be explained. The first model was a null model that included, for each predation rate, the abundance of corresponding emerged natural enemies, that is, natural enemies in the same ground or airborne compartment. Fifteen other models were then produced from that null model by adding every combination of one landscape variable among the five, and one farming practice variable among the three, and their interactions. The models considered potential spill-over processes and interactive effects between the landscape context and farming practices. Finally, averaged coefficients were calculated across all 16 models using the *model.avg* function of the MuMIn package in R (Ricci et al., 2019).

Similarly, the abundance of emerging natural enemies was modelled using GLMs with negative binomial error distribution. We use the negative binomial distribution because of the non-normality and the over-dispersion of data. The null model included the other families of overwintering natural enemies in the compartment considered at the same trophic level and the abundance of their own overwintering enemies at a higher trophic level. The following models were built from the null model by adding one landscape variable among the five and one farming practice variable among the three and their interactions. Averaged coefficients were calculated across all 16 models. Finally, models of the abundance of hyperparasitoids and parasitoids of natural enemies were built in the same way, as a function of landscape and farming practice variables using a negative binomial error distribution. All analyses were performed with R software version 3.6.2 (R Core Team, 2020).

RESULTS

Among the identified families, some were natural enemies and others were known to be their own parasitoids. Parasitoids were identified at the genus level: genera with known parasitic traits could be classified as parasitoids of natural enemies. Different levels of abundance were observed depending on family. A total of 7345 natural enemies were collected, of which 987 were from the top of emergence traps and 6358 in the pitfall traps.

Carabidae (mean = 9.0; SD = 11.1 individuals per field over the entire sampling period) and Staphylinidae (202.9 ± 113.1) were identified in the ground compartment (Supporting Information Appendix D1), whereas parasitoids belonging to the super-family of Chalcidoidea (9.7 ± 7.4) and family of Braconidae (2.4 ± 3.7), as well as generalist predators of the Cantharidae family (3.5 ± 5.1), were present in the airborne compartment. Members of the Platygasteridae family (0.41 ± 1.05) also emerged, but their abundance was very low (Supporting Information Appendix D2).

We found parasitoids of natural enemies in both compartments. In the ground compartment, individuals belonging to the Proctotrupidae family (0.53 ± 0.82) emerged, but their abundance was low (Supporting Information Appendix D1). In the airborne compartment, some hyperparasitoids and parasitoids identified as Chalcidoidea (2.3 ± 2.8) and Diapriidae (5.1 ± 3.4) emerged (Supporting Information Appendix D2). All entomological taxa sampled were considered in this analysis, except for hoverflies that made up, surprisingly compared with Raymond et al. (2014), only four individuals captured in total.

The mean predation rate over the two exposure periods varied depending on the sentinel prey concerned. The highest rate was found for aphids on the ground (0.85 ± 0.12), followed by *Ephestia* eggs in the crop (0.75 ± 0.08) and weed seeds on the ground (0.66 ± 0.17). The lowest rate was found for aphids in the crop, which were about three times less predated than other sentinel preys (0.26 ± 0.12). Predation rates for each of the two sessions are listed in Supporting Information Appendix D3. Sentinel prey cards exposing aphids did not reveal different predation rates between the two periods, whereas prey cards with *Ephestia* eggs and weed seeds showed higher predation rates in the second period. Correlations between the four types of prey cards ranged between 0.03 and 0.52 (Pearson's rho), and were not significant, except between aphids in the crop and aphids on the ground (Supporting Information Appendix C2).

In the following, we first present the results obtained using the complete data set. Second, we describe the differences observed between the complete season and the beginning of the spring season, that is, the first four emergence sampling periods and the first session of sentinel prey cards.

Prey cards and natural enemies in the ground compartment

The predation rate on aphids in the ground compartment was significantly positively influenced by the abundance of emerged carabid beetles, and by the cumulated tillage depth (Figure 1, Supporting Information Appendix E1), whereas the proportion of winter crops had a significant negative effect. The weed seed predation rate was not influenced by any factor considered in this study. The abundance of emerged Staphylinidae did not influence any predation rates
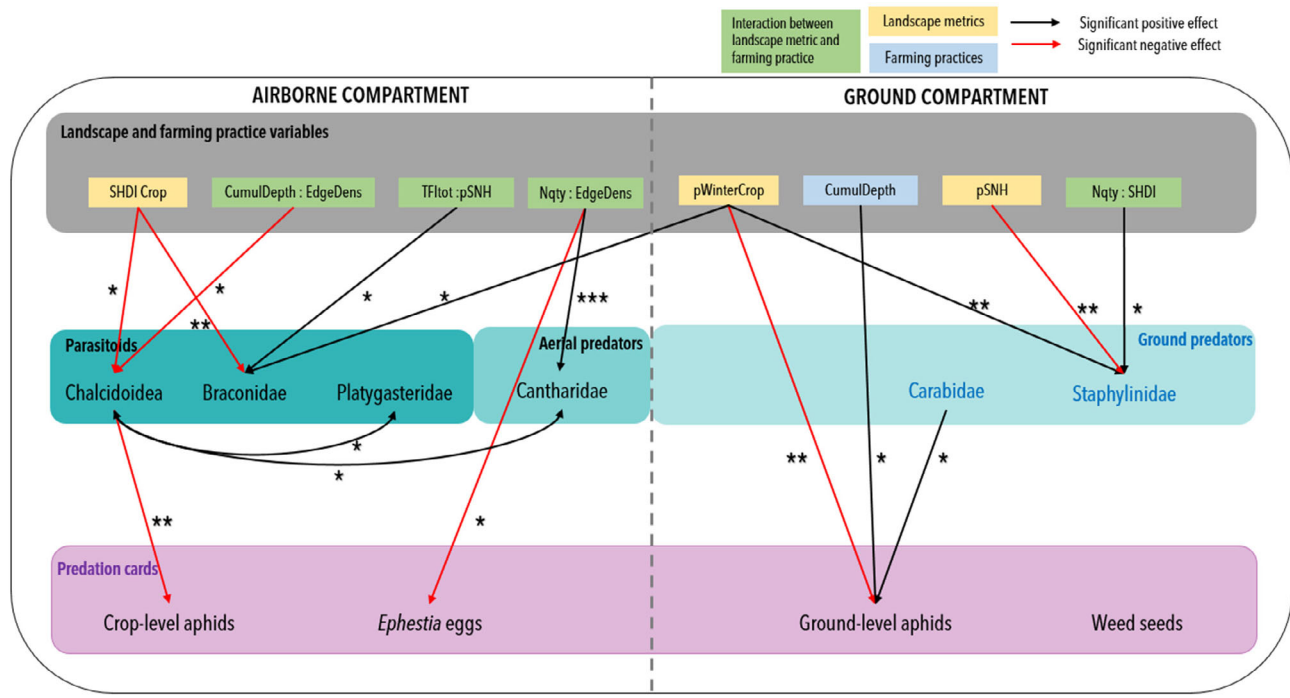
FIGURE 1 Effects of landscape and farming practices on the abundance of emerged natural enemies and their effects on biological control in the ground and airborne compartments measured using sentinel prey cards. Black arrows represent positive effects of variables or interactions between two variables, and red arrows represent negative effects. All the arrows show a significant effect from multi-model analysis based on GLM. Yellow rectangles correspond to landscape variables; blue rectangles correspond to farming practice variables; green rectangles correspond to interactions between one landscape and one farming practice variable. * p-value <0.05; ** p-value <0.01; *** p-value <0.001. Abbreviations used for explanatory variables are explained in Table 1. See Supporting Information Appendices E1, E2, F1 and F2 for complete results

measured using the two sentinel prey cards placed on the ground (Figure 1, Supporting Information Appendix E1).

The proportion of SNH significantly negatively influenced the abundance of emerged Staphylinidae (Figure 1, Supporting Information Appendix E2). In addition, the proportion of winter crops and the interaction between the quantity of nitrogen and the SHDI significantly and positively affected the abundance of emerged Staphylinidae (Figure 1, Supporting Information Appendix E2). This interaction indicates that smaller quantities of nitrogen had a significant positive effect on Staphylinidae abundance when the SHDI was low. The abundance of emerged Carabidae was not influenced by any landscape metrics or farming practices considered in this analysis (Figure 1, Supporting Information Appendix E2).

Prey cards and natural enemies in the airborne compartment

The predation rate of aphids present in the crop was significantly and negatively influenced by the abundance of emerged Chalcidoidea parasitoids (Supporting Information Appendix F2). The predation rate of *Ephestia* eggs was significantly and negatively affected by the interaction between quantity of nitrogen and edge density (Supporting Information Appendix F2). This interaction indicates that edge density had

a positive effect when the quantity of nitrogen in the crop fields was low.

The abundance of emerged Chalcidoidea parasitoids was significantly negatively affected by crop diversity (SHDI crop) and by the interaction between cumulated tillage depth and edge density (Figure 1, Supporting Information Appendix F2). This interaction indicates that the edge density had a significant positive effect in the case of low cumulated tillage depth. The abundance of emerged Braconidae was significantly negatively affected by the crop SHDI and positively affected by the proportion of winter crops (Figure 1, Supporting Information Appendix F2). There was also a significant interactive effect between the total TFI and the proportion of SNH, indicating that the proportion of SNH had a significant positive effect when the total TFI was high. The last group of parasitoids belonged to the family Platygasteridae and its abundance was not influenced by landscape metrics or farming practices (Figure 1, Supporting Information Appendix F2). The only predator group identified in the airborne compartment was the family Cantharidae, which was significantly affected by the interaction between the quantity of nitrogen and edge density, indicating edge density had a significant positive effect when the nitrogen quantity was high (Figure 1, Supporting Information Appendix F2).

Relationships between taxa of natural enemies were significant. Abundances of emerged Chalcidoidea and Platygasteridae were

correlated, as were abundances of emerged Chalcidoidea and Cantharidae (Figure 1, Supporting Information Appendix F2).

Hyperparasitoids and parasitoids of natural enemies in both compartments

Whether in the ground or the airborne compartment, the emerged taxonomic groups of hyperparasitoids and parasitoids of natural enemies had no effect on the abundance of emerged natural enemies (Supporting Information Appendices E2, F2).

The abundance of hyperparasitoids and parasitoids of groups of natural enemies was significantly influenced by interactions between landscape metrics and farming practices (Figure 2, Supporting Information Appendix G). The interaction between cumulated tillage depth and crop diversity had a significant negative effect on the abundance of emerged Chalcidoidea and a positive effect on Proctotrupidae (Figure 2, Supporting Information Appendix G). The interaction between cumulated tillage depth and the proportion of winter crops had a significant negative effect on the abundance of emerged Proctotrupidae (Figure 2, Supporting Information Appendix G). The abundance of emerged Diapriidae was significantly negatively influenced by the interaction between the total TFI and the edge density or the proportion of SNH. Another positive effect on the abundance of emerged Diapriidae was the interaction between nitrogen quantity and the proportion of winter crops (Figure 2, Supporting Information Appendix G).

Comparison between the beginning of the season and the complete season

The analysis carried out using the data from the beginning of the spring season (Supporting Information Appendices H1, H2) did not differ markedly from the analysis of all six sampling periods (Figure 1, Figure 2). For instance, in both, ground beetles were found to have a positive effect on aphid predation. A main difference was the positive effect of edge density on weed seed predation not observed in complete season analysis. The general effects of interactions between pairs landscape metrics and farming intensity variables on the different arthropod families remained similar. However, the exact variable involved in these interactions varied. Details concerning these results are presented in Supporting Information Appendices E2 and F2.

DISCUSSION

Contribution of emerged natural enemies to conservation biological control

Assessing CBC is complex because it involves multiple pests as well as many families of natural enemies. Our results reveal a diversity of responses measured using a set of complementary (noncorrelated) sentinel prey cards.

One of our main results was that emerged carabid beetles contributed to the biological control of aphids on the ground in spring, whereas
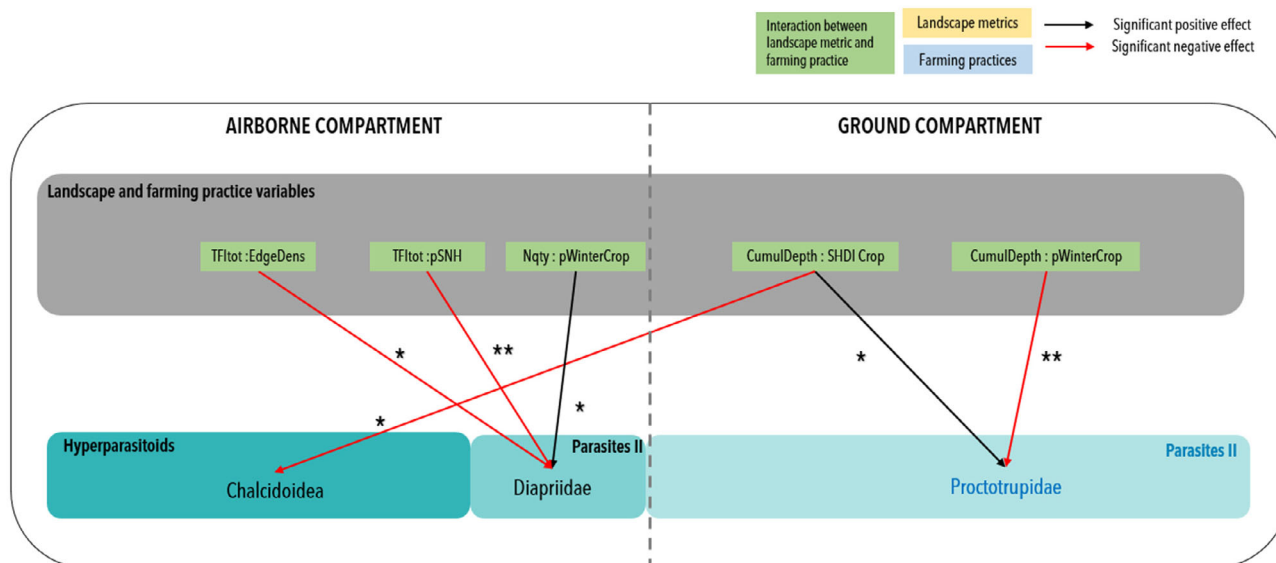

FIGURE 2 Effects of landscape and farming practices on emerged hyperparasitoids and parasitoids of natural enemies and their influence on the abundance of natural enemies in the ground and airborne compartments. Black arrows represent positive effects of variables or interactions between two variables, and red arrows represent negative effects. All the arrows showed a significant effect in the multi-model analysis based on GLM. Yellow rectangles correspond to landscape variables; blue rectangles correspond to farming practice variables (but none of the landscape or agricultural practice variables had a significant effect alone); green rectangles correspond to interactions between one landscape and one farming practice variable. * *p*-value <0.05; ** *p*-value <0.01; *** *p*-value <0.001. Abbreviations used for the explanatory variables are explained in Table 1. See Supporting Information Appendix G for complete results

staphylinids did not (Figure 1). This result is consistent with several studies that have shown the importance of generalist predators such as carabid beetles for aphid control in cereal fields (Schmidt et al., 2003; Symondson et al., 2002). However, staphylinids feed on many other types of preys, not measured by the sentinel prey cards, including slugs, snails and mites (Birken & Cloyd, 2007; Douglas & Tooker, 2012; Orth et al., 1975), and were, by far, the most abundant natural enemies found in the emergence traps. These results suggest that staphylinids are particularly adapted to living conditions in cereal fields and may greatly contribute to biological pest control. Whether we considered the beginning or the complete spring season, the effect of carabid beetles on aphid cards was still significant (Figure 1 and Supporting Information Appendix H1). Therefore, emerging carabids could play an important role as they may already reduce pest populations in early spring and continue predation until the beginning of the summer. The contribution of emerged carabids did not disappear even though their population could have been diluted by incoming carabids due to spill over from SNH or other crop fields. Neither agricultural practices nor the landscape context influenced the abundance of emerging ground beetles in our study. The primary role of overwintering carabid for CBC in spring has already been found in earlier studies (Holland et al., 2005; Marrec et al., 2015). Especially, landscape configuration such as edge density and field size has shown positive effects on carabid functional diversity (Gallé et al., 2018, 2019; Gayer et al., 2021). However, landscape composition and the intensity of farming practices may also influence their abundance (Duflot et al., 2016).

The predation rate of weed seeds at the beginning of the season differed from the rate estimated for the complete season (Figure 1; Supporting Information Appendix H1). None of the emerging taxa had a significant effect on seed predation, but we detected an effect of the landscape based on edge density, suggesting a spill over of seed-eaters from outside the fields. However, a subset of the emerging carabid communities may also have contributed. We were unable to test this effect as species-level identification is required to identify granivorous species among a community dominated by generalist predators (Trichard et al., 2013). In addition, predation on *Ephestia* eggs was also positively affected by edge density when the quantity of nitrogen was lower, suggesting a potential spill over of natural enemies in small fields with lower fertilization inputs. This influence of fertilization is difficult to interpret in a mechanistic way but gives an idea of the influence of the intensity of practices on the studied taxa and on potential pest predation. These results suggest the value of smaller fields to promote biological control by spill over of natural enemies (Martin et al., 2019).

The predation of aphids exposed in the crop canopy decreased with an increase in the abundance of emerged Chalcidoidea parasitoids. Parasitoids are considered prey specialists, but parasitism cannot be measured using sentinel prey cards, so we did not measure the biocontrol activity of these taxa. This result may suggest competition between parasitoids and aphid predators in favour of parasitoids as previously found with hoverflies (Almohamad et al., 2008; Vialatte et al., 2017), thus suppressing the effect of predators and resulting in a lower measured predation rate. In addition, the abundance of parasitoids depends on the density of aphids. More parasitoids may be associated with higher aphid abundance in the fields, resulting in a dilution effect of the prey cards, which in this case would be less predated. Measurement of aphid population in field may have uncovered this mechanism but was not performed here.

A diversity of natural enemies emerged in cereal fields in spring

This study showed that a diverse range of taxa overwinter in cereal fields as varying abundances of 10 different taxa were observed. A study by Raymond et al. (2014) in the same region highlighted the overwintering of hoverflies (Diptera: Syrphidae), a major predator family involved in pest control, especially aphid control (Schmidt et al., 2003; Tenhumberg & Poehling, 1995). Surprisingly, we observed very few individual Syrphidae (10 in total), maybe because fluctuating meteorological conditions affected their winter survival rate and/or their overwintering strategies (Raymond et al., 2013). Other well-known natural enemies such as true bugs, lacewings, spiders or ladybird were not found in the emergence traps, showing they most likely do not overwinter in the crop fields (at least in the range of farming practices studied here).

We observed marked variability both in the abundance of emerging taxa and in the seasonality of their emergence (Supporting Information Appendices D1, D2). Individuals belonging to the family Platygasteridae only emerged during the two final sampling periods, that is, in the last 2 weeks of May, and at a very low rate, whereas most individuals of Cantharidae emerged in early spring (i.e., mid-March and the end of April). Differences in the timing of the emergence of the various taxonomic groups sampled are linked to their phenology and life traits. It may be an advantage for the continuity of CBC if several predators of the same pest are present in successive periods.

Conversely, the presence of taxa belonging to high trophic levels may be detrimental to the CBC, as the abundance of emerging natural enemies may be reduced by parasitism by their own enemies. Nevertheless, statistical analysis performed in both ground and airborne compartments showed no significant effects of emerging hyperparasitoids or parasitoids on the abundance of emerging natural enemies.

In the airborne compartment, different taxa of natural enemies in the same trophic level co-occurred, as the abundance of the Chalcidoidea family was significantly correlated with the abundance of emerged Platygasteridae and Cantharidae (Figure 1). This was not the case in the ground compartment. Such relationships could mean that some natural enemy families may depend on the abundance of the same pest prey in crop fields in autumn, and/or by the same wintering conditions offered by crop fields.

Farming intensity modulates the response of natural enemies to the landscape context

Some overwintering natural enemies appear to be particularly adapted to winter crops, favoured by a higher proportion of winter crops in

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the landscape, mainly cereal fields in the study area, or negatively influenced by the heterogeneity of the crop mosaic characterized by the diversity of crop covers. Such relationships refer to overwintering staphylinids and some parasitoid families, that is, Chalcidoidea and Braconidae. These results suggest that these emerging natural enemies are relatively independent from SNH or may even be negatively influenced by them, as was the case for emerging staphylinids (Figure 1). Chalcidoidea.

In both compartments, many interactions between landscape elements and farming practices had a significant effect on the abundance of natural enemies. This relates to earlier works showing that, on the one hand, field-scale practices such as soil cultivation and grass cutting have direct and indirect negative effects on generalist predators (Thorbek & Bilde, 2004). Similarly, soil tillage and pesticide treatment have been found to strongly reduce parasitoid populations during the overwintering period and at emergence (Rusch et al., 2011; Tscharntke et al., 2016). On the other hand, at the landscape scale, surrounding semi-natural elements and diverse crop mosaics provide life support functions for many natural enemies species (Bianchi et al., 2006; Landis et al., 2000; Sirami et al., 2019). In a recent study, Ricci et al. (2019) pointed out that the effects of the landscape context on biological control are modified by the intensity of local pesticide use. Therefore, we expected a negative effect of higher intensity of practices that would counteract a potential positive effect of landscape heterogeneity on the abundance of emerging natural enemy communities. Surprisingly, we found the opposite trend, with positive interaction between landscape heterogeneity and farming practices intensity. Higher proportion of SNH or higher crop diversity, combined with more intense farming practices, had positive effects on the abundance of several emerging natural enemies. Many taxa of natural enemies are sensitive to farming intensity, as reported in several reviews (e.g., Geiger et al., 2010; Letourneau et al., 2011; Tscharntke, Klein, et al., 2005). However, our result suggests that the natural enemies that overwinter within crop fields may not follow this rule and are adapted to conventional farming practices. They may even benefit from lower inter-specific competition in landscapes where spill over is reduced (positive effect of high intensive practices in complex landscape). The high adaptive potential of natural enemy that overwinter in crop fields does not negate the importance of the spill over of natural enemies from outside the field for CBC as we found positive effect of edge density on some predation rates in low-intensity fields.

CONCLUSION

The present study highlights the potential contribution of natural enemies that overwinter within crop fields to biological control in spring. Nevertheless, we observed varied responses depending on taxa and the type of the sentinel prey card, which illustrate the complexity of conservation biological control. Considering the trophic chains in two specific compartments (ground and airborne) allowed an overall understanding of natural enemy interactions between each

other's, with their own enemies, and their effects on biological pest control.

Overwintering natural enemies seem adapted to winter crops and associated intensive farming practices, and relatively independent from SNH. These taxa were more abundant when higher crop diversity and edge density at landscape level were associated with more intense farming practices at field scale. These results suggest a potential trade-off between the community of natural enemies that overwinter within the fields and those arriving from outside the fields (spill over), with potential consequences on biological control. Further studies using exclusion cages are now required to quantify the contribution of emerging natural enemies to biological pest control relative to spill-over processes.

Better qualification of the trophic interactions between the numerous taxa found in crop fields would also facilitate the understanding of biological control mechanisms in the future. Advances in barcoding should enable the specific identification of the different taxa, while metabarcoding would improve the diet analyses of natural enemies, thereby allowing progress in the functional description of arthropod communities found in crop fields.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Data S1. Supporting Information.

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