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Natural enemies emerging in cereal fields in spring may contribute to biological control

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Abstract

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.

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.

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 landscape-scale lower crop diversity and higher edge density in combination with higher local-scale farming intensities. This suggests that they represent a subset of species adapted to intensified farming systems. This study highlights a broad taxonomic range of emerging natural enemies and their potential contribution to local pest predation.

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

1. 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 homogenisation 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 generate species movements between complementary landscape elements, 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 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, et al., 2005). For instance, grassy strips near large arable fields provide perennial vegetation and overwintering sites for natural enemies such as beetles *i.e.* beetle banks (MacLeod et al., 2004; Thomas, 2000). Thus predators disperse more or less far into the crop, depending on the species, and participate to 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). In 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, fertilisation, 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 semi-natural habitats (Rusch, Binet, et al., 2016; Rusch, Chaplin-Kramer, et al., 2016), and local farming practices may control the positive effect of semi-natural habitats 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 of the landscape context on the emergence of natural enemies and their own parasitoids or predators in crop fields. We hypothesised 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.

2. 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. Post 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 appendix A.

2.1. 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 m^2, Soil Emergence trap 96 x 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, *i.e.* 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 in 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, *i.e.* ground or airborne (Table1). The total abundance of each family was determined in each field.

Table 1: Life history traits of overwintering arthropods sampled in the study. Each taxon sampled was categorised as predator or parasitoid, and as belonging to the ground or airborne compartment according to its potential predation activity.

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]

2.2. 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 have 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 have known limitations (McHugh et al., 2020; Meyer et al., 2017) but allow collecting standardized data.

Four complementary types of sentinel preys were placed to monitor diverse predation potential at 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 x 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 to 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.

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, 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 the 24th to 28th April and from the 29th of May to the 2nd of June 2017. The total size of the dataset was 60 predation rates (30 fields, 2 sessions).

2.3. 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 digitised 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 semi-natural habitats and the crop mosaic are described using 13 landscape metrics. First, woodlands, hedgerows and permanent grasslands were grouped to calculate the proportion of semi-natural habitats, their mean patch size, the length of their edges and the length of edges at the interface of semi-natural habitats and crop fields. Second, land-cover categories were used to characterize the heterogeneity of the semi-natural habitats: the proportion of wooded habitats, permanent grasslands, and the total length of hedgerows. To describe crop heterogeneity, land cover was categorised 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, while the total length of edges, *i.e.* 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, *i.e.* 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 fertilisation 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, *i.e.* 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 non-correlated variables representative of the landscape context and farming practices, using Pearson's coefficients (Appendix B.1; Appendix B.2). After considering correlations between variables five landscape metrics, and three farming intensity variables were kept for further analyses ((Table 2; Appendix C.1).

Table 2: Definition of the non-correlated landscape metrics and farming intensity measures used in the study. See 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]

2.4. Statistical analysis

First, Pearson’s coefficients were calculated between the four types of prey cards to identify possible redundancies in what they measure, *i.e.* 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 (ii) the first four sampling periods corresponding to the beginning of the spring season and that took place before to the first session of predation measurements. In both cases, we modelled the ground and airborne compartments separately, which correspond to 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, *i.e.* 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 were 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).

3. Results

Among the identified families, some were natural enemies and others known to be their own parasitoids. Parasitoids were identified at 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 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 (Appendix D.1), while, parasitoids belonging to the super-familie 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 (Appendix D.2).

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 (Appendix D.1). In the airborne compartment, some hyperparasitoids and parasitoids identified as Chalcidoidea (2.3 ± 2.8) and Diapriidae (5.1 ± 3.4) emerged (Appendix D.2). All entomological taxa sampled were considered in this analysis, except for hoverflies that made up, surprisingly compared to Raymond *et al.* (2014), only 4 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 Appendix D.3. 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 (Appendix C.2).

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, *i.e.* the first four emergence sampling periods and the first session of sentinel prey cards.

3.1. 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 (Fig. 1, Appendix E.1), while 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 measured using the two sentinel prey cards placed on the ground (Fig. 1, Appendix E.1).

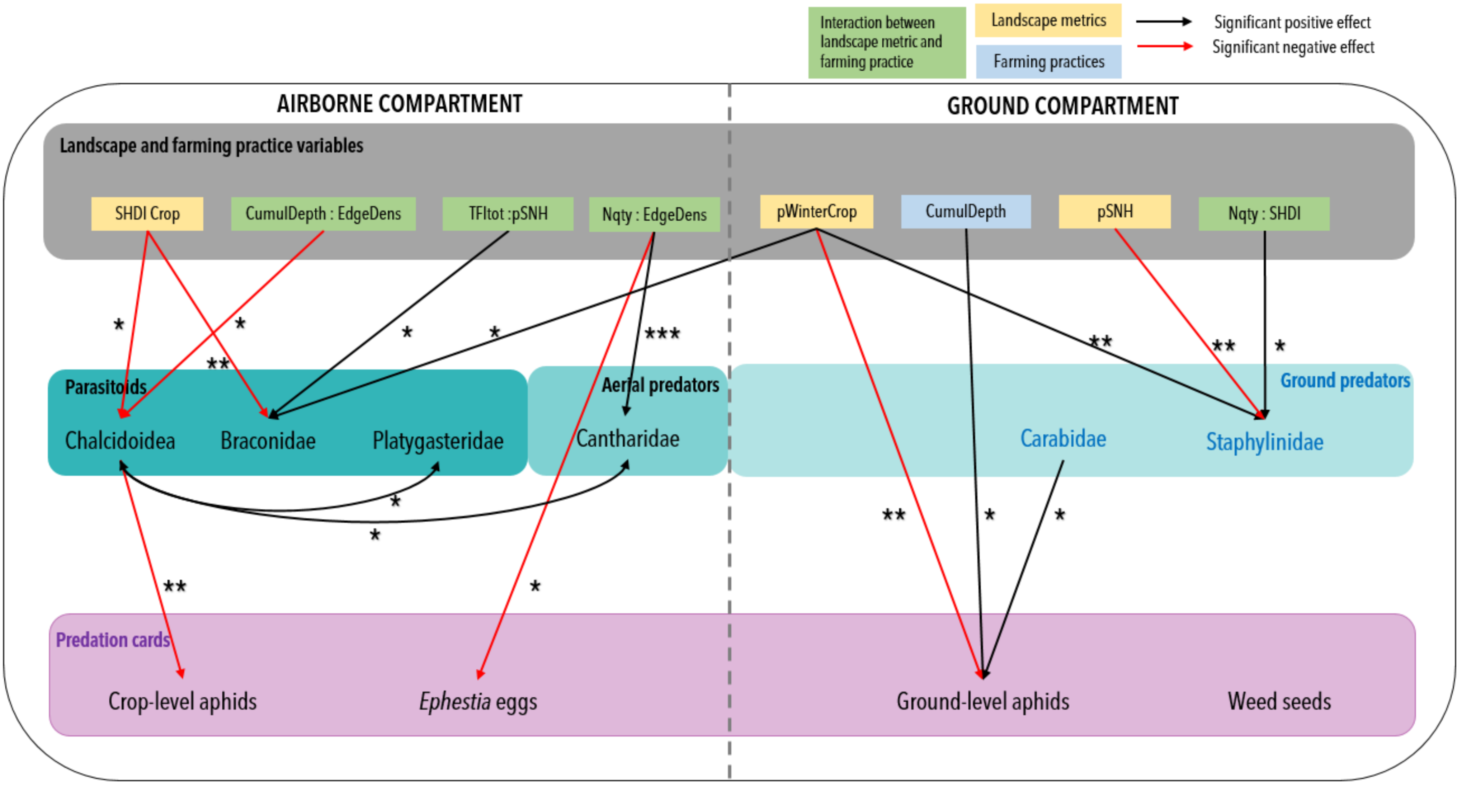

Figure 1: Effects of landscape and farming practices on the abundance of emerged natural enemies and their effects on biological control in the ground and airborne compartments measured using sentinel prey cards. Black arrows represent positive effects of variables or interactions between two variables, 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 appendix E.1, E.2, F.1 and F.2 for complete results.

The proportion of semi-natural habitats significantly negatively influenced the abundance of emerged Staphylinidae (Fig. 1, Appendix E.2). 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 (Fig. 1, Appendix E.2). 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 (Fig. 1, Appendix E.2).

3.2. 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 (Appendix F.2). The predation rate of *Ephestia* eggs was significantly and negatively affected by the interaction between quantity of nitrogen and edge density (Appendix F.2). 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 (Fig. 1, Appendix F.2). 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 (Fig. 1, Appendix F.2). There was also a significant interactive effect between the total TFI and the proportion of semi natural habitats, indicating that the proportion of semi natural habitats 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 (Fig. 1, Appendix F.2). 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 (Fig. 1, Appendix F.2).

Relationships between taxa of natural enemies, were significant. Abundances of emerged Chalcidoidea and Platygasteridae were correlated, as were abundances of emerged Chalcidoidea and Cantharidae (Fig. 1, Appendix F.2).

3.3. 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 (Appendix E.2; Appendix F.2).

The abundance of hyperparasitoids and parasitoids of groups of natural enemies was significantly influenced by interactions between landscape metrics and farming practices (Fig. 2, 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 (Fig. 2, 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 (Fig. 2, 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 semi natural habitats. Another positive effect on the abundance of emerged Diapriidae was the interaction between nitrogen quantity and the proportion of winter crops (Fig. 2, Appendix G).

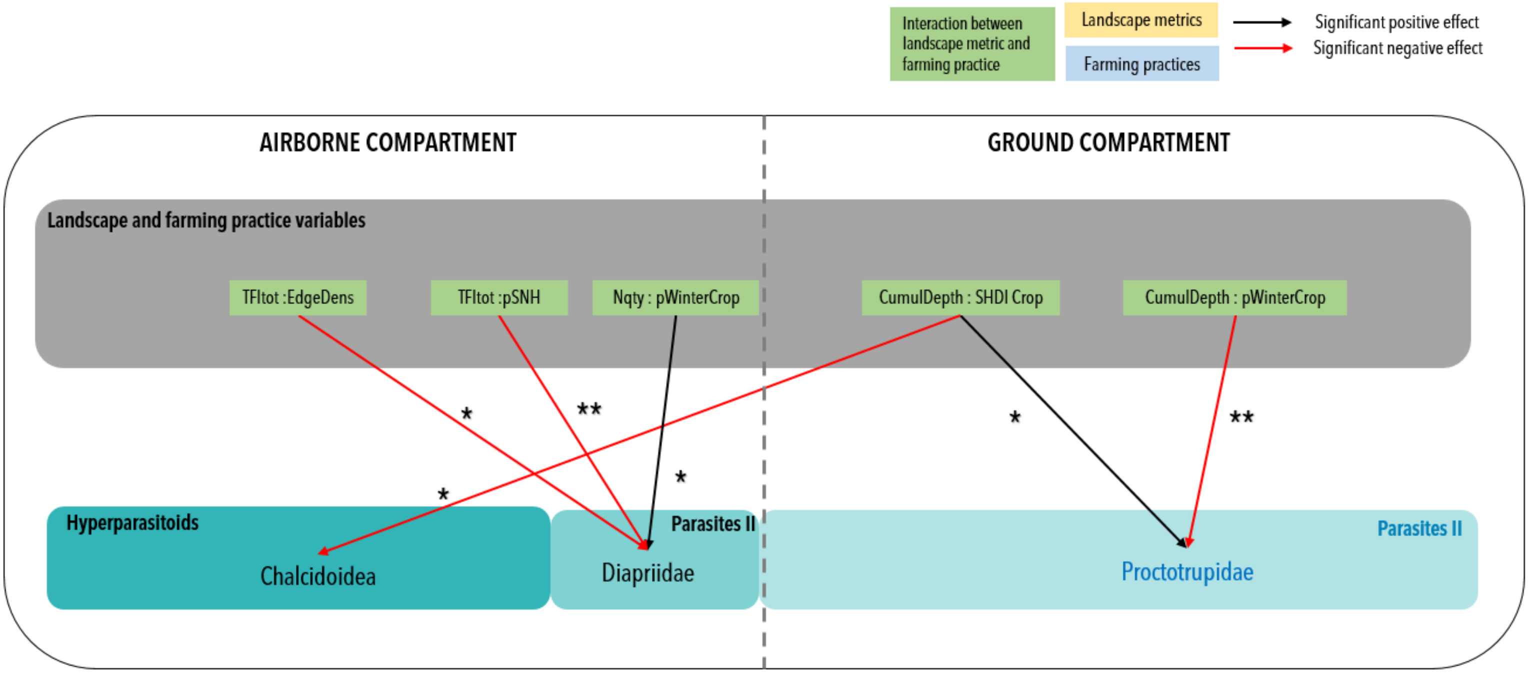

Figure 2: Effects of landscape and farming practices on emerged hyperparasitoids and parasitoids of natural enemies and their influence on the abundance of natural enemies in the ground and airborne compartments. Black arrows represent positive effects of variables or interactions between two variables, 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 appendix G for complete results.

3.4. 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 (Appendix H.1, Appendix H.2) did not differ markedly from the analysis of all six sampling periods (Fig. 1, Fig. 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 appendices E.2 and F.2.

4. Discussion

4.1. 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 (non-correlated) 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 staphylinids did not (Fig.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 type 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 (Fig. 1 and Appendix H.1). 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 semi-natural habitats 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 have 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 (Fig. 1; Appendix H.1). 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 seedeaters 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 give 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 spillover 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 uncover this mechanism but was not performed here.

4.2. 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 in here).

We observed marked variability both in the abundance of emerging taxa and in the seasonality of their emergence (Appendices D.1 and D.2). Individuals belonging to the family Platygasteridae only emerged during the two final sampling periods, *i.e.* in the last two 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 is 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 (Fig.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.

4.3. 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 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, *i.e.* Chalcidoidea and Braconidae. These results suggest that these emerging natural enemies are relatively independent from semi-natural habitats or may even be negatively influenced by them, as was the case for emerging staphylinids (Fig. 1). Chalcidoidea

In both compartments, many interactions between landscape elements and farming practices had a significant effect on the abundance of natural enemies. This relate 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 is 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 semi natural habitats 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 field.

5. 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 airborn) 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 semi-natural habitats. These taxa were more abundant when higher crop diversity and edge density at landscape-level was 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.

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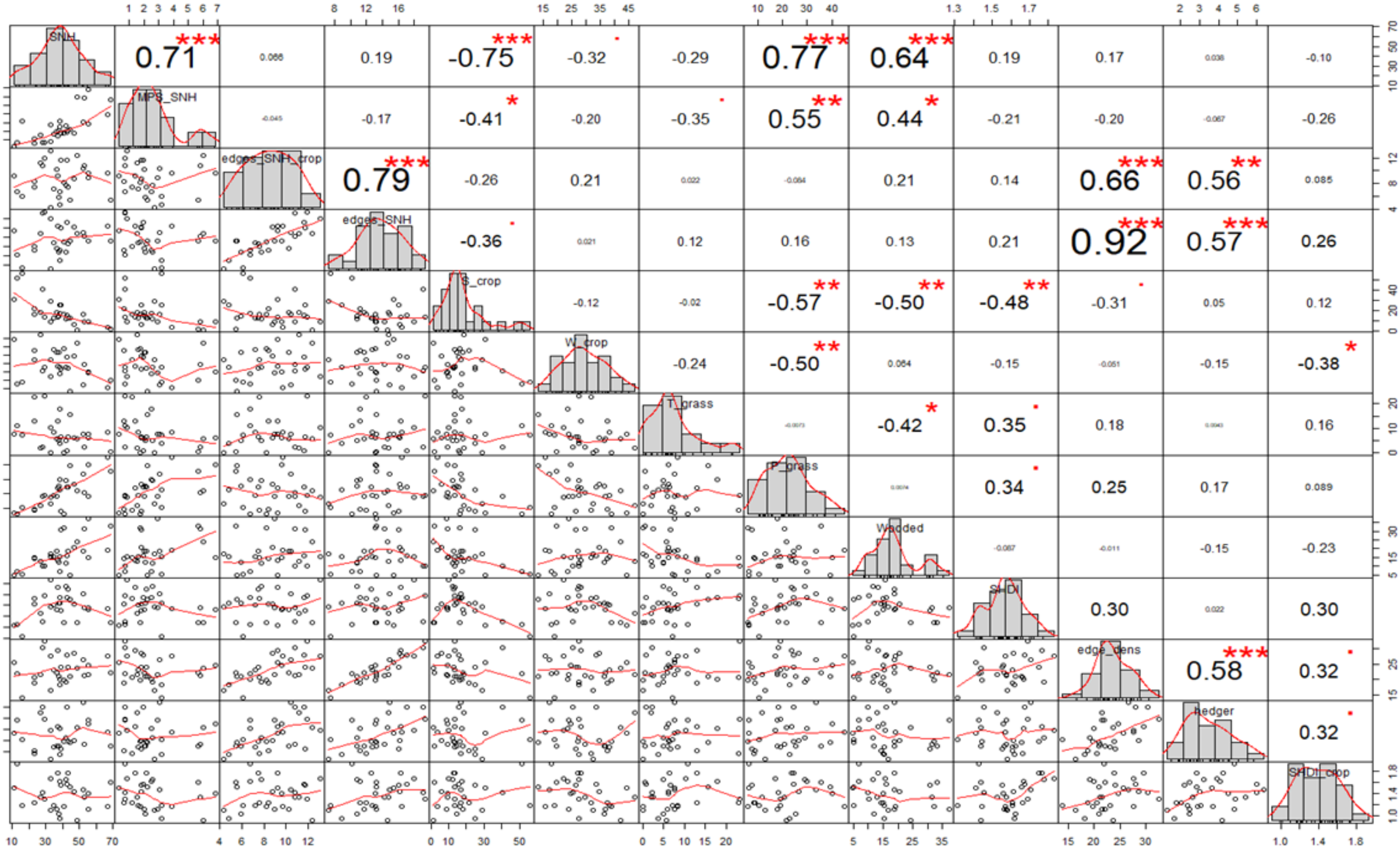
Appendices

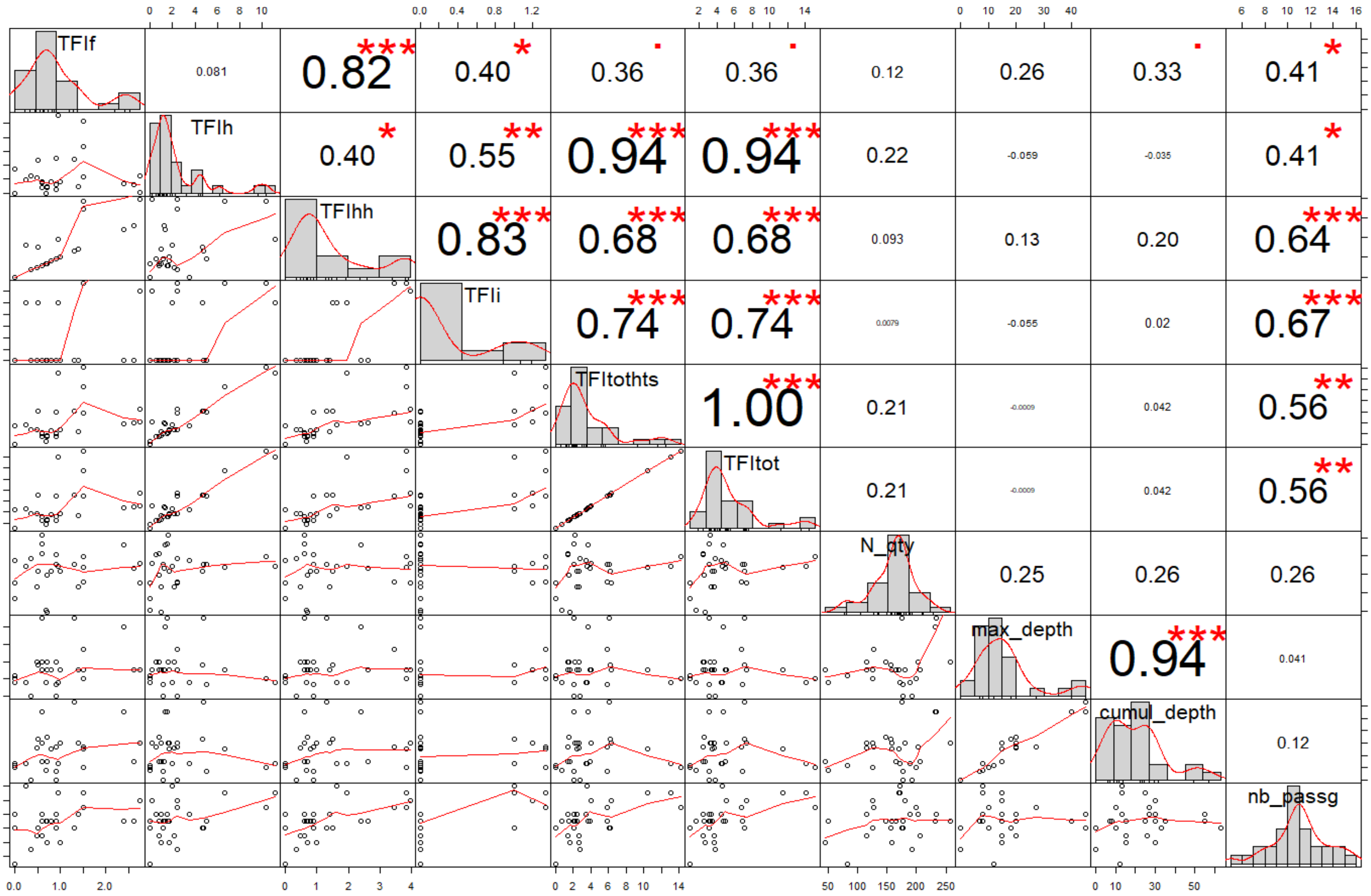
Appendix A: Complete list of variables calculated and surveyed, classified according to the latent variable to which they they belong, their unit of measure, and their range of variation.

	Latent variable (LV)	Manifest variable (MV)	Meaning	Unit	Mean [min-max]
	Agricultural production	Crop yield	estimated crop yield	Q/ha	71.4 [34.5;98.1]
AIRBORNE COMPARTMENT	Potential predation	Crop-level aphids	Predation rate of aphids at canopy position	ratio	0.26 [0.02;0.53]
		Ephestia eggs	Predation rate of lepidoptera eggs at canopy position	ratio	0.75 [0.60;0.95]
		Parasitoids	N° of parasitoids emerging	individual	12.1 [3.0;33.0]
		Abundance of Chalcidoidea (parasitoids)	N° of emerging individuals sampled	individual	9.7 [1;31.0]
		Abundance of Braconidae	N° of emerging individuals sampled	individual	2.4 [0;17.0]
		Abundance of Platygasteridae	N° of emerging individuals sampled	individual	0.41 [0 ; 5.0]
		Airborne predators	N° of predators emerging	individual	3.5 [0;19.0]
		Abundance of Cantharidae	N° of emerging individuals sampled	individual	3.5 [0;19.0]
		Airborne (Hyper)parasitoids	N° of hyperparasitoids or parasitoids II sampled	individual	6.0 [0;16.0]
		Abundance of Chalcidoidea (hyperparasitoids)	N° of emerging individuals sampled	individual	2.3 [0;11.0]
		Abundance of Diapriidae	N° of emerging individuals sampled	individual	5.2 [0;12.0]
GROUND COMPARTMENT	Potential predation	Ground-level aphids	Predation rate of aphids on the ground	ratio	0.85 [0.53;1]
		Weed seeds	Predation rate of seeds on the ground	ratio	0.66 [0.24;0.93]
		Predators on the ground	N° of predators emerging	individual	211.9 [48.0;548.0]
		Abundance of Carabidae	N° of emerging individuals sampled	individual	9.0 [0;59.0]
		Abundance of Staphylinidae	N° of emerging individuals sampled	individual	202.9 [43.0;547.0]
		(Hyper)parasitoids II on the ground	N° of hyperparasitoids or parasitoids II on the ground	individual	0.53 [0;3.0]
		Abundance of Proctotrupidae	N° of emerging individuals sampled	individual	0.53 [0;3.0]
	Farming intensity	Cumulated depth	Cumulated tillage depth	cm	22.2 [0;63.0]
		Maximum depth	maximum tillage depth	cm	15.8 [0;45.0]
		TFI.f	Treatment frequency index of fungicides	dose / ha	1.01 [0;2.75]
		TFI.h	Treatment frequency index of herbicides	dose / ha	2.5 [0;11.1]

		TFI.i	Treatment frequency index of insecticides	dose / ha	0.31 [0;1.33]
		TFI.hh	Total treatment frequency index not including herbicides	dose / ha	0.90 [0;3.95]
		TFItot	Total treatment frequency index including all types of treatments	dose / ha	4.9 [1;15.2]
		Nqty	Quantity of nitrogen provided in liquid form	kg / ha	162.4 [46.0;257.9]
		N° passage	Number of treatments	N°	11.1 [5.0;16.0]
	Landscape heterogeneity	% SNH	Proportion of semi-natural habitats	%	38.6 [11.2;68.8]
		MPS SNH	Mean patch size of semi-natural habitats	ha	2.5 [0.3;6.8]
		Edges SNH	Total length of SNH edges	km	13.5 [7.2;19.4]
		Edges SNH-crop	Length of edges between SNH and crops	km	8.7 [4.4;13.1]
		% S. crop	Proportion of spring crops	%	18.1 [1.3;56.0]
		% W. crop	Proportion of winter crops	%	29.1 [13.3;47.2]
		% T. grass	Proportion of temporary grasslands	%	7.7 [0;23.2]
		% P. grass	Proportion of permanent grasslands	%	21.0 [5.9;45.1]
		% Wooded	Proportion of wooded habitats	%	16.9 [4.7;37.3]
		SHDI	Shannon diversity index on % of land cover classes	-	1.6 [1.3;1.8]
		Edge density	Total length of edges – all types of edges types included	km/ha	23.2 [13.9;32.5]
		Hedgerows	Total length of hedgerows	km	3.5 [1.3;6.4]
		SHDI crops	Shannon diversity index of crops	-	1.37 [0.90;1.93]



Appendix B.1: Pairwise Pearson's correlations between landscape variables. * *p-value* < 0.05*;* ** *p-value* <0.01*;* *** *p-value* <0.001.



Appendix B.2: Pairwise Pearson's correlations between farming practice variables. * *p-value* < 0.05*;* ** *p-value* < 0.01*;* *** *p-value* < 0.001.

Appendix C.1: Pairwise Pearson's correlations between the explanatory variables used in the study.

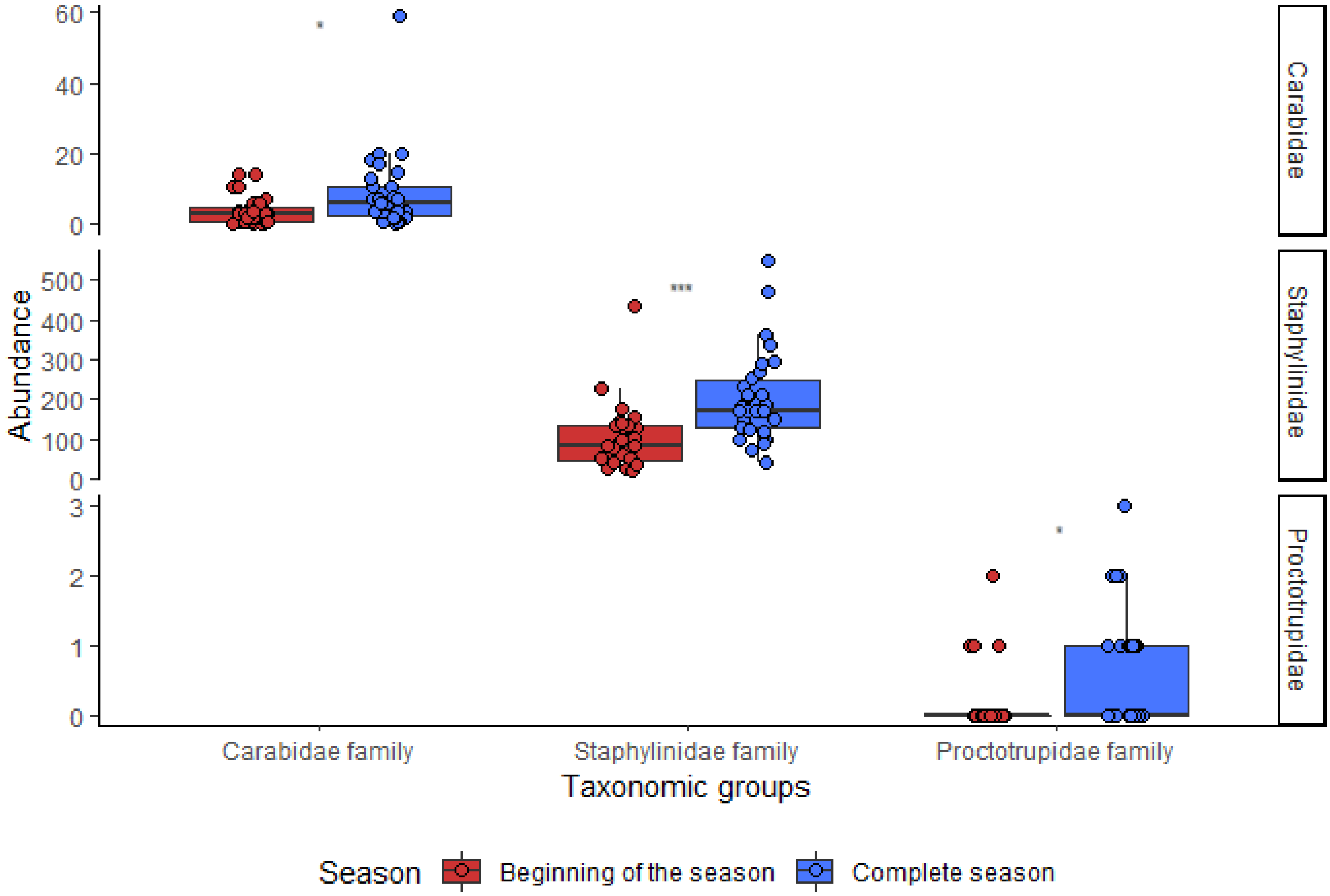
SHDI: Shannon diversity index of landscape in 1km² buffer; SHDI crop: Shannon diversity index of crops; pSNH: proportion of land covered by semi-natural habitats; pWinterCrop: proportion of winter crops similar; Edge dens: total length of edges including all types of edges; Cumul depth: cumulated tillage depth; N qty: quantity of nitrogen provided in liquid form; TFItot: total treatment frequency index (insecticides, fungicides and herbicides included).

	SHDI	SHDI crop	pSNH	pWinterCrop	Edge dens	Cumul depth	N qty
SHDI crop	0.30						
pSNH	0.19	-0.10					
pWinterCrop	-0.15	-0.38	-0.32				
Edge dens	0.30	0.32	0.17	-0.05			
Cumul depth	-0.05	0.08	-0.004	0.04	0.05		
N qty	-0.16	-0.11	-0.25	0.21	0.02	0.26	
TFItot	-0.29	-0.42	-0.17	0.46	-0.23	0.04	0.21

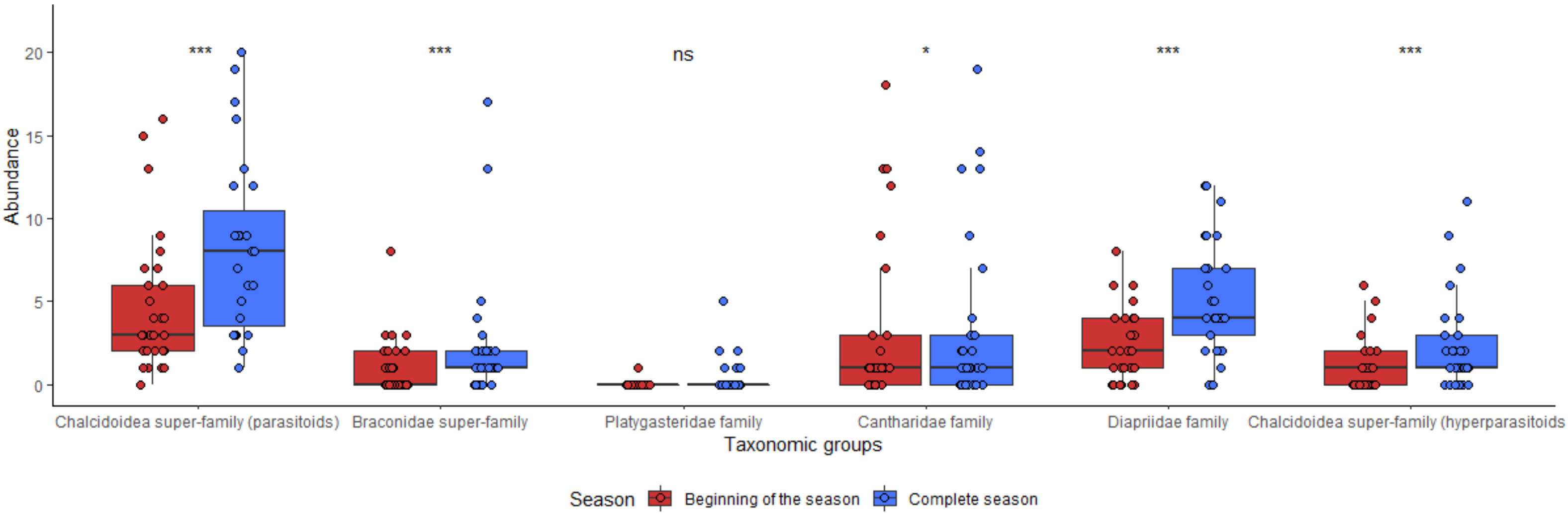
Appendix C.2: Pearson's correlations between predation rates.

Numbers in **bold** correspond to correlations among data for the complete season; numbers in *italics* correspond to the correlations among data for the beginning of the spring season. * *p-value* <0.05; ** *p-value* <0.01; *** *p-value <0.001*.

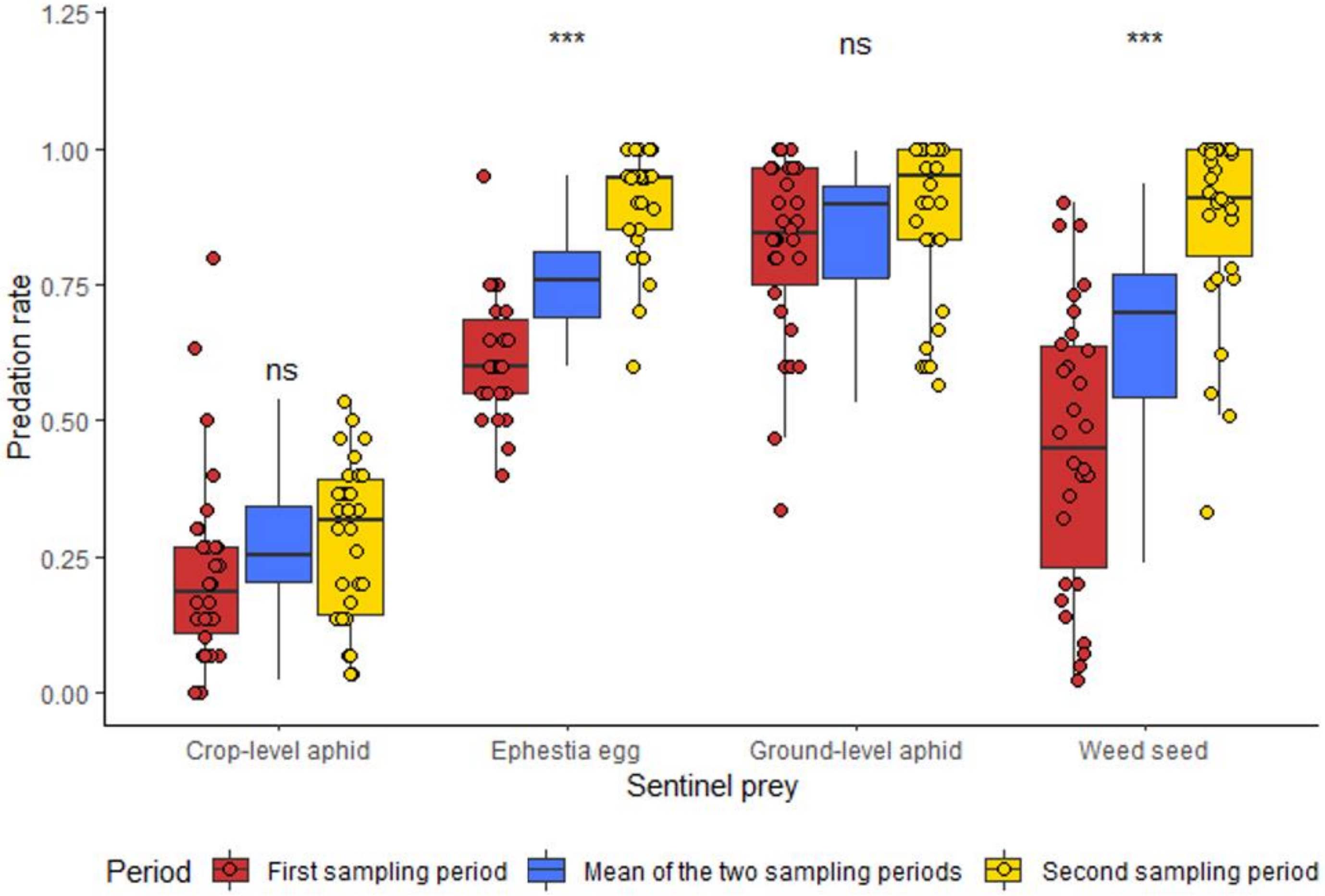
	Crop-level aphids	Ephestia eggs	Ground-level aphids
Ephestia eggs	**0.17** *0.23*		
Ground-level aphids	**0.52**** *0.48***	**0.24** *0.24*	
Weed seeds	**0.03** *0.25*	**0.04** *0.33*	**-0.32** *-0.021*



Appendix D.1: Emerging natural enemies and their own enemies' abundance at the beginning of the season and throughout the season in the ground compartment. The emergence of these taxa at the beginning of the season corresponds to the abundances measured in the first four sampling periods (from the 15th of March to the 26th of April). The emergence of the taxa throughout the season corresponds to all six sampling periods (from the 15th of March to the 23rd of May). The significance of the difference between abundances across spring was tested with a pairwise Wilcoxon's test. * *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001; ns, not significant.



Appendix D.2: Emerging natural enemies of pests and abundance of their own enemies at the beginning of the season and throughout the season in the airborne compartment. The emergence of these taxa at the beginning of the season corresponds to the abundances measured in the first four sampling periods (from the 15th of March to the 26th of April). The emergence of the taxa throughout the season corresponds to all six sampling periods (from the 15th of March to the 23rd of May). The significance of the difference between abundances across spring was tested with a pairwise Wilcoxon's test. * *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001; ns, not significant



Appendix D.3: Predation rates observed on different prey sentinel cards in two sampling periods. The significance of the difference was tested between the predation rates evaluated in the first sampling period (from the 24th to the 28th of April) and in the second sampling period at the end of May (from the 29th of May to the 2nd of June) using a pairwise Wilcoxon's test.* *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001; ns, not significant.

Appendix E.1: Averaged estimated effects of the abundance of overwintering natural enemies, farming practices, landscape variables and their interactions on the two predation rates in the ground compartment. For each explanatory variable or interaction, the averaged coefficient value ± error standard (s.e.) and its level of significance are given. **Bold** values correspond to averaged estimated effects calculated for the complete season; values in *italics* correspond to those calculated with data at the beginning of the season.* *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001.

Ground compartment				
	Weed seed		Ground-level aphid	
effect	estimate	s.e.	estimate	s.e.
Staphylinidae	**0.0003** *0.0007*	**0.0003** *0.0006*	**-0.0008** *-0.0005*	**0.0005** *0.0007*
Carabidae	**0.002** *0.010*	**0.003** *0.01*	**0.009*** **_0.03*_**	**0.004** **_0.01_**
TFItot	**0.03** *0.12*	**0.04** *0.11*	**-0.05** *-0.001*	**0.07** *0.13*
CumulDepth	**-0.01** *0.001*	**0.03** *0.02*	**0.10*** *-0.007*	**0.05** *0.03*
Nqty	**-0.02** *-0.003*	**0.04** *0.01*	**0.05** *-0.0003*	**0.05** *0.01*
SHDI	**0.02** *-0.36*	**0.03** *1.63*	**0.03** *-0.15*	**0.06** *1.12*
SHDICrop	**-0.05** *-0.17*	**0.04** *0.59*	**0.08** *-0.06*	**0.05** *0.42*
pSNH	**0.06** *0.01*	**0.04** *0.006*	**-0.07** *0.003*	**0.05** *0.009*
pWinterCrop	**0.03** *-0.008*	**0.04** *0.02*	**-0.12*** *-0.01*	**0.05** *0.01*
EdgeDens	**0.02** _0.05*_	**0.03** *0.02*	**0.08** *-0.03*	**0.05** *0.03*
TFItot*SHDI	**-0.02** *-0.09*	**0.05** *0.17*	**0.009** *-0.07*	**0.07** *0.19*
TFItot * SHDICrop	**0.06** *0.008*	**0.05** *0.08*	**0.08** *-0.06*	**0.07** *0.09*
TFItot * pSNH	**-0.02** *-0.001*	**0.03** *0.001*	**0.03** *0.002*	**0.05** *0.001*
TFItot * pWinterCrop	**0.01** *0.003*	**0.05** *0.002*	**-0.04** *-0.0002*	**0.06** *0.003*
TFItot *EdgeDens	**-0.08** *-0.008*	**0.04** *0.004*	**-0.004** *-0.002*	**0.06** *0.005*
CumulDepth*SHDI	**0.02** *-0.005*	**0.04** *0.03*	**0.03** *0.03*	**0.05** *0.03*
CumulDepth*SHDICrop	**-0.05** *-0.005*	**0.03** *0.01*	**0.05** *0.01*	**0.04** *0.01*
CumulDepth*pSNH	**0.02** *-0.0001*	**0.03** *0.0002*	**0.003** *-0.0001*	**0.04** *0.0002*
CumulDepth*pWinterCrop	**0.03** *-0.0001*	**0.04** *0.0005*	**0.04** *-0.0001*	**0.05** *0.0004*
CumulDepth*EdgeDens	**0.02** *0.0005*	**0.05** *0.001*	**0.10** *0.002*	**0.06** *0.001*
Nqty*SHDI	**0.07** *0.01*	**0.04** *0.01*	**-0.02** *-0.01*	**0.06** *0.01*
Nqty*SHDICrop	**-0.002** *0.001*	**0.04** *0.005*	**0.02** *0.002*	**0.06** *0.005*
Nqty*pSNH	**0.01** *-0.00005*	**0.03** *0.0001*	**-0.01** *-0.0001*	**0.05** *0.0001*
Nqty*pWinterCrop	**0.04** *0.0001*	**0.03** *0.0001*	**-0.04** *0.00002*	**0.04** *0.0001*
Nqty*EdgeDens	**-0.03** *-0.0001*	**0.05** *0.0003*	**0.06** *0.0006*	**0.07** *0.0004*

Appendix E.2: Averaged estimated effects of emerging natural enemies, farming practices, landscape variables and their interactions on the overwintering beneficials that emerged in the ground compartment. For each explanatory variable or interaction, the averaged coefficient value ± error standard (s.e.) and its level of significance are given. Numbers in **bold** correspond to averaged estimated effects calculated for the complete season; numbers in *italics* correspond to those calculated for the beginning of the season.* *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001.

	Staphylinidae			Carabidae	
effect	estimate	s.e.	effect	estimate	s.e.
Proctotrupidae	**0.07** *0.07*	**0.13** *0.29*	Proctotrupidae	**-0.16** *0.04*	**0.22** *0.39*
Carabidae	**0.01** *0.0361*	**0.008** *0.0338*	Staphylinidae	**0.003** *0.002*	**0.002** *0.002*
TFItot	**0.02** *0.01*	**0.12** *0.20*	TFItot	**-0.18** *-0.02*	**0.26** *0.27*
CumulDepth	**-0.04** *-0.11*	**0.09** *0.15*	CumulDepth	**-0.19** *-0.36*	**0.19** *0.20*
Nqty	**0.04** *0.18*	**0.10** *0.13*	Nqty	**-0.10** *-0.03*	**0.18** *0.21*
SHDI	**-0.06** *0.09*	**0.10** *0.14*	SHDI	**0.11** *0.02*	**0.19** *0.21*
SHDICrop	**-0.13** *-0.15*	**0.10** *0.14*	SHDICrop	**0.07** *-0.23*	**0.20** *0.20*
pSNH	**-0.25**** *-0.19*	**0.09** *0.13*	pSNH	**0.13** *0.13*	**0.21** *0.19*
pWinterCrop	**0.25**** *0.09*	**0.09** *0.14*	pWinterCrop	**-0.25** *-0.04*	**0.21** *0.20*
EdgeDens	**-0.16** *-0.26*	**0.11** *0.15*	EdgeDens	**-0.11** *-0.18*	**0.23** *0.22*
TFItot*SHDI	**0.20** *0.38**	**0.12** *0.16*	TFItot*SHDI	**-0.30** *0.12*	**0.24** *0.27*
TFItot*SHDICrop	**0.12** *0.05*	**0.14** *0.18*	TFItot*SHDICrop	**-0.11** *0.20*	**0.27** *0.28*
TFItot*pSNH	**-0.15** *-0.05*	**0.09** *0.13*	TFItot*pSNH	**0.19** *-0.13*	**0.20** *0.20*
TFItot*pWinterCrop	**-0.01** *-0.33**	**0.12** *0.17*	TFItot*pWinterCrop	**-0.15** *0.04*	**0.25** *0.28*
TFItot*EdgeDens	**-0.01** *0.07*	**0.13** *0.18*	TFItot*EdgeDens	**0.11** *-0.27*	**0.25** *0.28*
CumulDepth*SHDI	**0.02** *0.04*	**0.11** *0.15*	CumulDepth*SHDI	**-0.22** *-0.17*	**0.21** *0.22*
CumulDepth*SHDICrop	**-0.11** *-0.12*	**0.11** *0.13*	CumulDepth*SHDICrop	**0.06** *0.01*	**0.21** *0.21*
CumulDepth*pSNH	**-0.09** *-0.13*	**0.08** *0.10*	CumulDepth*pSNH	**-0.10** *0.003*	**0.16** *0.17*
CumulDepth*pWinterCrop	**0.20ns** *0.17*	**0.13** *0.16*	CumulDepth*pWinterCrop	**-0.14** *0.04*	**0.28** *0.25*
CumulDepth*EdgeDens	**-0.17** *-0.36**	**0.12** *0.16*	CumulDepth*EdgeDens	**-0.43** *-0.38*	**0.23** *0.25*
Nqty*SHDI	**0.22*** *0.13*	**0.11** *0.15*	Nqty*SHDI	**-0.33** *0.68**	**0.19** *0.30*
Nqty*SHDICrop	**-0.17** *-0.06*	**0.11** *0.15*	Nqty*SHDICrop	**0.15** *0.21*	**0.21** *0.22*
Nqty*pSNH	**0.01** *-0.01*	**0.09** *0.12*	Nqty*pSNH	**-0.24** *0.14*	**0.17** *0.20*
Nqty*pWinterCrop	**-0.02** *-0.02*	**0.09** *0.12*	Nqty*pWinterCrop	**0.22** *-0.05*	**0.17** *0.19*
Nqty*EdgeDens	**-0.02** *0.22*	**0.14** *0.19*	Nqty*EdgeDens	**0.27** *-0.10*	**0.24** *0.30*

Appendix F.1: Averaged estimated effects of the abundance of overwintering natural enemies, farming practices, landscape variables and their interactions on the two predation rates at the crop level in the airborne compartment. For each explanatory variable or interaction, the averaged coefficient value ± error standard (s.e.) and its level of significance are given. Values in **bold** correspond to averaged estimated effects calculated for the complete season; values in *italics* correspond to those calculated with data at the beginning of the spring season.* *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001.

Airborne compartment				
	Ephestia egg		Crop-level aphid	
effect	estimate	s.e.	estimate	s.e.
Chalcidoidea	__-0.00060__ _-0.0037_	__0.003__ _0.0063_	__-0.011**__ _-0.018*_	__0.004__ _0.009_
Braconidae	__-0.006__ _-0.01_	__0.005__ _0.015_	__-0.008__ _-0.014_	__0.006__ _0.021_
Platygasteridae	__-0.03__ -	__0.021__ -	__0.001__ -	__0.026__ -
Cantharidae	__0.006__ _0.008_	__0.004__ _0.036_	__0.005__ _0.002_	__0.005__ _0.008_
TFItot	__-0.04__ _-0.02_	__0.03__ _0.03_	__-0.03__ _-0.03_	__0.03__ _0.05_
CumulDepth	__-0.006__ _0.02_	__0.02__ _0.03_	__0.0003__ _0.008_	__0.03__ _0.04_
Nqty	__-0.001__ _-0.01_	__0.02__ _0.03_	__-0.02__ _0.002_	__0.02__ _0.04_
SHDI	__0.001__ _-0.01_	__0.02__ _0.03_	__0.02__ _0.04_	__0.02__ _0.04_
SHDICrop	__-0.006__ _-0.04_	__0.02__ _0.02_	__0.02__ _-0.002_	__0.03__ _0.05_
pSNH	__0,0002__ _0.02_	__0.02__ _0.03_	__0.0001__ _0.02_	__0.03__ _0.04_
pWinterCrop	__0.01__ _-0.02_	__0.02__ _0.02_	__0.002__ _-0.04_	__0.03__ _0.04_
EdgeDens	__0.009__ _0.01_	__0.02__ _0.03_	__-0.001__ _0.001_	__0.02__ _0.04_
TFItot*SHDI	__0.01__ _0.009_	__0.02__ _0.06_	__-0.05__ _0.0001_	__0.03__ _0.05_
TFItot * SHDICrop	__0.01__ _0.04_	__0.03__ _0.03_	__-0.05__ _0.02_	__0.04__ _0.08_
TFItot * pSNH	__-0.03__ _-0.03_	__0.02__ _0.03_	__0.02__ _-0.0004_	__0.03__ _0.04_
TFItot * pWinterCrop	__0.04__ _0.04_	__0.02__ _0.03_	__0.004__ _-0.02_	__0.03__ _0.05_
TFItot *EdgeDens	__-0.02__ _-0.02_	__0.02__ _0.03_	__-0.005__ _-0.01_	__0.03__ _0.05_
CumulDepth*SHDI	__-0.01__ -0.01	__0.02__ 0.03	__-0.02__ -0.003	__0.03__ 0.04
CumulDepth*SHDICrop	__0.01__ _0.02_	__0.02__ _0.02_	__-0.02__ _-0.02_	__0.02__ _0.04_
CumulDepth*pSNH	__-0.02__ _-0.01_	__0.01__ _0.02_	__-0.02__ _0.01_	__0.02__ _0.03_
CumulDepth*pWinterCrop	__0.01__ _0.02_	__0.02__ _0.04_	__0.02__ _0.02_	__0.03__ _0.04_
CumulDepth*EdgeDens	__-0.02__ _-0.02_	__0.02__ _0.03_	__-0.02__ _0.02_	__0.03__ _0.05_
Nqty*SHDI	__0.002__ _0.02_	__0.02__ _0.02_	__-0.005__ _0.02_	__0.03__ _0.04_
Nqty*SHDICrop	__0.02__ _0.05_	__0.02__ _0.02_	__0.01__ _0.03_	__0.03__ _0.04_
Nqty*pSNH	__-0.02__ _-0.02_	__0.02__ _0.03_	__0.02__ _0.01_	__0.02__ _0.03_
Nqty*pWinterCrop	__0.02__ _0.02_	__0.02__ _0.03_	__-0.04__ _-0.03_	__0.02__ _0.03_
Nqty*EdgeDens	__-0.06*__ _-0.08_	__0.03__ _0.006_	__0.06__ _0.09_	__0.04__ _0.06_

Appendix F.2: Averaged estimated effects of hyperparasitoids and parasitoids of natural enemies, farming practices, landscape variables and their interactions on the abundance of overwintering natural enemies in the airborne compartment. For each explanatory variable or interaction, the averaged coefficient value ± error standard (s.e.) and its level of significance are given. Values in **bold** correspond to averaged estimated effects calculated for the complete season; values in *italics* correspond to those calculated at the beginning of the season.* *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001.

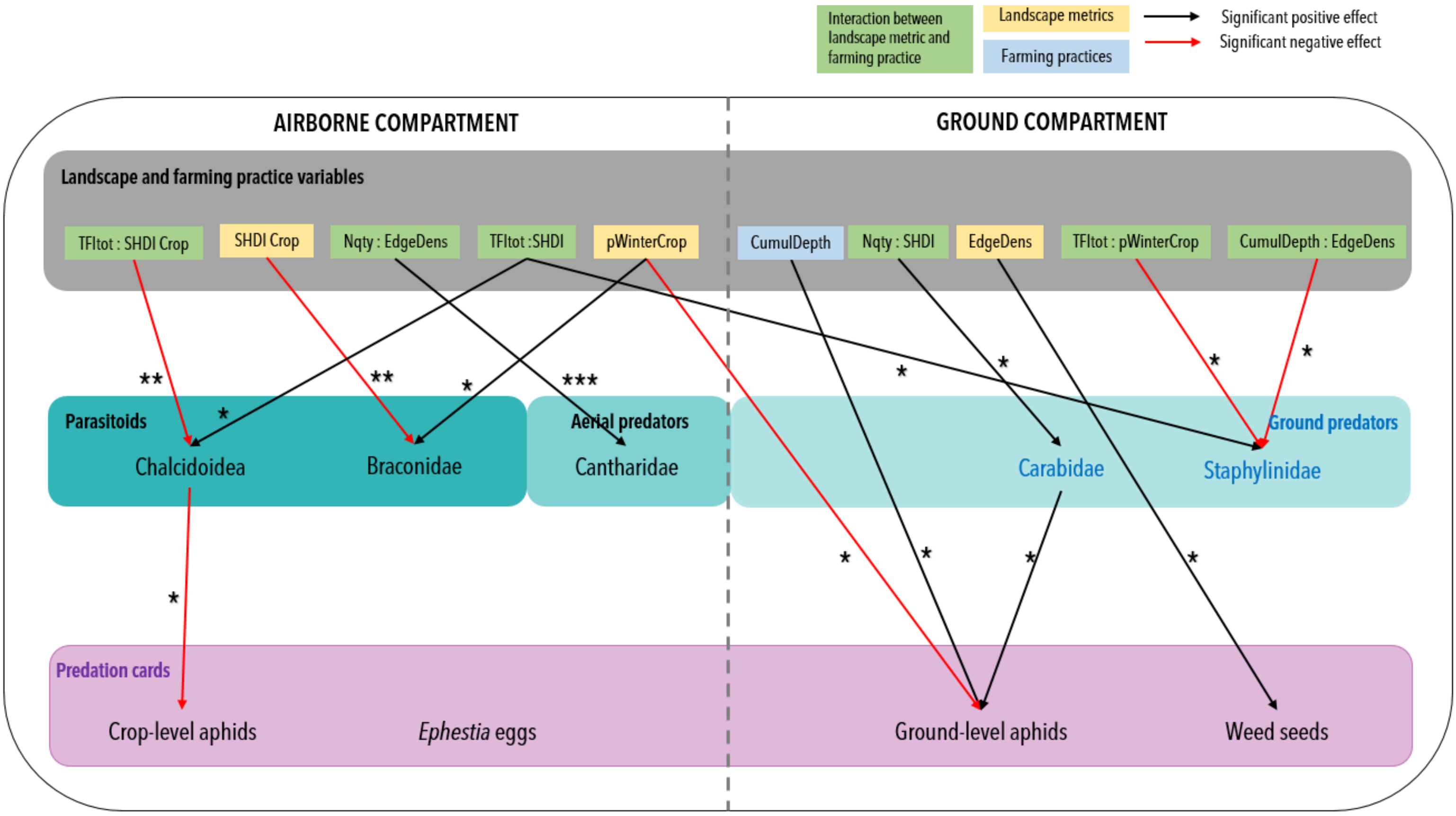
	Chalcidoidea (parasitoids)			Braconidae			Platygasteridae			Cantharidae	
effect	estimate	s.e.	effect	estimate	s.e.	effect	estimate	s.e.	effect	estimate	s.e.
Chalcidoidea (Hyperparasitoids)	__0.05__ _0.04_	__0.04__ _0.09_	Chalcidoidea (Hyperparasitoids)	__0.02__ _-0.01_	__0.08__ _0.20_	Chalcidoidea (Hyperparasitoids)	__0.07__ -	__0.20__ -	Diapriidae	__0.02ns__ _0.12ns_	__0.07__ _0.12_
Braconidae	__-0.02__ _-0.20_	__0.04__ _0.11_	Chalcidoidea	__-0.02__ _-0.09_	__0.05__ _0.11_	Chalcidoidea	__0.12__* -	__0.05__ -	Braconidae	__0.08ns__ _0.20ns_	__0.06__ _0.12_
Platygasteridae	__0.23__* -	__0.10__ -	Platygasteridae	__-0.43__ -	__0.43__ -	Braconidae	__-0.76__ -	__0.56__ -	Chalcidoidea	__0.07ns__ _0.09ns_	__0.04__ _0.05_
Cantharidae	__0.05__* _0.05_	__0.02__ _0.03_	Cantharidae	__0.02__ _0.09_	__0.05__ _0.06_	Cantharidae	__0.02__ -	__0.09__ -	Platygasteridae	__0.02ns__ -	__0.22__ -
TFItot	__-0.008__ _-0.28_	__0.20__ _0.22_	TFItot	__-0.30__ _-0.13_	__0.39__ _0.55_	TFItot	__0.68__ -	__1.83__ -	TFItot	__-0.29ns__ _-0.73ns_	__0.42__ _0.46_
CumulDepth	__0.037__ _0.06_	__0.13__ _0.15_	CumulDepth	__-0.19__ _-0.06_	__0.26__ _0.28_	CumulDepth	__-0.66__ -	__1.14__ -	CumulDepth	__-0.13ns__ _-0.27ns_	__0.30__ _0.31_
Nqty	__0.02__ _0.18_	__0.13__ _0.16_	Nqty	__0.21ns__ _-0.03_	__0.21__ _0.27_	Nqty	__-0.29__ -	__0.80__ -	Nqty	__-0.22ns__ _-0.41ns_	__0.22__ _0.22_
SHDI	__-0.08__ _-0.19_	__0.13__ _0.15_	SHDI	__-0.36__ _-0.35_	__0.25__ _0.33_	SHDI	__1.48__ -	__1.60__ -	SHDI	__0.40ns__ _0.40ns_	__0.29__ _0.32_
SHDICrop	__-0.27__* _-0.49_**	__0.14__ _0.15_	SHDICrop	__-0.74__** _-1.04_**	__0.25__ _0.36_	SHDICrop	__0.27__ -	__0.58__ -	SHDICrop	__-0.09ns__ _0.22ns_	__0.33__ _0.32_
pSNH	__-0.06__ _-0.05_	__0.14__ _0.15_	pSNH	__0.18__ _-0.08_	__0.27__ _0.32_	pSNH	__1.31__ -	__0.80__ -	pSNH	__0.13ns__ _0.10ns_	__0.31__ _0.31_
pWinterCrop	__0.18__ _0.03_	__0.14__ _0.19_	pWinterCrop	__0.63__* ___0.64___*	__0.25__ ___0.30___	pWinterCrop	__-1.22__ -	__1.09__ -	pWinterCrop	__0.20ns__ _0.12ns_	__0.32__ _0.35_
EdgeDens	__-0.04__ _-0.20_	__0.12__ _0.16_	EdgeDens	__-0.35__ _-0.37_	__0.24__ _0.29_	EdgeDens	__0.13__ -	__0.58__ -	EdgeDens	__0.17ns__ _0.23ns_	__0.19__ _0.21_
TFItot*SHDI	__0.008__ _0.32_*	__0.16__ _0.16_	TFItot*SHDI	__-0.07__ _0.29_	__0.31__ _0.32_	TFItot*SHDI	__3.21__ -	__2.45__ -	TFItot*SHDI	__-0.47ns__ _-0.31ns_	__0.35__ _0.39_
TFItot* SHDICrop	__-0.32__ _-0.71_**	__0.20__ _0.22_	TFItot* SHDICrop	__-0.59__ _-0.77_	__0.37__ _0.50_	TFItot* SHDICrop	__0.35__ -	__1.18__ -	TFItot* SHDICrop	__-0.58ns__ _-0.05ns_	__0.50__ _0.68_
TFItot*pSNH	__0.04__ _0.05_	__0.14__ _0.16_	TFItot*pSNH	__0.55__* _0.39_	__0.28__ _0.29_	TFItot*pSNH	__1.26__ -	__1.19__ -	TFItot*pSNH	__0.21ns__ _-0.15ns_	__0.36__ _0.35_
TFItot* pWinterCrop	__0.06__ _-0.07_	__0.17__ _0.21_	TFItot* pWinterCrop	__-0.18__ _-0.47_	__0.38__ _0.46_	TFItot* pWinterCrop	__-0.46__ -	__1.16__ -	TFItot* pWinterCrop	__0.27ns__ _0.44ns_	__0.35__ _0.37_

TFItot*EdgeDens	**-0.007** *0.10*	**0.15** *0.20*	TFItot*EdgeDens	**0.41** *0.43*	**0.32** *0.37*	TFItot*EdgeDens	**0.45** -	**0.69** -	TFItot*EdgeDens	**-0.14ns** *-0.26ns*	**0.41** *0.42*
CumulDepth*SHDI	**0.004** *-0.09*	**0.14** *0.16*	CumulDepth*SHDI	**0.08** *-0.24*	**0.27** *0.32*	CumulDepth*SHDI	**1.36** -	**0.98** -	CumulDepth*SHDI	**0.11ns** *0.36ns*	**0.31** *0.34*
CumulDepth*SHDICrop	**0.05** *0.13*	**0.13** *0.16*	CumulDepth*SHDICrop	**0.29** *-0.17*	**0.25** *0.57*	CumulDepth*SHDICrop	**0.35** -	**0.62** -	CumulDepth*SHDICrop	**-0.39ns** *-0.30ns*	**0.30** *0.26*
CumulDepth*pSNH	**-0.17** *-0.23*	**0.1** *0.12*	CumulDepth*pSNH	**0.10** *0.56*	**0.22** *0.29*	CumulDepth*pSNH	**0.26** -	**0.77** -	CumulDepth*pSNH	**0.19ns** *-0.14ns*	**0.24** *0.23*
CumulDepth*pWinterCrop	**0.06** *0.04*	**0.15** *0.19*	CumulDepth*pWinterCrop	**-0.40** *-0.48*	**0.25** *0.30*	CumulDepth*pWinterCrop	**-1.30** -	**1.03** -	CumulDepth*pWinterCrop	**-0.16ns** *-0.10ns*	**0.33** *0.34*
CumulDepth*EdgeDens	**-0.35*** *-0.32*	**0.15** *0.20*	CumulDepth*EdgeDens	**-0.15** *0.05*	**0.32** *0.38*	CumulDepth*EdgeDens	**0.32** -	**0.75** -	CumulDepth*EdgeDens	**0.50ns** *0.50ns*	**0.33** *0.34*
Nqty*SHDI	**-0.02** *0.009*	**0.14** *0.15*	Nqty*SHDI	**0.03** *0.15*	**0.27** *0.31*	Nqty*SHDI	**0.23** -	**0.58** -	Nqty*SHDI	**-0.03ns** *0.07ns*	**0.26** *0.26*
Nqty*SHDICrop	**0.08** *0.24*	**0.14** *0.17*	Nqty*SHDICrop	**-0.47** *-0.51*	**0.28** *0.33*	Nqty*SHDICrop	**-0.20** -	**0.64** -	Nqty*SHDICrop	**-0.40ns** *-0.44ns*	**0.32** *0.30*
Nqty*pSNH	**-0.09** *-0.10*	**0.12** *0.15*	Nqty*pSNH	**0.33** *0.26*	**0.25** *0.33*	Nqty*pSNH	**1.06** -	**0.86** -	Nqty*pSNH	**0.08ns** *-0.10ns*	**0.25** *0.25*
Nqty*pWinterCrop	**0.007** *-0.12*	**0.11** *0.15*	Nqty*pWinterCrop	**-0.12** *0.07*	**0.21** *0.24*	Nqty*pWinterCrop	**-0.006** -	**0.69** -	Nqty*pWinterCrop	**-0.04ns** *0.25ns*	**0.27** *0.27*
Nqty*EdgeDens	**-0.30** *-0.16*	**0.21** *0.27*	Nqty*EdgeDens	**-0.26** *-0.53*	**0.44** *0.53*	Nqty*EdgeDens	**-0.30** -	**0.90** -	Nqty*EdgeDens	**1.02***** *0.99****	**0.24** *0.26*

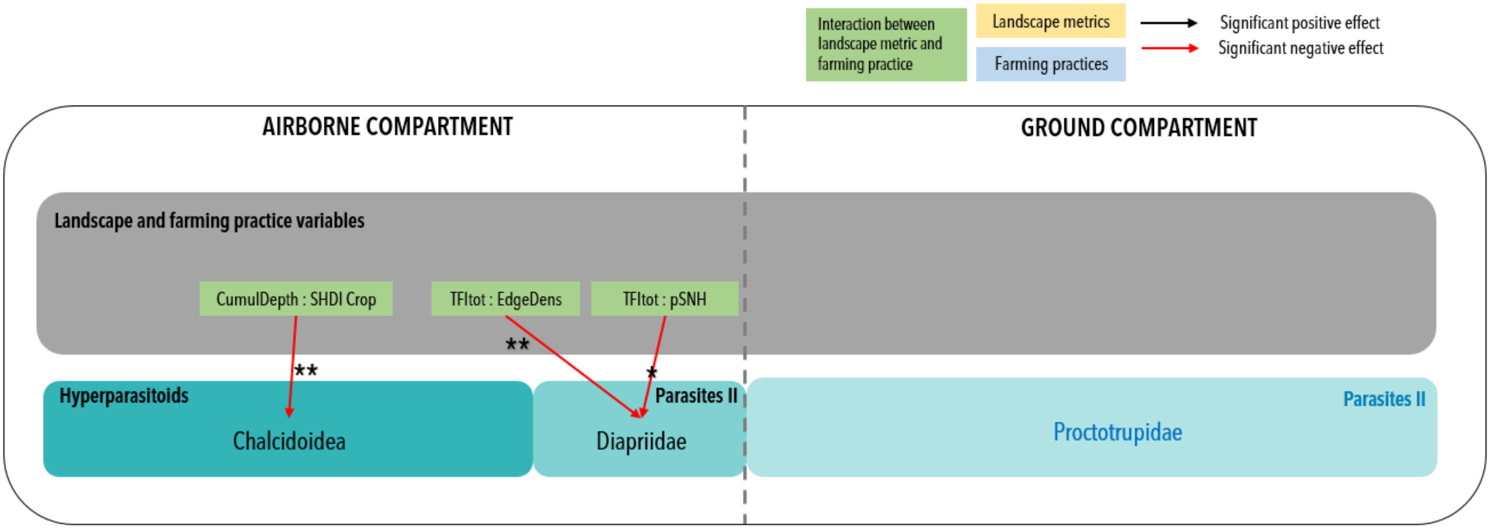
Appendix G: Averaged estimated effects of farming practices, landscape variables and their interactions on the hyperparasitoids or parasitoids of the natural enemies, which emerged in both ground and airborne compartments. Values in **bold** correspond to averaged estimated effects calculated for the complete season; values in *italics* correspond to those calculated for the beginning of the spring season. * *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001.

Airborne compartment						Ground compartment		
	Chalcidoidea (Hyperparasitoids)			Diapriidae			Proctotrupidae	
effect	estimate	s.e.	effect	estimate	s.e.	effect	estimate	s.e.
TFItot	**0.34**	**0.30**	TFItot	**0.19***	**0.09**	TFItot	**-0.49**	**0.50**
	0.09	*0.39*		*0.34***	*0.12*		*-0.44*	*0.72*
CumulDepth	**0.56***	**0.19**	CumulDepth	**-0.19**	**0.14**	CumulDepth	**-0.31**	**0.31**
	0.25	*0.27*		*-0.19*	*0.20*		*-0.14*	*0.66*
Nqty	**-0.06**	**0.24**	Nqty	**-0.06**	**0.13**	Nqty	**0.04**	**0.32**
	-0.06	*0.30*		*0.18*	*0.20*		*0.32*	*0.62*
SHDI	**0.10**	**0.23**	SHDI	**0.12**	**0.15**	SHDI	**-0.11**	**0.35**
	0.39	*0.32*		*0.20*	*0.19*		*1.29*	*0.81*
SHDICrop	**-0.15**	**0.19**	SHDICrop	**-0.01**	**0.14**	SHDICrop	**0.05**	**0.34**
	-0.33	*0.25*		*-0.009*	*0.21*		*-0.14*	*0.56*
pSNH	**0.33**	**0.22**	pSNH	**0.23***	**0.10**	pSNH	**-0.37**	**0.31**
	0.50ns	*0.30*		*0.40***	*0.14*		*-0.17*	*0.55*
pWinterCrop	**-0.003**	**0.23**	pWinterCrop	**-0.09**	**0.14**	pWinterCrop	**0.05**	**0.33**
	0.05ns	*0.31*		*-0.26*	*0.21*		*-0.07*	*0.55*
EdgeDens	**-0.10**	**0.23**	EdgeDens	**-0.03**	**0.13**	EdgeDens	**0.33**	**0.31**
	-0.08	*0.29*		*0.03*	*0.17*		*0.48*	*0.56*
TFItot*SHDI	**0.22**	**0.28**	TFItot*SHDI	**0.06**	**0.16**	TFItot*SHDI	**0.03**	**0.57**
	-0.16	*0.34*		*0.19*	*0.20*		*0.42*	*1.30*
TFItot*SHDICrop	**0.10**	**0.32**	TFItot*SHDICrop	**-0.06**	**0.18**	TFItot*SHDICrop	**0.57**	**0.65**
	-0.41	*0.38*		*0.10*	*0.25*		*0.21*	*0.89*
TFItot*pSNH	**0.12**	**0.22**	TFItot*pSNH	**-0.24****	**0.08**	TFItot*pSNH	**-0.12**	**0.49**
	0.26	*0.31*		*-0.28***	*0.09*		*0.38*	*0.84*
TFItot*pWinterCrop	**-0.42**	**0.31**	TFItot*pWinterCrop	**0.20**	**0.16**	TFItot*pWinterCrop	**0.14**	**0.44**
	-0.11	*0.40*		*0.10*	*0.22*		*-0.45*	*0.91*
TFItot*EdgeDens	**0.20**	**0.30**	TFItot*EdgeDens	**-0.35***	**0.15**	TFItot*EdgeDens	**-0.10**	**0.44**
	-0.08	*0.38*		***-0.48****	***0.20***		*-0.90*	*0.68*
CumulDepth*SHDI	**0.03**	**0.24**	CumulDepth*SHDI	**0.20**	**0.16**	CumulDepth*SHDI	**-0.37**	**0.32**
	0.26	*0.34*		*0.20*	*0.23*		*1.28*	*0.76*
CumulDepth* SHDICrop	**-0.5***	**0.25**	CumulDepth* SHDICrop	**-0.17**	**0.15**	CumulDepth* SHDICrop	**0.53***	**0.22**
	-1.10**	***0.41***		*-0.10*	*0.21*		*0.10*	*0.46*
CumulDepth* pSNH	**-0.08**	**0.16**	CumulDepth* pSNH	**0.02**	**0.11**	CumulDepth* pSNH	**-0.42**	**0.29**
	0.02	*0.24*		*0.10*	*0.17*		*0.08*	*0.38*
CumulDepth* pWinterCrop	**0.15**	**0.27**	CumulDepth* pWinterCrop	**0.09**	**0.17**	CumulDepth* pWinterCrop	**-0.83****	**0.27**
	0.02	*0.36*		*-0.16*	*0.23*		*-0.58*	*0.51*
CumulDepth* EdgeDens	**-0.14**	**0.28**	CumulDepth* EdgeDens	**0.004**	**0.17**	CumulDepth* EdgeDens	**0.02**	**0.38**
	-0.19	*0.38*		*0.13*	*0.24*		*0.62*	*0.59*
Nqty*SHDI	**0.31**	**0.29**	Nqty*SHDI	**0.16**	**0.15**	Nqty*SHDI	**0.27**	**0.44**
	0.24	*0.34*		*0.32*	*0.25*		*0.86*	*1.04*
Nqty*SHDICrop	**0.23**	**0.26**	Nqty*SHDICrop	**-0.15**	**0.16**	Nqty*SHDICrop	**0.05**	**0.35**
	0.19	*0.33*		*0.008*	*0.22*		*0.002*	*0.59*
Nqty*pSNH	**0.35**	**0.24**	Nqty*pSNH	**-0.13**	**0.12**	Nqty*pSNH	**-0.09**	**0.29**
	0.37	*0.32*		*-0.18*	*0.16*		*0.13*	*0.52*
Nqty*pWinterCrop	**-0.15**	**0.24**	Nqty*pWinterCrop	**0.25***	**0.11**	Nqty*pWinterCrop	**-0.38**	**0.35**

	-0.11	*0.29*		*0.30*	*0.16*		*-0.18*	*0.52*
Nqty*EdgeDens	**0.01**	**0.31**	Nqty*EdgeDens	**-0.13**	**0.18**	Nqty*EdgeDens	**0.11**	**0.38**
	0.30	*0.39*		*-0.35*	*0.26*		*0.94*	*0.57*



Appendix H.1: Effects of landscape and farming practices on the abundance of emerged natural enemies and their consequences for biological control in the ground and airborne compartments measured using sentinel prey cards. The results are for the beginning of the spring season. Black arrows represent a positive effect of the variable or the interaction between two variables. Red arrows represent a negative effect. All arrows show a significant effect. Yellow rectangles correspond to a landscape variable; blue rectangles correspond to a farming practice variable; green rectangles correspond to the interaction between one landscape and one farming practice variable. * p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001. Abbreviations for explanatory variables are explained in Table 1. See appendices E.1, E.2, F.1 and F.2 for the complete results.



Appendix H.2: Effects of landscape and farming practices on emerged hyperparasitoids and parasitoids of natural enemies and their consequences for the abundance of natural enemies in the ground and airborne compartments. The results are for the beginning of the spring season. Black arrows represent a positive effect of the variable or the interaction between two variable. Red arrows represent a negative effect. All arrows show a significant effect. Yellow rectangles correspond to a landscape variable; blue rectangles correspond to a farming practice variable; green rectangles correspond to the interaction between one landscape and one farming practice variable. * *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001. Abbreviations for explanatory variables are explained in Table 1. See appendix G for complete results.