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Multi-scale approach to biodiversity proxies of biological control service in European farmlands

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Abstract

Intensive agriculture has profoundly altered biodiversity and trophic relationships in agricultural landscapes, leading to the deterioration of many ecosystem services such as pollination or biological control. Information on which spatio-temporal factors are simultaneously affecting crop pests and their natural enemies is required to improve conservation biological control practices. We conducted a study in 80 winter wheat crop fields distributed in three regions of North-western Europe (Brittany, Hauts-de-France and Wallonia), along intra-regional gradients of landscape complexity. Five taxa of major crop pests (aphids and slugs) and natural enemies (spiders, carabids, and parasitoids) were sampled three times a year, for two consecutive years. We analysed the influence of regional (meteorology), landscape (structure in both the years n and $n-1$) and local factors (hedge or grass strip field boundaries, and distance to boundary) on the abundance and species richness of crop-dwelling organisms, as proxies of the service/disservice they provide. Firstly, there was higher biocontrol potential in areas with mild winter climatic conditions. Secondly, natural enemy communities were less diverse and had lower abundances in landscapes with high crop and wooded continuities (sum of interconnected crop or wood surfaces), contrary to slugs and aphids. Finally, field boundaries with grass strips were more favourable to spiders and carabids than boundaries formed by hedges, while the opposite was found for crop pests, with the latter being less abundant towards the centre of the fields. We also revealed temporal modulation—and sometimes reversion—of the impact of local elements on crop biodiversity. To some extent, these results cause controversy because they show that hedgerows and woodlots should not be the unique cornerstones of agro-ecological landscape design strategies. We point out that combining woody and grassy habitats to take full advantage of the features and ecosystem services they both provide (biological pest control, windbreak effect, soil stabilization) may promote sustainable agricultural ecosystems. It may be possible to both reduce pest pressure and promote natural enemies by accounting for taxa-specific antagonistic responses to multi-scale environmental characteristics.

Keywords: Landscape; Semi-natural habitat; Conservation Biological Control; Disservice; Edge effect; Woody elements

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1. Introduction

Biodiversity has been put in jeopardy over the past 70 years in agroecosystems as a direct consequence of farm intensification combined with climate change, and destruction of natural ecosystems (Kleijn et al., 2009; Raven and Wagner, 2021). Conservation of farmland biodiversity is a major and timely issue because of the ecosystem services it supplies, such as crop pollination and biological control of pests and pathogen vectors (Dainese et al., 2019). The biological control service against pests is largely delivered by naturally occurring beneficial predatory or parasitic arthropods, and is considered as one of the most important regulation services supplied by biodiversity (Bale et al., 2008). Yet, it is put at risk, not only because of biodiversity loss, but also because of diverse and sometimes asymmetric responses of pests and natural enemies to environmental changes (Damien and Tougeron, 2019; Karp et al., 2018).

Protecting biodiversity from habitat loss and environmental disturbances is part of conservation biological control (CBC) strategies. They consist in both limiting the action and outbreak of crop pests, and enabling natural enemies by providing them habitats and resources to survive and grow their populations (Jonsson et al., 2008). CBC services provided by agro-biodiversity can be enhanced by reducing chemical inputs, using alternative farm practices and diversifying landscape elements such as semi-natural habitats surrounding the fields (Holland et al., 2016; Lichtenberg et al., 2017; Muneret et al., 2018). Abundance, species richness and functional diversity of crop pests and natural enemies (parasitoids and predators) are all influenced by both field-level and landscape-level characteristics, although not necessarily to the same extent (Jonsson et al., 2015; Larsen and Noack, 2020), consequently affecting the service/disservice balance of CBC strategies. Degrees of biological control potentially achieved in a field are thus dependent on how different taxonomic groups respond to these multi-scale factors, so determining the ideal agricultural landscape that would favour natural enemies and disadvantage crop pests becomes a complex task (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Karp et al., 2018).

Heterogeneous landscapes support greater arthropod biodiversity (Sirami et al., 2019), increase the potential of resident predators and parasitoids (Gagic et al., 2012), and are less exposed to pest outbreaks (Tschardt et al., 2005). Rusch et al. (2016) reported a 46 % lower biological control level in homogeneous landscapes dominated by cultivated areas, compared to landscapes with a high proportion of semi-natural habitats, such as grasslands and woody elements (hedges, woodlots, forests), facilitating species movement and year-long access to resources (French et al., 2001). The spatial and temporal organization of cropping systems in the farmland mosaic is also a key factor in establishment and persistence of pest and natural enemy populations in crops (Bertrand et al., 2016; Marrec et al., 2017). However, landscape-level effects can also be taxa- and trait-dependent because of variability in dispersal capacities or in specialization degree to habitat type among species (Chaplin-Kramer et al., 2011). For example, some studies have shown greater abundances of ground beetles in open landscapes than in complex landscapes (Aviron et al., 2005), and others have found higher fitness of wolf spiders sampled in homogenous landscapes than in heterogenous landscapes (Öberg, 2009).

At the local scale, crop field interfaces with other fields and with semi-natural areas are important to consider for assessing species spatio-temporal dynamics. Many species move to adjacent habitats when the quality of the former habitat deteriorates (Burel et al., 2013; Macfadyen and Muller, 2013). Hedges and grassy or flowering strip borders around crops can act as stable refuges and interfaces facilitating population movements between semi-natural vegetation and crops (Marshall and Moonen, 2002; Pecheur et al., 2020). Such borders are also habitats that provide food sources, overwintering sites (Sarhou et al., 2014), and may affect the potential for biological control service in several ways (Albrecht et al., 2020; Gurr et al., 2017; Montgomery et al., 2020). On the one hand, semi-natural habitats and crop boundaries can increase the presence and abundance of natural enemies such as parasitoids, spiders, carabids, syrphids or staphylinids (Chaplin-Kramer et al., 2011; Haenke et al., 2014; Landis et al., 2000). On the other hand, they can be reservoirs for crop pests such as rodents, slugs or aphids (Bianchi et al., 2006; Michel et al., 2007; Thies et al., 2005), and therefore generate a disservice. In addition, hedges and grassy field boundaries are very

contrasted habitats, harboring distinct structure, configuration, and plant composition, in a way that each boundary type may only be favorable to some taxa (Fusser et al., 2016; Meek et al., 2002).

The effects of regional, landscape, or local factors should be considered at the scale of the community, because the outcome in terms of biological control ultimately depends on trophic and non-trophic links within interaction networks (De Heij and Willenborg, 2020; Derocles et al., 2014; Martin et al., 2013). Functional diversity and redundancy levels are directly linked to species diversity (Jonsson et al., 2017; Rosenfeld, 2002), and there can be additive and synergistic effects among complementary species of natural enemies (*e.g.*, presence of specialists of different pest species, or better spatial and temporal coverage) (Dainese et al., 2017), therefore providing altogether a better control of crop pests (Roubinet et al., 2018). On a temporal scale, abundance and species richness of pests and natural enemies change over the years and seasons, and the way they respond to multiple external factors (*i.e.* weather, landscape, agricultural practices) can also vary over time, which is a rarely addressed but important element to consider (Alignier et al., 2014; Plečáš et al., 2014; Welch and Harwood, 2014).

In this study, we focused on two cereal crop pest groups (aphids and slugs, Glen and Moens, 2002; Van Emden and Harrington, 2017), two ground-dwelling generalist predatory groups (carabid beetles and spiders), and one specialist natural enemy group (aphid parasitoids). Evidence for key roles of carabids, spiders, and parasitoids in pest suppression is accumulating (De Heij and Willenborg, 2020; Denys and Tschardtke, 2002; Michalko et al., 2019), and the link between diversity and abundance of natural enemies and the control of pest populations has been established (Tschardtke et al., 2008; Dainese et al., 2019). However, most studies focus on single or a few taxa, or on single or few environmental variables, putting forward the necessity for multi-taxonomic and multi-factorial approach on aboveground crop biodiversity. There is a need to better measure the extent to which the environment, at different spatial and temporal scales, can modulate the potential for biological control by considering the relative responses of different taxa, and how the effects of agro-ecological infrastructures on these organisms may deviate from general expectations from the literature (Bianchi et al., 2006; Holland et al., 2016; Karp et al., 2018; Tschardtke et al., 2012). We considered landscape heterogeneity not just in terms of composition, as it is often the case (relative proportion of semi-natural elements), but in terms of configuration, particularly by considering the effect of wooded elements. Using a community approach, we investigated which local to landscape factors could positively or negatively influence the potential for biological control at different spatial and temporal scales, with the aim to minimize abundances of crop-dwelling pests and maximize species diversity and abundance of their predatory or parasitic natural enemies.

We aimed at explaining activity-density, abundance, and species richness of five major taxa in winter wheat fields in contrasting agricultural landscapes in regions with diverging temperature conditions in North-western Europe. More specifically, we addressed the following research hypotheses: (i) the abundance of each taxon varies from one region to another, with an earlier activity in regions with mild winter conditions (Andrade et al., 2015; Honek et al., 2018; Tougeron et al., 2018); (ii) more complex landscapes support a greater natural enemy biodiversity (Thies et al., 2005) and improve the potential for biological control, for example through higher parasitism rates. In addition, we investigated the local influence of two types of field boundary (hedges and grass strip) and of the distance to the boundary. We suggest that (iii) crop pests are more abundant in the borders than in the middle of the fields, particularly in early spring due to the refuge they provide (Tschardtke et al., 2016); (iv) abundance of natural enemies is greater close to grass strips and to the middle of the fields than close to hedges and field boundaries, because of the affinity of most field-dwelling predatory species with open habitats, although differences between taxa are expected (Derocles et al., 2014; Fusser et al., 2016; Holland et al., 2007; Mestre et al., 2018).

2. Material & Methods

2.1. Study regions and field selection

We conducted this study in 2017 and 2018, in three regions along a mesoclimatic gradient. The first region was Brittany, western France, and sampling was carried out in the *Zone Atelier Armorique* (European LTER Network; osur.univ-rennes1.fr/za-armorique/) (48°36'N, 1°32'W) (mean annual temperature: $11.74 \pm 0.21^\circ\text{C}$, mean rainfall level: 2.24 ± 0.16 mm). This area is characterized by an oceanic climate and a North-South landscape complexity gradient from open, large-field landscapes to more complex landscapes with small fields and an important hedgerow network. Moreover, this area is dominated by mixed farming; the dominant crops are grasslands, winter cereals and maize. The second region was Hauts-de-France, northern France, and sampling was done in the North-East of Aisne (49°56'N, 3°54'E) (mean annual temperature: $10.92 \pm 0.25^\circ\text{C}$, mean rainfall level: 1.74 ± 0.12 mm). This area is characterized by an East-West landscape complexity gradient, from highly complex pasture lands with mixed farming, to open landscapes dominated by arable lands, especially cereals, sugar beet and oilseed rape. The third region was Wallonia, Belgium, and sampling was carried out in the Hainaut and Walloon-Brabant provinces (50°48'N, 4°45'E) (mean annual temperature: $11.11 \pm 0.20^\circ\text{C}$, mean rainfall level: 1.84 ± 0.11 mm). This industrialized upland area is characterized by a North-South landscape gradient, from simple landscapes and intensive crops mostly covered with cereals, to areas with more woods and hedgerows.

We selected three 5 x 5 km wide windows in both Brittany and Wallonia along an *a priori* gradient of landscape complexity (open, intermediate, and complex window types), and two in Hauts-de-France (open and complex window types). In each window, five winter wheat fields were randomly selected each year, except for Brittany in 2017 for which three fields in complex landscape, four fields in intermediate landscape, and eight fields in open landscape were selected. Each field had at least one boundary as a hedge and one as a grass strip. Landcover in each window for each year was obtained from the OCS-CESBIO Theia landcover database for France (theia-land.fr/en/) and PAC SIGEC for Wallonia (geoportail.wallonie.be/) of 2016 to 2018, and then classified into six different categories: summer crop (e.g., corn, rapeseed, beetroot), winter crop (e.g., winter wheat), woodland, grassland and other (roads, buildings, artificial structures) (**Figure 1**).

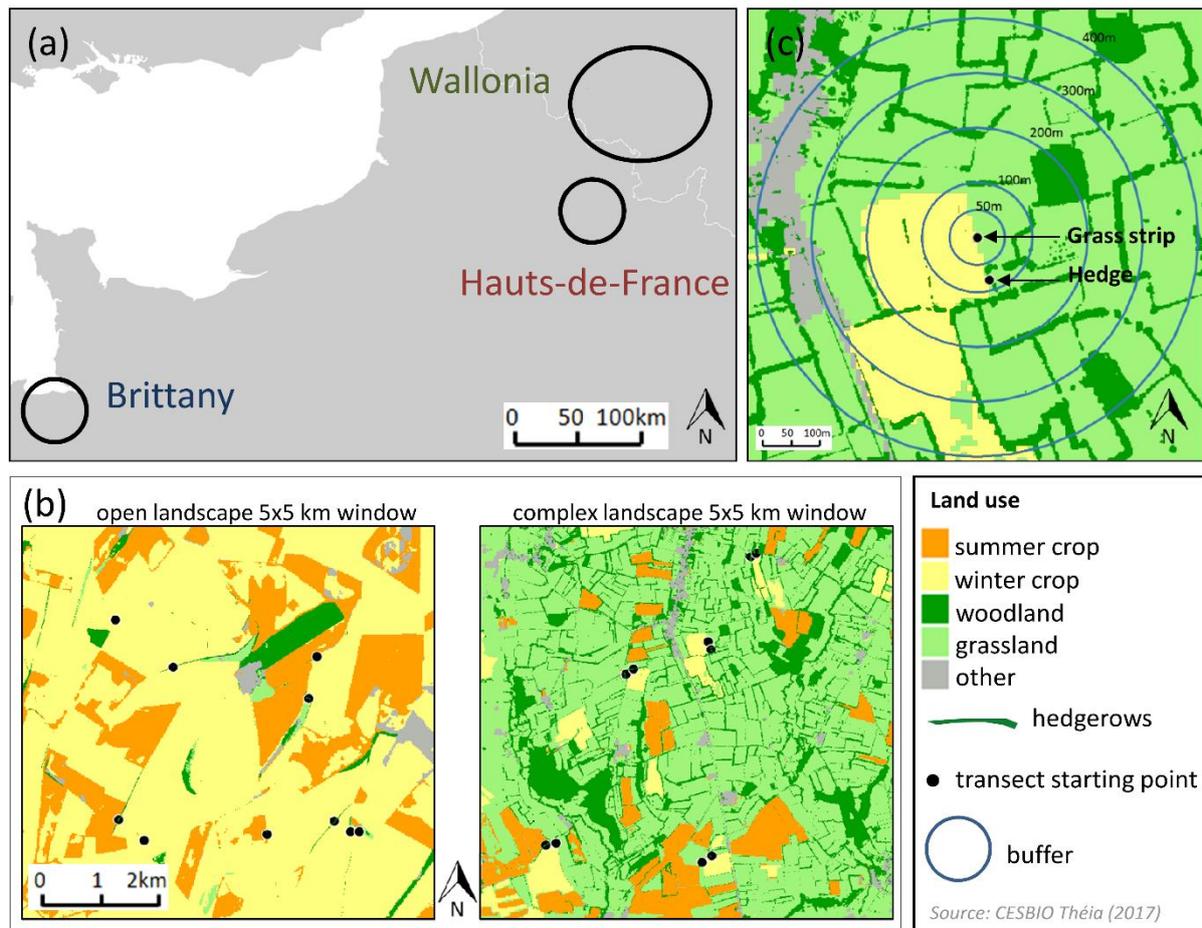


Figure 1: Study area and sampling design. (a) Location of the three study regions across the European gradient (Brittany, Hauts-de-France, and Wallonia). (b) Typical examples of an open landscape (on the left) and a complex landscape window (on the right), showing the different land-use types: summer crop (e.g., corn, rapeseed, beetroot ...), winter crop in which sampling was done (e.g., winter wheat), woodland (e.g., woodlots, forests), grassland (perennial or temporary) and other (e.g., buildings). This is here represented for the region Hauts-de-France in 2017 (black dots = sampling locations: transect starting points). The sampling fields are within 5 x 5 km window but the frames represent a larger area to facilitate the visualization of the surrounding landscape. (c) Sampling design at the field level, in the complex landscape window, with one sampling transect starting from a hedge and another from a grass strip. Metrics characterizing the surrounding landscape were calculated within concentric buffers (50 m to 400 m radius) around each sampling point.

2.2. Sampling design

We established two transects in each wheat field: one from the hedge, the second from the grass strip, both towards the middle of the field, and each at least 50m away from the other (**Figure 1**). Each transect comprised three sampling points, at 0 m (within the boundary) or 1 m from the boundary for aphid sampling, at 15 m, and at 40 m from each type of boundary. Sampling was repeated three times, in mid-April, end of May and end of June of each year (2017 and 2018).

We sampled ground-dwelling spiders and carabid beetles using two pitfall traps (\varnothing 9 cm, height: 11 cm) placed 1 m apart at each sampling point to increase capture rates. Data of both traps were pooled for each sampling point and date. Spiders were only kept in 2018. Pitfall trapping is dependent on both population density and on organism's activity, thus allowing measure of the 'activity-density' of species, which will be

the term used in this article to align with the majority of the existing literature. That said, we point out that these capture methods rather reflect an ‘abundance-activity’—which is a less used but probably more correct term—because a density would imply a measurement on a given surface. However, this capture surface depends on the species, the topography of the environment, and many other abiotic parameters that are not controlled when using pitfall traps. Each trap was filled with 200 mL of water saturated with salt and a few drops of detergent to reduce surface tension, and protected from litter and rainfall by an aluminium roof. Traps were left open for two weeks before collection. Carabid beetles and spiders were identified to the species level (Jeannel (1941, 1942), Roger et al., (2013), for carabids, and Nentwig et al., (2019), for spiders). Both taxa are known to form guilds feeding on both slugs and aphids (Greenstone and Shufran, 2003; Harwood and Obrycki, 2013; Nyffeler and Symondson, 2001; Symondson et al., 2002). However, to consider only natural enemies with a potential biological control effect on these preys, stenophagous spider species *Zodarium italicum* (Araneae: Zodariidae) and *Dysdera erythrina* (Araneae: Dysderidae) were removed from the dataset because they are myrmecophagous and crustaceophagous, respectively (Pekár and Toft, 2015). For carabid beetles, we removed 26 species from genera *Amara*, *Harpalus*, *Ophonus* and *Pseudoophonus*, known to be strictly or predominantly herbivorous (Honek et al., 2011, 2013; Saska et al., 2014). The other species were considered generalist predators, even if community-dependent and seasonal opportunistic facets of their diet has been reported (Gray et al., 2021; Holland, 2002; Ikeda et al., 2010; Šerić Jelaska et al., 2014; Zalewski et al., 2014). Analyses were done on a total of 156 spider species dominated by Linyphiidae (52.7% of the total abundance), and 104 carabid species, for which *Poecilus cupreus* accounted for 46.4% of the total abundance. Among Linyphiidae, we counted 80% of Erigoninae (dominant genera *Erigone* and *Oedothorax*) and 20% of other groups (e.g., genera *Leptyphantes*, *Tenuiphantes*). Spider and carabid species common to all three regions accounted for 95.7% and 96.0% of the total abundances, respectively.

Slugs (mostly *Arion* sp.) were collected at each sampling point using one pitfall trap protruding 5 cm from ground surface and filled with 200 mL of 4.4° beer, known as a slug attractant and commonly used to catch them (Dankowska, 2011). Traps were left open for one week before collection.

Aphids were counted on a defined number of wheat plants at each sampling point; 200 plants in April, 50 in May and 15 in June, to match sampling efforts with expected aphid population growth across the season (Andrade et al., 2015). Counting was carried out at 2 m from the pitfall traps to avoid the trampled area near sampling points. Collected data included the total number of aphids and the number of mummies (i.e., parasitized aphids). Parasitism rate was calculated at each sampling point as: number of mummies / total number of aphids and mummies. All six primary parasitoid species (*Aphidius avenae*, *Aphidius ervi*, *Aphidius rhopalosiphii*, *Aphidius matricariae*, *Praon volucre* and *Ephedrus plagiator*) and all three aphid species identified (*Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi*) were found in the three regions and landscape types, although at different relative abundances.

It is important to note that, like many studies on CBC, ours assumes a link between the presence of natural enemies and pest control, but we did not directly measure the value of the biological control service; we only measured a service potential (Bianchi et al., 2006; Holland et al., 2016; Jonsson et al., 2017).

2.3. Landscape metrics

For each field, metrics were calculated to characterize the surrounding landscape using concentric buffers centred on the starting point of each transect (i.e., both around the hedge and the grass strip starting point) using the *Chloe - Landscape Metrics* software (Boussard and Baudry, 2019). Landscape variables correlogram is presented in **Figure S1**. We considered:

- (1) the *landscape grain* in concentric buffers of 100, 200, 300, and 400 m radius, as a measure of landscape openness and as a proxy of microclimatic effects of surrounding landscape elements (e.g.,

windbreak effect, humidity retention). The grain accounts for both the composition and the configuration of woody elements and represents a sort of “local wooded proximity” to the point of analysis. Landscape grain ranges from 0 to 1, with low values in landscapes with a high density of intricate wooded elements which divide fields, and high values in landscapes with low densities of woody elements that do not divide fields. The more wooded elements that are interconnected, the finer the non-wooded landscape matrix between them, and the fewer wooded elements the coarser the matrix (i.e., the landscape grain is the size of the mesh formed by wooded element network, from many small elements (fine grain close to 0) to few large ones (coarse grain close to 1)) (Vannier et al., 2011) (**Figure S2** for details);

(2) the *continuity of wooded surfaces (wooded continuity)* is measured in two steps. First, clusters of interconnected wooded surfaces such as hedgerows and woodlots (in hectares) are generated in a buffer of 1 km radius around the sampling point. Then, the total area of the cluster overlapping concentric buffers of 50, 100, 150, and 200 m radius is measured (**Figure S3**);

(3) the *continuity of crop surfaces (crop continuity)*, calculated from the sum of interconnected winter crops and interconnected summer crops surfaces (in hectares) included in a buffer of 1 km radius and overlapping concentric buffers of 50, 100, 150, and 200 m radius in years n and $n-1$ (same principle as for the continuity of wooded surfaces, **Figure S3**);

and (4) the *length of crop interface (crop interface)*, calculated from the sum of the length (m) of the interface between adjacent fields of winter and summer crops in concentric buffers of 50, 100, 200, 300, and 400 m radius in years n and $n-1$.

The relevance of these two last metrics relies on the assumption that cereal aphids, their parasitoids and predators such as carabids move during the growing season from one crop to the next when resources are exhausted or after major disturbances, especially from ripe or harvested winter crops to fully developed summer crops. In addition, such seasonal movements have consequences on the success of survival and reproduction and the distribution of individuals in the following year (Bertrand et al., 2016; Burel et al., 2013; Duflot et al., 2016; Marrec et al., 2017). The value of continuity of crop surface will increase as the surface of crops increases in the landscape and as crops with similar calendar (summer or winter crops) are clustered, leading to more homogeneous, intensively cropped landscapes. On the other hand, the length of crop interface will increase as summer and winter crops are more intricate in the landscape mosaic and less separated by non-cropped elements.

2.4. Meteorological data

To consider the effect of meteorological conditions on plants and insects, data for the winter season (December-March 2016-2017 and 2017-2018) and for the sampling spring season (April-July, 2017 and 2018) were collected from automatic weather stations of Météo-France (for both French regions) and of the Royal Meteorological Institute (for Belgium). The weather stations were chosen to cover the sampling area in each region. Daily minimal and mean temperatures and rainfall amounts were collected, and data were averaged for the three to five weather stations of a region (**Table S1**). Finally, heating degree-days were calculated for each region at each date, using 4°C (DD4) as baseline, roughly corresponding to most plant growing threshold, and most arthropod development and activity thresholds (Briere et al., 1999; Jarošík et al., 2004).

2.5. Statistical analyses

We conducted all statistical analyses using R v4.0 (R Core Team, 2020). For each analysis, terms and interactions from global models were removed using a backward selection procedure, and models were

compared and sequentially selected according to best fit AIC (Burnham and Anderson, 2004) using the *MuMIn*, *MASS* and *buildmer* packages (Barton and Barton, 2019; Ripley et al., 2013; Voeten, 2019). The significance of each variable was then checked with the Anova function (type II, $\alpha = 0.05$) from the *car* package (Fox and Weisberg, 2011). Analyses were followed by Tukey multiple post-hoc comparison tests from the *emmeans* package (Lenth et al., 2019), to assess pairwise differences between modalities of significant factors. Model goodness of fit were assessed using the *DHARMA* package (Hartig, 2020).

2.5.1. Meteorological conditions

To make the “time of the year” comparable between years, the Julian date was used. Cumulated DD4 were calculated for each day, starting December 1st of each year, and for each region. For each year, we analysed December 1st to March 21st data independently from March 22nd to June 30th data (*i.e.*, before and during the sampling period). Differences in daily mean temperatures, average minimal temperatures, and precipitation rates were compared between years and regions, using the date as a quadratic covariate, with a two-degree scaled polynomial to allow non-linear variations, and including three-way interactions (\sim Region * Year * (Date + Date²)). To analyse trends in DD4 cumulation, the date as a quadratic covariate was removed from the models. Details concerning meteorological data analyses are provided in **Supplementary Material**. In short, we used Generalized Least Squares linear models (GLS) fit by maximized log-likelihoods, with autoregressive processes (AR) of order p (Metcalfe and Cowpertwait, 2009) for the residual series using the *nlme* package (Pinheiro et al., 2014). Left-censored Tobit regression models for zero-inflated continuous distributions from the *censReg* package (Henningsen, 2017) were used to analyse daily rainfall data.

2.5.2. Effects of spatio-temporal environmental factors on pests and natural enemies

Cumulated DD4 for each region was used as an explanatory variable instead of the sampling date to correct for differences in seasonal advance among regions. Landscape metrics and other covariates were scaled (with mean = 0) to avoid scaling issues in the models. Sample sizes (number of sampling points including all years, regions, landscape windows, fields, sampling rounds, boundary type and distances to the boundary) are N = 714 (spiders), N = 1361 (carabids), N = 1422 (parasitoids), N = 1422 (aphids) and N = 1421 (slugs).

For each taxon separately, Generalized Linear Mixed Models (GLMMs) with a negative binomial family and a log-link function due to overdispersion (Ver Hoef and Boveng, 2007) were fitted to the activity-density, abundance, and species richness data using the *MASS* and *lme4* packages (Bates et al., 2007; Ripley et al., 2013). Differences in parasitism rates (*i.e.*, parasitism probability) were analysed using a GLMM with a binomial family and a logit-link function. We tested for the effect of the following explanatory variables: region, year, cumulated DD4, landscape grain, wooded continuity, crop continuity in year n and $n-1$, crop interface in year n and $n-1$, boundary type (hedge or grass strip), and distance to the boundary (as a covariate, 0, 15, and 40 m). Interaction effects between cumulated DD4 and local factors were also tested and are detailed in the full model below. The identity of the landscape window of each region for each year (N = 16) was used as a random effect in the models, to account for repeated measures at the landscape level. To select the best buffer radius scale at which landscape metrics had to be considered at year n and $n-1$, for each taxon, we fitted successive GLMMs with only one landscape metric included as fixed effect at a time (*e.g.*, landscape grain at 100 m radius, then at 200 m, etc.), and the random effect, and models were compared based on AIC values (**Table S2**). Graphic representation of model estimates and model predicted values (marginal means), and interpretation of interaction effects were partly done using the *ggeffects* and *sjPlot* packages (Lüdtke, 2018a, 2018b). For interactions with covariates, we used the mean value of the continuous variable as well as the minimum and maximum values to plot the effect (Lüdtke, 2018a). Nakagawa’s marginal and conditional coefficients of determination R^2 (Nakagawa et al., 2017) are provided for each model and were computed using the *performance* package (Lüdtke et al., 2020). Before stepwise selection, the full models were built as follow:

Response variable \sim Year + Region

- + Cumulated DD4 * Boundary type * Distance to the boundary
- + Grain + Wooded continuity
- + Crop continuity [n] + Crop continuity [$n-1$]
- + Crop interface [n] + Crop interface [$n-1$]
- + (1 | Landscape window_year)

3. Results

3.1. Meteorological conditions

For the winter period (December 1st to March 21st) and for both years, Brittany was on average warmer (6.12 ± 0.24 °C) than both Hauts-de-France (3.98 ± 0.25 °C, t -ratio = -3.8, $p < 0.01$) and Wallonia (4.14 ± 0.24 °C, t -ratio = -3.5, $p < 0.01$). As a consequence, DD4 cumulated faster in Brittany, for both years. Note that relatively severe cold snaps occurred in each region on 2016-12-31 (< -3.0 °C) and on 2017-01-20 (< -2.6 °C), while cold snaps occurred later for the second sampling year, on 2018-03-01 (< -4.3 °C in Wallonia, < -2.6 °C in other regions). For the sampling period (March 22nd to June 30th), mean temperatures did not differ among years or regions and DD4 did not cumulate faster in any of the regions. For both the winter and the sampling period, no regional effect was found on precipitation rates, but 2017 was dryer than 2018 (all regions confounded). Details concerning meteorological data results are provided in **Supplementary Material (Figure S4, and Table S3 for statistical results)**.

3.2. Effects of spatio-temporal environmental factors on crop pests and natural enemies

The term ‘abundance’ is used as a generic term in the result section to designate ‘activity-density’ of carabids, spiders, and slugs, ‘parasitism rate’ of parasitoids, and ‘abundance’ of aphids, to facilitate reading. Environmental variables influenced the abundances of every taxon, as well as the species richness of both carabids and spiders. Summary statistical results of the full models are provided in **Table S4**.

3.2.1. Region, year, and cumulated degree-days effects

A regional effect was found on the abundance of every taxon but slugs; abundances were greater in Brittany than in either Wallonia (carabids) or Hauts-de-France (spiders and aphids), or both (parasitoids). Spider species richness was also greater in Brittany, followed by Wallonia, and then Hauts-de-France, but no regional difference was found in carabid species richness. Abundance of aphids was lower in 2018 than in 2017, but there were no differences between years for other taxa. Finally, the abundance of all taxa but spiders significantly increased with cumulated degree-days, indicative of the seasonal advance at each sampling location. Besides, the increase in cumulated degree-days had a significant negative impact on both carabid and spider species richness (**Table 1**).

3.2.2. Landscape effects

Carabid beetles were more abundant in coarse grain landscapes (*i.e.*, high values, fields with less dense and more isolated woody elements). Parasitism rates and aphid abundances were higher in fine grain landscapes (*i.e.*, low values, fields with denser and less isolated woody elements). In addition, the greater the continuity of wooded surfaces around the sampling point, the lower were the abundance and species richness of natural enemies (carabids, spiders, parasitoids) and the greater were the abundances of crop pests (aphids and slugs). The effect of both of these landscape metrics (grain and continuity of wooded surface) indicate that natural enemies are generally favoured by open landscapes, whereas crop pests are favoured by closed landscapes

with higher continuous wooded surface and more complex organisation of woody elements (**Table 1, Figure 2**).

Carabid and spider abundances decreased with increasing crop continuity in year n , but this metric did not influence the abundance of other taxa. Increasing crop continuity in year $n-1$ had a negative effect on carabid abundances, a positive effect on spider abundances, and did not influence other taxa. Higher length of crop interface in year n had a negative influence on carabid abundances, carabid species richness, and spider species richness, but a positive influence on slug abundances. Finally, in year $n-1$, the length of the crop interface was positively related to parasitism rate, and negatively related to the abundance of slugs. These effects indicate that natural enemies are disadvantaged by agricultural landscapes with homogeneous crop cover in a given year, but that crop rotation (year $n-1$) affects abundances in different ways, depending on the considered taxon (**Table 1, Figure 2**).

Refer to Table S2 for the scale at which landscape variables had an effect on each taxon. There was no common best scale response of the different biotic variables studied, for each of the landscape variables considered. Therefore, we did not find an absolute value at which it could be recommended to manage the landscape for high biological control potential.

3.2.3. *Local factors and temporal effects*

The local environment (type of boundary and distance to the boundary) differently affected the abundance and species richness of crop pests and natural enemies. The increase in the distance to the field boundary had a significant positive impact on carabid beetle abundances (especially late in the sampling season and on the grass strip side of the fields), and on parasitism levels (especially late in the sampling season). Another reading is that carabid abundances mostly increased with increasing cumulated degree-days far from the boundary but remained more stable over time close to it.

Greater distances from the boundary had a negative impact on spider abundances early in the season, whereas it had a positive impact late in the season (*i.e.*, with higher cumulated degree-days), regardless of the type of boundary. In other words, spider abundances decreased close to the boundary with cumulated degree-days, but increased at greater distances from the boundary with cumulated degree-days (**Table 1, Figure 3**).

Carabid species richness increased moving away from hedge boundaries in early season, and moving away from grass strip boundaries in late season. Spider species richness was globally greater on the grassy strip side of the fields. It remained stable on the hedge side of fields, but it decreased with the distance to the boundary on the grass strip side of fields, regardless of the sampling period (**Table 1, Figure 3**).

Abundances of both crop pests (aphids and slugs) decreased away from the crop boundary, and slugs were more abundant close to the hedge boundary, regardless of the distance to the boundary (**Table 1, Figure 3**).

To summarize, natural enemies were mostly favoured towards the centre of the field, especially on the grassy strip side, while crop pests were favoured close to the field boundaries, especially on the hedge side. In addition, a strong temporal component was found as local effects on carabids, spiders, and parasitoids were dependent on the seasonal advance (*i.e.*, interaction effects with “number of cumulated degree-days”) (**Table 1, Figure 3**).

Table 1: Statistical results of binomial (parasitism rates, logit link function) or negative binomial (all other taxa, log link function) generalized linear mixed models on the effect of environmental variables on activity-density, abundance or parasitism rate of all taxa, and species richness of carabids and spiders. Significant variables and interactions based on type II Wald statistics are highlighted in bold (*i.e.*, predictors that add significantly to the model). Grey boxes correspond to explanatory variables that were removed from the full model after backward AIC selection, and to one variable that could not be tested (year effect for spiders). Nakagawa's conditional and marginal coefficients of determination R^2 are provided for each model. See Table S2 for landscape metric scale selection. (*) Models concerning spiders were done for 2018 data only. DF = 1 except for the regional effect where DF = 2. Carabids (total abundances = 49,381 and 104 species), spiders (total abundances = 26,661 and 156 species), parasitoids (total abundances = 1,693), aphids (total abundances = 13,173) and slugs (total abundances = 9,049).

Dependent variable	Taxon	Carabids		Spiders (*)		Parasitoids		Aphids		Slugs		
	Selected explanatory variables	χ^2	p(> χ^2)	χ^2	p(> χ^2)	χ^2	p(> χ^2)	χ^2	p(> χ^2)	χ^2	p(> χ^2)	
Activity-density, abundance or parasitism rate	Region	39.4	<0.001	13.1	<0.01	54.9	<0.001	23.6	<0.001			
	Year							48.6	<0.001			
	Cumulated degree-day	83.2	<0.001	1.1	0.29	523.2	<0.001	292.4	<0.001	10.9	<0.001	
	Edge type	7.8	<0.01	3.9	<0.05	2.8	0.09			6.5	<0.05	
	Position to the edge	84.8	<0.001	0.02	0.9	176.1	<0.001	21.7	<0.001	52.1	<0.001	
	Landscape grain	14.8	<0.001			7.4	<0.01	10.3	<0.01			
	Continuity of wooded surface	25.6	<0.001	5.3	<0.05	26.4	<0.001	5.6	<0.05	3.9	<0.05	
	Continuity of crop surface year <i>n</i>	7.9	<0.01	5.5	<0.05							
	Continuity of crop surface year <i>n-1</i>	15.1	<0.001	9.7	<0.01							
	Length of crop interface year <i>n</i>	34.2	<0.001							12.3	<0.001	
	Length of crop interface year <i>n-1</i>					7.7	<0.01	3.3	0.07	7.6	<0.01	
	Edge type x Position to the edge	1.2	0.26	13.1	<0.01					3.4	0.07	
	Cumulated degree-day x Edge type	0.06	0.80									
	Cumulated degree-day x Position to the edge	23.0	<0.001	28.3	<0.001	11.2	<0.001					
	Cumulated degree-day x Edge type x Position to the edge	9.1	<0.01									
	model conditional - marginal Nakagawa's R^2		0.42 - 0.29		0.38 - 0.27		0.49 - 0.45		0.57 - 0.55		0.41 - 0.14	
	Species richness	Region			47.5	<0.001						
Year												
Cumulated degree-day		20.2	<0.001	30.1	<0.001							
Edge type		0.9	0.32	5.2	<0.05							
Position to the edge		15.4	<0.001	14.2	<0.001							
Landscape grain												
Continuity of wooded surface		12.3	<0.001	16.8	<0.001							
Continuity of crop surface year <i>n</i>												
Continuity of crop surface year <i>n-1</i>												
Length of crop interface year <i>n</i>		14.4	<0.001	10.2	<0.01							
Length of crop interface year <i>n-1</i>												
Edge type x Position to the edge		5.8	<0.05	22.6	<0.001							
Cumulated degree-day x Edge type		3.8	<0.05									
Cumulated degree-day x Position to the edge		0.2	0.63									
Cumulated degree-day x Edge type x Position to the edge	8.3	<0.01										
model conditional - marginal Nakagawa's R^2		0.39 - 0.08		0.41 - 0.35								

Figure 2: Generalized linear mixed model estimates of the effects of landscape variables (landscape grain, wooded continuity, crop continuity at years n and $n-1$, and crop interface at years n and $n-1$) on **A.** activity-density, abundance or parasitism rate of all taxa, and **B.** species richness of carabids and spiders. Raw (non-transformed) estimates values $\pm 95\%$ confidence intervals from reduced models (Table 2) are presented. For each landscape term in the models, red dots indicate significant negative effects, blue dots indicate significant positive effects, and grey dots indicate non-significant effects or terms that were not included in the selected best model. Carabids (total abundances = 49,381 and 104 species), spiders (total abundances = 26,661 and 156 species), parasitoids (total abundances = 1,693), aphids (total abundances = 13,173) and slugs (total abundances = 9,049). Pictogram credits to: CC BY 3.0; M. Dahirel (carabid), M. Broussard (parasitoid), G. Monger (slug), CC BY-NC-SA 3.0; J. Hughes (aphid), and CC0 1.0 (spider).

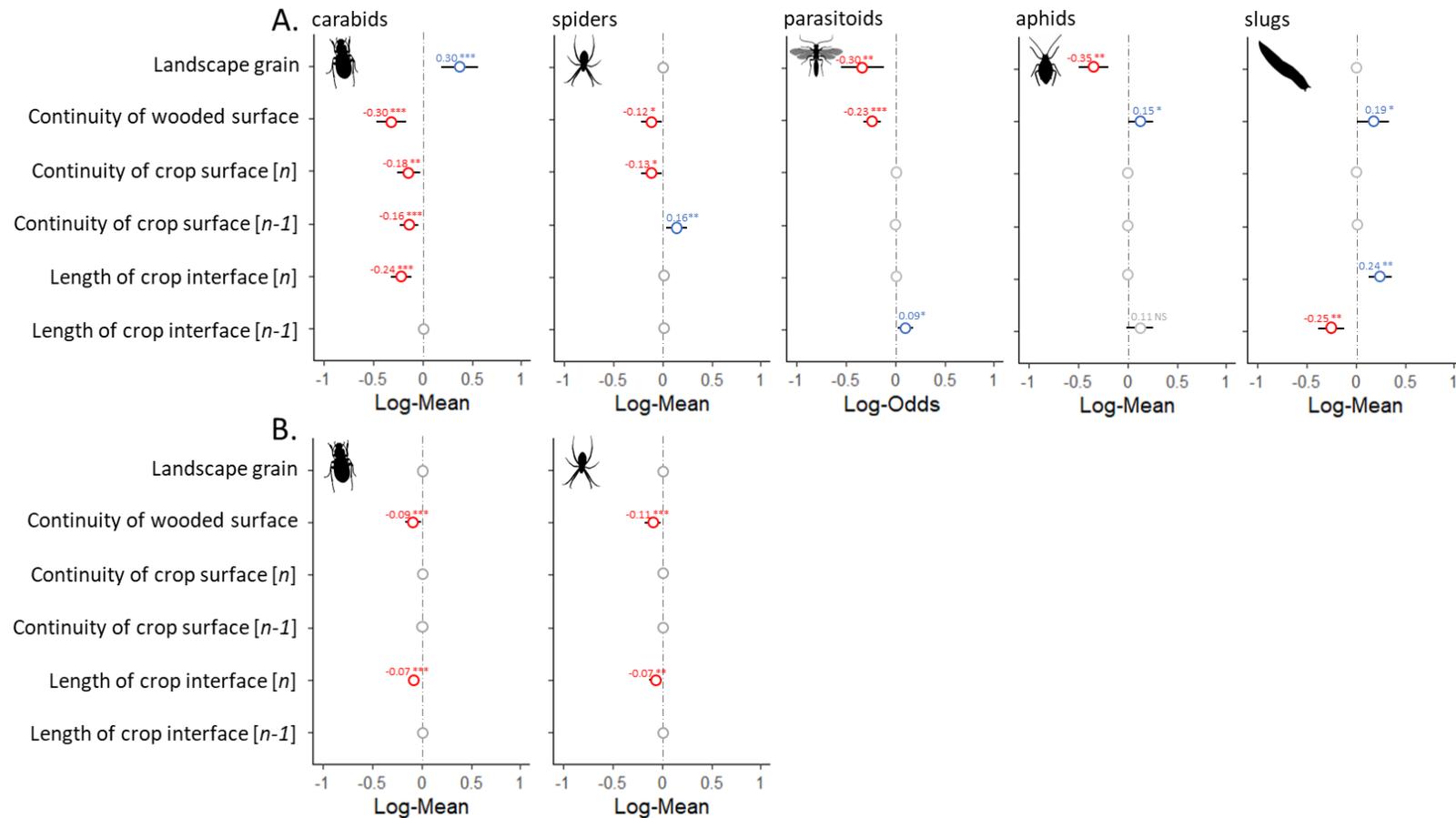
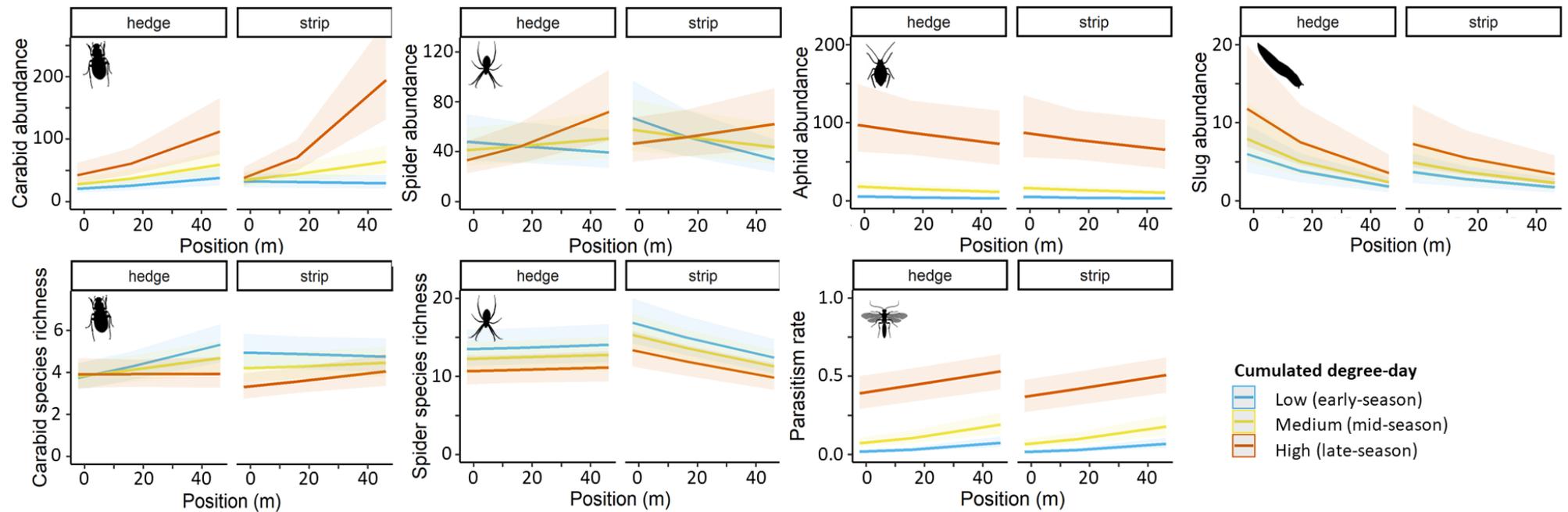


Figure 3: Estimated marginal means (predicted values) of the effects of local variables (type of boundary: hedge or grass strip, and position to the boundary: 0 to 40 m) on activity-density, abundance or parasitism rate of all taxa, and species richness of carabids and spiders, from generalized linear mixed models (binomial for parasitism rates and negative binomial for other taxa). Predicted values come from reduced models, as presented in Table 2, and not all two-way or three-way interactions were significant. For aphids, the “edge type” predictor had to be added in the reduced model to plot the effect. For each estimated term in the model, the interaction effect with cumulated degree-days is shown (*i.e.*, proxy of the “seasonal advance”). We used the minimum (365 °C, blue), median (731 °C, yellow) and maximum (1261 °C, red) values of the cumulated degree-day variable to plot interaction effects, representing early-sampling-season (April), mid-season (May) and late-season (June), respectively. Shaded areas around the lines represent 95% confidence intervals based on standard errors of model estimates. Pictogram credits same as in Figure 2.



4. Discussion

Our study aimed at identifying the environmental factors, at multiple scales, that could act on both reducing the presence of crop pests (slugs and aphids) and increasing the pressure level by natural enemies (carabid beetles, spiders and parasitoids), which indirectly determines the value of the biological control service provided. We predict the potential for biological control to be maximized towards the interior of the fields, in the presence of grass strip boundaries, and in landscapes with low continuities of wooded surface, low continuities of crop surface, and reduced lengths of crop interface. We also observed temporal effects modulating the impact of local elements on crop biodiversity, which is an aspect that is rarely addressed. Our results at the community level therefore suggest that landscape and crop management in line with CBC strategies could possibly be implemented to disadvantage crop pests and favour their natural enemies.

Our study shows effects on natural enemies that are quite unusual with regards to the existing literature on the effects of semi-natural habitats, yet not so unexpected. When landscape heterogeneity is defined as the proportion of semi-natural elements relative to cropped ones (*i.e.*, heterogeneity of landscape composition), as usually done, many studies show favourable impact on biological control or biodiversity in general. Here, we explicitly integrated configuration as a level of landscape heterogeneity, characterized by the extent of continuities of similar elements and length of crop interfaces, and highlighted the detrimental influence clustered landscapes can have on the potential for biological control. Hedges and woodlots can have a positive effect globally, at the landscape scale (resulting in a richer 'gamma' landscape-level species pool), but as we focused on field-dwelling natural enemies, it is clear that they were favoured by field-like open habitats.

4.1. Region, year, and cumulated degree-days effects

Differences in abundance, activity-density, parasitism rate, and species richness could be explained by mesoclimatic and meteorological factors, and in particular differences in winter conditions among sampled regions, in addition to regional agricultural and landscape histories. Each year, the winter period preceding the sampling period was warmer in Brittany than in other regions, and degree-days cumulated faster in Brittany than in the two other regions.

Some taxa, such as some parasitoid species sampled in our study, are particularly sensitive to winter conditions, and mild temperature can help building natural enemy populations faster, or maintain their populations onsite throughout the winter, leading to an early control of crop pests in the following spring (Andrade et al., 2016; Plantegenest et al., 2001). Differences in aphid abundances between years could be due to differences in precipitation rates, but also to cold snaps that occurred late in 2018 compared to 2017. Although such events remain relatively soft in temperate latitudes, they represent one of the main drivers of aphid-parasitoid community shifts across years (Tougeron et al., 2018).

Finally, we showed that carabid abundances increased with cumulated degree-days, which represents the dynamics of population growth and crop colonisation by natural enemies. However, species richness of both carabids and spiders decreased over time, indicating that ground-dwelling natural enemy communities became dominated by some species that would have been favoured by the crop habitat and the wheat phenological advance; the strength of such habitat filter may increase in late-spring (Marrec et al., 2021a).

4.2. Landscape effects

Larger surfaces of continuous woody elements surrounding the field benefited all crop pests but disadvantaged the natural enemy community, and could therefore provide a disservice, for example because large patches of woody elements can deter carabid movements (Thomas et al., 1998). Coarser landscape grain (*i.e.*, more open field and meadow matrix, with less dense and more isolated woody elements) also benefited carabids, but not parasitoids nor aphids. These two metrics give complementary information

because the landscape grain metric not only accounts for composition in woody elements, but also for their configuration (Vannier et al., 2011). For example, parasitism rates were low in areas with high wooded continuities, but were high in fine grain landscapes; parasitoids may have benefited from locally denser woody element networks (i.e., fine grain) to build up their populations, providing alternative hosts, food and shelters. As ground-dwelling predators were favoured by more open areas, it suggests that biological control would be provided by species adapted to meadow and crop-like open habitats, and not by wood or forest species (Aviron et al., 2018).

Slugs and aphids benefited from high surfaces of connected wooded areas in terms of abundance, and aphids also benefited from dense networks of woody elements (i.e., finer landscape grain). Slugs such as *Arion* sp. benefit from resource and microclimatic shelters of woody habitats close to the field (Fusser et al., 2016), from which they can colonise crops. Continuous wooded areas and hedgerows can also act as barriers increasing aphid abundances on the leeward side of such obstacles, therefore preventing, to some extent, aphids from entering field crops, or trapping them close to the woody elements (Hooks and Fereres, 2006; Van Emden and Harrington, 2017). Alignier et al. (2014) also showed that early but not late spring abundance of aphids was positively related to wood cover, which, along with our results, could suggest that colonisation sites of aphids are located mostly at field boundaries and are favoured by the presence of woody elements.

Potential effects of microclimatic conditions provided by woody elements have to be considered (Chen et al., 1999; De Frenne et al., 2021), because microclimates act on crop phenology, on behavior and physiology of species from different trophic levels, and on food-web structure, which in turn could influence the potential for biological pest control (Bernaschini et al., 2020; Tougeron et al., 2016). Existence of microclimatic conditions in the surrounding could partly explain the opposite response of natural enemies and crop pests to wooded areas, because not all taxa and species respond in the same way to such conditions (Alford et al., 2017). In any case, considering management of microclimatic shelters in agricultural landscapes could be valuable to protect biodiversity, for example from winter cold snaps (Vermunt et al., 2012).

High crop continuity in year n negatively affected ground-dwelling carabid and spider abundance-activities, suggesting dilution processes among winter and spring crops (habitat quantity), which is more likely to occur whenever short crop rotations and crop homogeneity dominate the agricultural landscape (Marrec et al., 2017; Tschardt et al., 2012). The length of crop interfaces was negatively related to carabid activity-density, and to carabid and spider species richness. Duflot et al. (2016) showed similar results on carabids in spring, suggesting a sink effect of adjacent maize fields. The opposite effect can be observed in species with relatively low dispersal abilities that benefit from resource supplementation in summer crops after the harvest of winter crops (Aviron et al., 2018; Marrec et al., 2021a). Higher length of crop interfaces positively affected slug abundance; as slugs colonize fields from their edges and have low dispersal capacities, they may rely more on small-scale connectivity between similar resource plots to build-up their populations. However, not all pest taxa respond the same way to landscape homogenization, and in some cases resource concentration can reduce crop pest pressure, as shown for example for the Andean potato weevil whose densities decrease with increasing amounts of potato fields in the landscape (i.e., monoculture) (Parsa et al., 2011).

In year $n-1$, landscape effects usually reveal dispersal processes in the fall or in early spring from former, potentially disappeared source habitats to newly sown crops (Marrec et al., 2017). Interannual between-field population movements play an important role in farmland community dynamics, and can ultimately affect biological control depending on the rate of success of redistribution and spill-over processes (Burel et al., 2013; Vasseur et al., 2013). For both metrics (crop continuity and crop interface) in year $n-1$, we found contrasted effects among taxa. Crop continuity in year $n-1$ had a positive effect on spider activity-density

but a negative effect on carabid activity-density. Spider species able to long-distance passive dispersal, such as Linyphiidae, usually balloon (Lafage *et al.*, 2015). In open, continuously cropped landscapes, such interannual dispersal is facilitated as no aerial barriers may block individuals on their way (contrary to wooded continuities as explained above). On the contrary, interannual ground dispersal is the most common in carabids. Consequently, they highly depend on the nature and structure of elements they move through. Previous studies highlighted the need for these species to encounter diversified habitats—summer and winter crops, semi-natural habitats—over relatively small range distances (Marrec 2015, Duflot 2016, Aviron 2018), which is not allowed when crop continuity in the year $n-1$ is high. In year $n-1$, high length of crop interfaces allowed colonization of wheat fields by more parasitoids and, although with a marginally non-significant effect, by more aphids. Aphid abundances in the focus field—and associated parasitoids emerging from winter diapause—could be favoured by cereal regrowth from the previous year's cultures, or by other landscape factors potentially correlated with this metric but not measured, such as for example grassland regrowth (Brewer *et al.*, 2008). The negative effect of high length of crop interfaces on slug activity-density is likely due to their need for wooded refuges after summer crops are harvested (Eggenschwiler *et al.*, 2013; Fusser *et al.*, 2016), and before entering newly sown winter crops, so that long crop interfaces without hedges or wood edges in-between may be detrimental for them.

Finally, for 11 of the 42 tests performed on the buffer scales to be considered in our models, the best AIC value was for the largest scale, which may suggest that a larger effect could have been observed beyond the maximum buffer radius studied (Jackson and Fahrig, 2015).

4.3. Local factors and temporal effects

At the local scale, the influence of the type of boundary (for carabid activity-density and species richness) or of the distance to the boundary (for carabid and spider activity-density, and parasitism rate) depended on cumulated degree-days. Therefore, we stress for considering intra-seasonal dynamics (*e.g.*, crop phenology, population growth), in addition to interannual dynamics, when evaluating species responses to local environmental variables. For example, some carabid beetle species use grassy field margins during the beginning of their activity period although no positive effect of grassy field margins on their abundance can be detected later in the season (Labruyere *et al.*, 2016). To the same extent, Roubinet *et al.* (2018) found a within-season variation in interaction strength between predators and aphid pests, due to time-specific functional redundancy in the predator community.

Results on carabids highlighted a habitat preference effect, as their activity-density was higher on the grass strip side of the fields; hedgerows usually favour population growth of forest species that are not found in the field, while grass strips provide a suitable habitat from which open-habitat species can thrive and colonize the field (Burel *et al.*, 2000; French *et al.*, 2001; Marrec *et al.*, 2015). These species benefit from better refuges, they benefit from higher plant densities and diversity (Fusser *et al.*, 2016), the latter being an essential element for overwintering of some species (Geiger *et al.*, 2009; Pfiffner and Luka, 2000). Some carabid beetle species such as *P. cupreus* and *Pterostichus melanarius*, which were the most abundant species in our sample, and others such as *Anchomenus dorsalis*, overwinter mainly within the fields or grassy areas, and are open-habitat species which benefit little from hedge boundaries (Holland *et al.*, 2007; Marrec *et al.*, 2015).

Spiders showed a shift of activity-density from the boundaries in early season towards the middle of the fields later in the wheat growing season. Spiders can, to some extent, overwinter within the fields, but we also suggest that semi-natural herbaceous elements could promote biological pest control by spiders by spillover to nearby crops early in the season (Mestre *et al.*, 2018; Pfiffner and Luka, 2000). For example, Linyphiidae spiders, representing more than half of the total activity-density in our study, prefer herbaceous and grassy field margins to hedges, particularly for overwintering (Geiger *et al.*, 2009). In addition, ground-dwelling spider species richness was higher in grass strips than in hedges, but we showed spider species

richness to decrease with distance to the boundary in grass strip field margins, but not in hedge margins. Therefore, semi-natural woody elements may be important for the conservation of diverse spider communities, distinct from those that inhabit grass strips (Mestre et al., 2018), and for maintaining spider species diversity within crops over time.

The dominance of Linyphiidae has been observed with more inclusive sampling methods in cereal crops such as D-vacs and quadrat sampling (Djoudi et al., 2018; Lafage and Pétillon, 2016; Pluess et al., 2010) but could appear surprising using pitfall traps. We encourage readers to consider that the sampling methods used here are not appropriate for all Linyphiidae spider species, which are mostly sheet web builders, but are appropriate for the subfamily Erigoninae, which accounted for 80% of the total Linyphiidae abundance sampled in our pitfall traps. In addition, around two-third of the spiders collected were males, which consume about half of the prey the females do (Harwood et al., 2004), and it is therefore necessary to point out that they would provide less pest control than females. These caveats hold for all the taxa presented here, whose probability of capture is obviously related to the method used. It should be kept in mind that the conclusions for carabid beetles, spiders and slugs are therefore only valid for species easily captured by the pitfall trap method.

Field boundaries may provide an appropriate environment for crop pests (Carrière et al., 2012; Eggenschwiler et al., 2013; Tschamtker et al., 2016). In aphids, landing sites during crop colonisation in spring are mostly located at field boundaries, from which populations grow and spread to the rest of the field (Dean, 1973; Van Emden and Harrington, 2017). Slugs were particularly more abundant close to hedgerows, which is consistent with results found for crop interface. The opposite was found for parasitism rates and predator species activity-density, especially late in the season. This indicates that natural enemy communities that control crop pests have open-area habitat preferences and find appropriate resources towards the interior of wheat crops (Derocles et al., 2014; Thiele, 1977), where their dominant hunting strategies and diets differ from field borders (Gallé et al., 2019). In lowbush blueberry fields, Loureiro et al. (2020) found that carabid beetle diversity does not change with distance from field border or with time, but their activity-density increases with distance from field border. One complementary explanation for parasitoids may be the increasing presence of hyperparasitoids close to the field boundaries, especially in Wallonia (data not shown here), which could have impaired parasitoid populations and disrupted biological control (Tougeron and Tena, 2018).

4.4. Multi-scale summary

Quite unexpectedly, continuity of wooded surfaces at the landscape scale and hedgerows at the local scale appeared favourable to crop pests, while they did not promote the potential of biological control by ground-dwelling spiders, carabids or parasitoids. However, even if natural enemies globally prefer open habitats such as grass strips and tend to move towards the interior of the fields, hedgerows, woodlands, and forest fragments still play important roles and are necessary for maintaining biodiversity onsite in agroecosystems (*e.g.*, species reservoir, dispersal corridors, overwintering and microclimatic shelters, water retention and windbreak effects) (Baudry et al., 2000; Burel et al., 2000; Marrec et al., 2021b; Montgomery et al., 2020), which can lead to an overall better regulation of pests than in simple agricultural landscapes (Bianchi et al., 2006). In addition, our metrics on woody elements did not inform on the quantity of non-wooded semi-natural habitats at the landscape scale, such as grassy or flower strips, or even meadows, which play an important role in maintaining biodiversity in and around the crops, and in providing ecosystem services (Albrecht et al., 2020; Labruyere et al., 2016).

In this perspective, improving biological control could be achieved by considering management of both woody and open habitat semi-natural elements at both the local and landscape scale. To improve biological control, it could therefore be recommended in policy-making to combine different field margin habitats along the same field boundary (*e.g.*, associating a hedge and a grass or flowering strip). This may promote

more diverse natural enemy communities and allow the coexistence of species with overlapping functional niches, such as both canopy-active specialists and ground-active generalist predators (Denys and Tschirntke, 2002; Gallé et al., 2019; Mansion-Vaquié et al., 2017), and may support regulation of pests before they enter crops. It would allow taking advantage of grassy elements, which would be favourable to both grassland and field species, while conserving the other benefits of woody habitats on biodiversity and on other ecosystem services (e.g., carbon storage, soil stabilization, temperature regulation, windbreak effect).

Of course, there is no "one-size-fits-all" answer to the preservation of biodiversity and ecosystem services in agricultural landscapes. It is not surprising that different taxa of arthropods respond differently to landscape variables or local elements, depending on their traits, such as habitat preference and movement capacities (Djoudi et al., 2019; Duflot et al., 2014; Lafage et al., 2015). Therefore, finding the "ideal landscape" will require consideration of the best agriculture-biodiversity and services-disservices trade-offs (e.g., adding hedges for windbreak effect may result in higher slug abundances close to the field border).

5. Conclusion

To conclude, carefully assessing the response of multiple taxa to environmental variations at multiple spatio-temporal scales is crucial to evaluate the efficiency of biological pest control in the context of global change and biodiversity crisis. Hedgerows and woody elements provide in some contexts excellent regulation services, but their optimal quality and density for balancing different ecosystem services, including biological pest control, should be better assessed. Additionally, our vision of semi-natural elements such as hedgerows and woodlands as unique cornerstones of agro-ecological infrastructures must evolve towards better considering their diversity and their potential to serve or impede biological control through their effect on biodiversity, in association with other local and landscape elements.

Data availability

Our dataset has been made publicly and freely available at the following link: <https://doi.org/10.5281/zenodo.5905416>

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References

- Albrecht, M., Williams, N.M., Tschumi, M., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecology Letters* 11, 1488-1498.
- Alford, L., Tougeron, K., Pierre, J.-S., Burel, F., Van Baaren, J., 2017. The effect of landscape complexity and microclimate on the thermal tolerance of a pest insect. *Insect Science* 25, 905–915.

- Alignier, A., Raymond, L., Deconchat, M., Menozzi, P., Monteil, C., Sarthou, J.-P., Vialatte, A., Ouin, A., 2014. The effect of semi-natural habitats on aphids and their natural enemies across spatial and temporal scales. *Biological Control* 77, 76–82.
- Andrade, T.O., Krespi, L., Bonnardot, V., van Baaren, J., Outreman, Y., 2016. Impact of change in winter strategy of one parasitoid species on the diversity and function of a guild of parasitoids. *Oecologia* 180, 877–888. <https://doi.org/10.1007/s00442-015-3502-4>
- Andrade, T.O., Outreman, Y., Krespi, L., Plantegenest, M., Vialatte, A., Gauffre, B., van Baaren, J., 2015. Spatiotemporal variations in aphid-parasitoid relative abundance patterns and food webs in agricultural ecosystems. *Ecosphere* 6, art113. <https://doi.org/10.1890/ES15-00010.1>
- Aviron, S., Burel, F., Baudry, J., Schermann, N., 2005. Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agriculture, Ecosystems & Environment* 108, 205–217. <https://doi.org/10.1016/j.agee.2005.02.004>
- Aviron, S., Lalechère, E., Dufлот, R., Parisey, N., Poggi, S., 2018. Connectivity of cropped vs. semi-natural habitats mediates biodiversity: a case study of carabid beetles communities. *Agriculture, Ecosystems & Environment* 268, 34–43.
- Bale, J.S., van Lenteren, J.C., Bigler, F., 2008. Biological control and sustainable food production. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363, 761–776. <https://doi.org/10.1098/rstb.2007.2182>
- Barton, K., Barton, M.K., 2019. Package ‘MuMIn.’ R package version 1.
- Bates, D., Sarkar, D., Bates, M.D., Matrix, L., 2007. The lme4 package. R package version 2.
- Baudry, J., Bunce, R.G.H., Burel, F., 2000. Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* 60, 7–22. <https://doi.org/10.1006/jema.2000.0358>
- Bernaschini, M.L., Valladares, G., Salvo, A., 2020. Edge effects on insect–plant food webs: assessing the influence of geographical orientation and microclimatic conditions. *Ecological Entomology* 45, 806–820.
- Bertrand, C., Burel, F., Baudry, J., 2016. Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landscape Ecology* 31, 451–466. <https://doi.org/10.1007/s10980-015-0259-4>
- Bianchi, F.J.J.A., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences* 273, 1715–1727. <https://doi.org/10.1098/rspb.2006.3530>
- Boussard, H., Baudry, J., 2019. Chloé4.0: A software for landscape pattern analysis. Available at: https://www6.rennes.inrae.fr/bagap_eng/PRODUCTIONS/Softwares
- Brewer, M.J., Noma, T., Elliott, N.C., Kravchenko, A.N., Hild, A.L., 2008. A landscape view of cereal aphid parasitoid dynamics reveals sensitivity to farm-and region-scale vegetation structure. *EJE* 105, 503–511.
- Briere, J.-F., Pracros, P., Le Roux, A.-Y., Pierre, J.-S., 1999. A Novel Rate Model of Temperature-Dependent Development for Arthropods. *Environ Entomol* 28, 22–29. <https://doi.org/10.1093/ee/28.1.22>
- Burel, F., Aviron, S., Baudry, J., Le Féon, V., Vasseur, C., 2013. The structure and dynamics of agricultural landscapes as drivers of biodiversity, in: *Landscape Ecology for Sustainable Environment and Culture*. Springer, The Netherlands, pp. 285–308.
- Burel, F., Baudry, J., Delettre, Y., Petit, S., Morvan, N., 2000. Relating insect movements to farming systems in dynamic landscapes, in: *Interchanges of Insects between Agricultural and Surrounding Landscapes*. Springer, The Netherlands, pp. 5–32.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociological methods & research* 33, 261–304.

- Carrière, Y., Goodell, P.B., Eilers-Kirk, C., Larocque, G., Dutilleul, P., Naranjo, S.E., Ellsworth, P.C., 2012. Effects of Local and Landscape Factors on Population Dynamics of a Cotton Pest. *PLoS ONE* 7, e39862. <https://doi.org/10.1371/journal.pone.0039862>
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity: Pest and natural enemy response to landscape complexity. *Ecology Letters* 14, 922–932. <https://doi.org/10.1111/j.1461-0248.2011.01642.x>
- Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Broszofski, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in Forest Ecosystem and Landscape Ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience* 49, 288–297.
- Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. *Science advances* 5, eaax0121.
- Dainese, M., Schneider, G., Krauss, J., Steffan-Dewenter, I., 2017. Complementarity among natural enemies enhances pest suppression. *Scientific reports* 7, 1–8.
- Damien, M., Tougeron, K., 2019. Prey–predator phenological mismatch under climate change. *Current Opinion in Insect Science* 35, 60–68. <https://doi.org/10.1016/j.cois.2019.07.002>
- Dankowska, E., 2011. Effectiveness of beer traps and molluscicides as means of gastropod control. *Folia Malacologica* 19, 273–275. <https://doi.org/10.2478/v10125-011-0012-9>
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M.B., Christiansen, D.M., Decocq, G., De Pauw, K., 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology* 27, 2279–2297.
- De Heij, S.E., Willenborg, C.J., 2020. Connected Carabids: Network Interactions and Their Impact on Biocontrol by Carabid Beetles. *BioScience* 70, 490–500. <https://doi.org/10.1093/biosci/biaa039>
- Dean, G.J., 1973. Aphid colonization of spring cereals. *Annals of Applied Biology* 75, 183–193.
- Denys, C., Tschardtke, T., 2002. Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia* 130, 315–324. <https://doi.org/10.1007/s004420100796>
- Derocles, S.A.P., Le Ralec, A., Besson, M.M., Maret, M., Walton, A., Evans, D.M., Plantegenest, M., 2014. Molecular analysis reveals high compartmentalization in aphid-primary parasitoid networks and low parasitoid sharing between crop and noncrop habitats. *Molecular Ecology* 23, 3900–3911. <https://doi.org/10.1111/mec.12701>
- Djoudi, E.A., Marie, A., Mangenot, A., Puech, C., Aviron, S., Plantegenest, M., Pétilion, J., 2018. Farming system and landscape characteristics differentially affect two dominant taxa of predatory arthropods. *Agriculture, Ecosystems & Environment* 259, 98–110. <https://doi.org/10.1016/j.agee.2018.02.031>
- Djoudi, E.A., Plantegenest, M., Aviron, S., Pétilion, J., 2019. Local vs. landscape characteristics differentially shape emerging and circulating assemblages of carabid beetles in agroecosystems. *Agriculture, Ecosystems & Environment* 270–271, 149–158. <https://doi.org/10.1016/j.agee.2018.10.022>
- Duflot, R., Ernoul, A., Burel, F., Aviron, S., 2016. Landscape level processes driving carabid crop assemblage in dynamic farmlands. *Popul Ecol* 58, 265–275. <https://doi.org/10.1007/s10144-015-0534-x>
- Duflot, R., Georges, R., Ernoul, A., Aviron, S., Burel, F., 2014. Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica* 56, 19–26. <https://doi.org/10.1016/j.actao.2014.01.004>
- Eggenschwiler, L., Speiser, B., Bosshard, A., Jacot, K., 2013. Improved field margins highly increase slug activity in Switzerland. *Agronomy for sustainable development* 33, 349–354.
- Fox, J., Weisberg, S., 2011. *An R Companion to Applied Regression*, Second. ed. Sage, Thousand Oaks, CA, USA.

- French, B.W., Elliott, N.C., Berberet, R.C., Burd, J.D., 2001. Effects of riparian and grassland habitats on ground beetle (Coleoptera: Carabidae) assemblages in adjacent wheat fields. *Environmental Entomology* 30, 225–234.
- Fusser, M.S., Pfister, S.C., Entling, M.H., Schirmel, J., 2016. Effects of landscape composition on carabids and slugs in herbaceous and woody field margins. *Agriculture, Ecosystems & Environment* 226, 79–87. <https://doi.org/10.1016/j.agee.2016.04.007>
- Gagic, V., Hänke, S., Thies, C., Scherber, C., Tomanović, Ž., Tscharnkte, T., 2012. Agricultural intensification and cereal aphid–parasitoid–hyperparasitoid food webs: network complexity, temporal variability and parasitism rates. *Oecologia* 170, 1099–1109. <https://doi.org/10.1007/s00442-012-2366-0>
- Gallé, R., Happe, A., Baillod, A.B., Tscharnkte, T., Batáry, P., 2019. Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *Journal of Applied Ecology* 56, 63–72. <https://doi.org/10.1111/1365-2664.13257>
- Geiger, F., Wäckers, F.L., Bianchi, F.J.J.A., 2009. Hibernation of predatory arthropods in semi-natural habitats. *BioControl* 54, 529–535. <https://doi.org/10.1007/s10526-008-9206-5>
- Glen, D., Moens, R., 2002. Agriolimacidae, Arionidae and Milacidae as pests in Western European cereals. In: *Molluscs as crop pests*, Barker, G. M. (Ed.), CABI press, Wallingford, United-Kingdom, pp 271–300.
- Gray, C., Ma, A., McLaughlin, O., Petit, S., Woodward, G., Bohan, D.A., 2021. Ecological plasticity governs ecosystem services in multilayer networks. *Commun Biol* 4, 75. <https://doi.org/10.1038/s42003-020-01547-3>
- Greenstone, M.H., Shufan, K.A., 2003. Spider predation: species-specific identification of gut contents by polymerase chain reaction. *The journal of arachnology* 31, 131–134.
- Gurr, G.M., Wratten, S.D., Landis, D.A., You, M., 2017. Habitat Management to Suppress Pest Populations: Progress and Prospects. *Annu. Rev. Entomol.* 62, 91–109. <https://doi.org/10.1146/annurev-ento-031616-035050>
- Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tscharnkte, T., Holzschuh, A., 2014. Landscape configuration of crops and hedgerows drives local syrphid fly abundance. *Journal of applied ecology* 51, 505–513.
- Hartig, F., 2020. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.3.3.0.
- Harwood, J.D., Sunderland, K.D., Symondson, W.O.C., 2004. Prey selection by linyphiid spiders: molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. *Molecular Ecology*, 13: 3549–3560.
- Harwood, J.D., Obrycki, J.J., 2013. Quantifying aphid predation rates of generalist predators in the field. *EJE* 102, 335–350.
- Henningsen, A., 2017. censReg: Censored Regression (Tobit) Models. R package version 0.5.
- Holland, J.M., 2002. *The agroecology of carabid beetles*. Intercept Limited, Andover, United Kingdom.
- Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. *Pest management science* 72, 1638–1651.
- Holland, J.M., Thomas, C.F.G., Birkett, T., Southway, S., 2007. Spatio-temporal distribution and emergence of beetles in arable fields in relation to soil moisture. *Bulletin of Entomological Research* 97, 89–100. <https://doi.org/10.1017/S0007485307004804>
- Honek, A., Martinková, Z., Jarošík, V., 2013. Ground beetles (Carabidae) as seed predators. *EJE* 100, 531–544.
- Honek, A., Martinkova, Z., Saska, P., 2011. Effect of size, taxonomic affiliation and geographic origin of dandelion (*Taraxacum* agg.) seeds on predation by ground beetles (Carabidae, Coleoptera). *Basic and Applied Ecology* 12, 89–96.

- Honek, A., Martinkova, Z., Saska, P., Dixon, A.F.G., 2018. Aphids (Homoptera: Aphididae) on Winter Wheat: Predicting Maximum Abundance of *Metopolophium dirhodum*. *J Econ Entomol* 111, 1751–1759.
- Hooks, C.R., Fereres, A., 2006. Protecting crops from non-persistently aphid-transmitted viruses: a review on the use of barrier plants as a management tool. *Virus research* 120, 1–16.
- Ikeda, H., Kubota, K., Kagawa, A., Sota, T., 2010. Diverse diet compositions among harpaline ground beetle species revealed by mixing model analyses of stable isotope ratios. *Ecological Entomology* 35, 307–316. <https://doi.org/10.1111/j.1365-2311.2010.01182.x>
- Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography* 24, 52–63. <https://doi.org/10.1111/geb.12233>
- Jarošík, V., Kratochvíl, L., Honěk, A., Dixon, A.F., 2004. A general rule for the dependence of developmental rate on temperature in ectothermic animals. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271, S219–S221.
- Jeannel, R., 1942. Coléoptères Carabiques II, Faune de France. Lechevalier, Paris, France.
- Jeannel, R., 1941. Coléoptères Carabiques, Faune de France. Lechevalier, Paris, France.
- Jonsson, M., Kaartinen, R., Straub, C.S., 2017. Relationships between natural enemy diversity and biological control. *Current Opinion in Insect Science* 20, 1–6. <https://doi.org/10.1016/j.cois.2017.01.001>
- Jonsson, M., Straub, C.S., Didham, R.K., Buckley, H.L., Case, B.S., Hale, R.J., Gratton, C., Wratten, S.D., 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *Journal of Applied Ecology* 52, 1274–1282.
- Jonsson, M., Wratten, S.D., Landis, D.A., Gurr, G.M., 2008. Recent advances in conservation biological control of arthropods by arthropods. *Biological control* 45, 172–175.
- Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., O'Rourke, M.E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J.A., Schellhorn, N.A., Tschirntke, T., Wratten, S.D., Zhang, W., Iverson, A.L., Adler, L.S., Albrecht, M., Aligned, A., Angelella, G.M., Zubair Anjum, M., Avelino, J., Batáry, P., Baveco, J.M., Bianchi, F.J.J.A., Birkhofer, K., Bohnenblust, E.W., Bommarco, R., Brewer, M.J., Caballero-López, B., Carrière, Y., Carvalheiro, L.G., Cayuela, L., Centrella, M., Četković, A., Henri, D.C., Chabert, A., Costamagna, A.C., De la Mora, A., de Kraker, J., Desneux, N., Diehl, E., Diekötter, T., Dormann, C.F., Eckberg, J.O., Entling, M.H., Fiedler, D., Franck, P., Frank van Veen, F.J., Frank, T., Gagic, V., Garratt, M.P.D., Getachew, A., Gonthier, D.J., Goodell, P.B., Graziosi, I., Groves, R.L., Gurr, G.M., Hajian-Forooshani, Z., Heimpel, G.E., Herrmann, J.D., Huseth, A.S., Inclán, D.J., Ingraio, A.J., Iv, P., Jacot, K., Johnson, G.A., Jones, L., Kaiser, M., Kaser, J.M., Keasar, T., Kim, T.N., Kishinevsky, M., Landis, D.A., Lavandero, B., Lavigne, C., Le Ralec, A., Lemessa, D., Letourneau, D.K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K., Madeira, F., Mader, V., Cortesero, A.M., Marini, L., Martinez, E., Martinson, H.M., Menozzi, P., Mitchell, M.G.E., Miyashita, T., Molina, G.A.R., Molina-Montenegro, M.A., O'Neal, M.E., Opatovsky, I., Ortiz-Martinez, S., Nash, M., Östman, Ö., Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perović, D.J., Peterson, J.A., Petit, S., Philpott, S.M., Plantegenest, M., Plečáň, M., Pluess, T., Pons, X., Potts, S.G., Pywell, R.F., Ragsdale, D.W., Rand, T.A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.-P., Saulais, J., Schäckermann, J., Schmidt, N.P., Schneider, G., Schüepp, C., Sivakoff, F.S., Smith, H.G., Stack Whitney, K., Stutz, S., Szendrei, Z., Takada, M.B., Taki, H., Tamburini, G., Thomson, L.J., Tricault, Y., Tsafack, N., Tschumi, M., Valantin-Morison, M., Van Trinh, M., van der Werf, W., Vierling, K.T., Werling, B.P., Wickens, J.B., Wickens, V.J., Woodcock, B.A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A., Zou, Y., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proc Natl Acad Sci USA* 115, E7863–E7870. <https://doi.org/10.1073/pnas.1800042115>
- Kleijn, D., Kohler, F., Baldi, A., Batary, P., Concepcion, E.D., Clough, Y., Diaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovacs, A., Marshall, E.J.P., Tschirntke, T., Verhulst, J., 2009. On the relationship

- between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B: Biological Sciences* 276, 903–909. <https://doi.org/10.1098/rspb.2008.1509>
- Labruyere, S., Ricci, B., Lubac, A., Petit, S., 2016. Crop type, crop management and grass margins affect the abundance and the nutritional state of seed-eating carabid species in arable landscapes. *Agriculture, Ecosystems & Environment* 231, 183–192. <https://doi.org/10.1016/j.agee.2016.06.037>
- Lafage, D., Maugenest, S., Bouzillé, J.-B., Pétilion, J., 2015. Disentangling the influence of local and landscape factors on alpha and beta diversities: opposite response of plants and ground-dwelling arthropods in wet meadows. *Ecol Res* 30, 1025–1035. <https://doi.org/10.1007/s11284-015-1304-0>
- Lafage, D., Pétilion, J., 2016. Relative importance of management and natural flooding on spider, carabid and plant assemblages in extensively used grasslands along the Loire. *Basic and Applied Ecology* 17, 535–545.
- Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual review of entomology* 45, 175–201. <https://doi.org/10.1146/annurev.ento.45.1.175>
- Larsen, A.E., Noack, F., 2020. Impact of local and landscape complexity on the stability of field-level pest control. *Nat Sustain* 4, 120–128. <https://doi.org/10.1038/s41893-020-00637-8>
- Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M. 2019. emmeans: Estimated marginal means, aka least-squares means. R package version 1.3.4.
- Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N.A., Carvalheiro, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.-M., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E., Memmott, J., Morandin, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pockock, M.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardiñas, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tscharrntke, T., Veselý, M., Weisser, W.W., Wilson, J.K., Crowder, D.W., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Glob Change Biol* 23, 4946–4957. <https://doi.org/10.1111/gcb.13714>
- Loureiro, A.M., Nams, V.O., White, S.N., Cutler, G.C., 2020. Short-Term Dispersal and Long-Term Spatial and Temporal Patterns of Carabidae (Coleoptera) in Lowbush Blueberry Fields. *Environmental Entomology* 49, 572–579.
- Lüdecke, D., 2018a. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *JOSS* 3, 772. <https://doi.org/10.21105/joss.00772>
- Lüdecke, D., 2018b. sjPlot: Data visualization for statistics in social science. R package version 2.
- Lüdecke, D., Makowski, D., Waggoner, P., Patil, I., 2020. performance: assessment of regression models performance. R package version. 0.4. 7.
- Macfadyen, S., Muller, W., 2013. Edges in agricultural landscapes: species interactions and movement of natural enemies. *PloS one* 8, e59659.
- Mansion-Vaquíe, A., Ferrante, M., Cook, S., Pell, J., Lövei, G., 2017. Manipulating field margins to increase predation intensity in fields of winter wheat (*Triticum aestivum*). *Journal of Applied Entomology* 141, 600–611.
- Marrec, R., Badenhauer, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N., Gauffre, B., 2015. Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape. *Agriculture, Ecosystems & Environment* 199, 282–289. <https://doi.org/10.1016/j.agee.2014.10.005>

- Marrec, R., Caro, G., Miguet, P., Badenhausser, I., Plantegenest, M., Vialatte, A., Bretagnolle, V., Gauffre, B., 2017. Spatiotemporal dynamics of the agricultural landscape mosaic drives distribution and abundance of dominant carabid beetles. *Landscape Ecology* 32, 2383–2398. <https://doi.org/10.1007/s10980-017-0576-x>
- Marrec, R., Gross, N., Badenhausser, I., Dupeyron, A., Caro, G., Bretagnolle, V., Roncoroni, M., Gauffre, B., 2021a. Functional traits of carabid beetles reveal seasonal variation in community assembly in annual crops. *bioRxiv* 2021.02.04.429696. <https://doi.org/10.1101/2021.02.04.429696>
- Marrec, R., Le Roux, V., Martin, L., Lenoir, J., Brunet, J., Cousins, S.A., De Smedt, P., Deconchat, M., Diekmann, M., Ehrmann, S., 2021b. Multiscale drivers of carabid beetle (Coleoptera: Carabidae) assemblages in small European woodlands. *Global Ecology and Biogeography* 30, 165–182.
- Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment* 89, 5–21. [https://doi.org/10.1016/S0167-8809\(01\)00315-2](https://doi.org/10.1016/S0167-8809(01)00315-2)
- Martin, E.A., Reineking, B., Seo, B., Steffan-Dewenter, I., 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences* 110, 5534–5539.
- Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., Nowakowski, M., 2002. The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation* 106, 259–271. [https://doi.org/10.1016/S0006-3207\(01\)00252-X](https://doi.org/10.1016/S0006-3207(01)00252-X)
- Mestre, L., Schirmel, J., Hetz, J., Kolb, S., Pfister, S.C., Amato, M., Sutter, L., Jeanneret, P., Albrecht, M., Entling, M.H., 2018. Both woody and herbaceous semi-natural habitats are essential for spider overwintering in European farmland. *Agriculture, Ecosystems & Environment* 267, 141–146. <https://doi.org/10.1016/j.agee.2018.08.018>
- Metcalf, A.V., Cowpertwait, P.S.P., 2009. *Introductory Time Series with R*. Springer New York, New York, NY, USA. <https://doi.org/10.1007/978-0-387-88698-5>
- Michalko, R., Pekár, S., Entling, M.H., 2019. An updated perspective on spiders as generalist predators in biological control. *Oecologia* 189, 21–36. <https://doi.org/10.1007/s00442-018-4313-1>
- Michel, N., Burel, F., Legendre, P., Butet, A., 2007. Role of habitat and landscape in structuring small mammal assemblages in hedgerow networks of contrasted farming landscapes in Brittany, France. *Landscape Ecology* 22, 1241–1253.
- Montgomery, I., Caruso, T., Reid, N., 2020. Hedgerows as Ecosystems: Service Delivery, Management, and Restoration. *Annu. Rev. Ecol. Evol. Syst.* 51, 012120-100346. <https://doi.org/10.1146/annurev-ecolsys-012120-100346>
- Muneret, L., Mitchell, M., Seufert, V., Aviron, S., Djoudi, E.A., Pétilion, J., Plantegenest, M., Thiéry, D., Rusch, A., 2018. Evidence that organic farming promotes pest control. *Nature Sustainability* 1, 361–368. <https://doi.org/10.1038/s41893-018-0102-4>
- Nakagawa, S., Johnson, P.C., Schielzeth, H., 2017. The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface* 14, 20170213.
- Nentwig, W., Blick, T., Gloor, D., Hänggi, A., Kropf, C., 2019. *Araneae Spiders of Europe*. URL <https://araneae.nmbe.ch/> (accessed 5.3.19).
- Nyffeler, M., Symondson, W.O., 2001. Spiders and harvestmen as gastropod predators. *Ecological Entomology* 26, 617–628.
- Öberg, S., 2009. Influence of landscape structure and farming practice on body condition and fecundity of wolf spiders. *Basic and Applied Ecology* 10, 614–621.
- Parsa, S., Ccanto, R., Rosenheim, J.A., 2011. Resource concentration dilutes a key pest in indigenous potato agriculture. *Ecological Applications* 21, 539–546.

- Pecheur, E., Piqueray, J., Monty, A., Dufrêne, M., Mahy, G., 2020. The influence of ecological infrastructures adjacent to crops on their carabid assemblages in intensive agroecosystems. *PeerJ* 8, e8094. <https://doi.org/10.7717/peerj.8094>
- Pekár, S., Toft, S., 2015. Trophic specialisation in a predatory group: the case of prey-specialised spiders (Araneae): Prey-specialised spiders (Araneae). *Biol Rev* 90, 744–761. <https://doi.org/10.1111/brv.12133>
- Pfiffner, L., Luka, H., 2000. Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agriculture, Ecosystems & Environment* 78, 215–222. [https://doi.org/10.1016/S0167-8809\(99\)00130-9](https://doi.org/10.1016/S0167-8809(99)00130-9)
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1-117.
- Plantegenest, M., Pierre, J.S., Dedryver, C.A., Kindlmann, P., 2001. Assessment of the relative impact of different natural enemies on population dynamics of the grain aphid *Sitobion avenae* in the field. *Ecological Entomology* 26, 404–410. <https://doi.org/10.1046/j.1365-2311.2001.00330.x>
- Plećaš, M., Gagić, V., Janković, M., Petrović-Obradović, O., Kavallieratos, N.G., Tomanović, Ž., Thies, C., Tscharncke, T., Četković, A., 2014. Landscape composition and configuration influence cereal aphid–parasitoid–hyperparasitoid interactions and biological control differentially across years. *Agriculture, Ecosystems & Environment* 183, 1–10. <https://doi.org/10.1016/j.agee.2013.10.016>
- Pluess, T., Opatovsky, I., Gavish-Regev, E., Lubin, Y., Schmidt-Entling, M.H., 2010. Non-crop habitats in the landscape enhance spider diversity in wheat fields of a desert agroecosystem. *Agriculture, ecosystems & environment* 137, 68–74.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences* 118.
- Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., Ripley, M.B., 2013. Package ‘mass.’
- Roger, J.-L., Jambon, O., Bouger, G., 2013. Clé de détermination des Carabides-Paysages agricoles du nord ouest de la France. Retrieved at: http://grenha.fr/documents/CarabidaeUniv_Rennes-JL_Roger_INRA.pdf
- Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. *Oikos* 98:1, 156–162.
- Roubinet, E., Jonsson, T., Malsher, G., Staudacher, K., Traugott, M., Ekbom, B., Jonsson, M., 2018. High redundancy as well as complementary prey choice characterize generalist predator food webs in agroecosystems. *Scientific reports* 8, 1–10.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., Thies, C., Tscharncke, T., Weisser, W.W., Winqvist, C., Woltz, M., Bommarco, R., 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystems & Environment* 221, 198–204. <https://doi.org/10.1016/j.agee.2016.01.039>
- Sarthou, J.-P., Badoz, A., Vaissière, B., Chevallier, A., Rusch, A., 2014. Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats. *Agriculture, Ecosystems & Environment* 194, 17–28. <https://doi.org/10.1016/j.agee.2014.04.018>
- Saska, P., Němeček, J., Koprudová, S., Skuhrovec, J., Káš, M., 2014. Weeds determine the composition of carabid assemblage in maize at a fine scale. *Sci. Agric. Bohem* 45, 85–92.
- Šerić Jelaska, L., Franjević, D., Jelaska, S.D., Symondson, W.O.C., 2014. Prey detection in carabid beetles (Coleoptera: Carabidae) in woodland ecosystems by PCR analysis of gut contents. *EJE* 111, 631–638. <https://doi.org/10.14411/eje.2014.079>

- Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences* 116, 16442–16447.
- Symondson, W.O., Glen, D.M., Ives, A.R., Langdon, C.J., Wiltshire, C.W., 2002. Dynamics of the relationship between a generalist predator and slugs over five years. *Ecology* 83, 137–147.
- Thiele, H.-U., 1977. *Carabid Beetles in their Environments: a Study on Habitat Selection by Adaptations in Physiology and Behaviour*. Springer-Verlag, Berlin, Germany.
- Thies, C., Roschewitz, I., Tschamntke, T., 2005. The landscape context of cereal aphid-parasitoid interactions. *Proceedings of the Royal Society B: Biological Sciences* 272, 203–210. <https://doi.org/10.1098/rspb.2004.2902>
- Thomas, C.F.G., Parkinson, L., Marshall, E.J.P., 1998. Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. *Oecologia* 116, 103–112. <https://doi.org/10.1007/s004420050568>
- Tougeron, K., Damien, M., Le Lann, C., Brodeur, J., van Baaren, J., 2018. Rapid Responses of Winter Aphid-Parasitoid Communities to Climate Warming. *Frontiers in Ecology and Evolution* 6, 173. <https://doi.org/10.3389/fevo.2018.00173>
- Tougeron, K., Tena, A., 2018. Hyperparasitoids as new targets in biological control in a global change context? *Biological Control* 130, 164–171.
- Tougeron, K., van Baaren, J., Burel, F., Alford, L., 2016. Comparing thermal tolerance across contrasting landscapes: first steps towards understanding how landscape management could modify ectotherm thermal tolerance. *Insect Conservation and Diversity* 9, 171–180. <https://doi.org/10.1111/icad.12153>
- Tschamntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S., Vidal, S., 2008. Reprint of “Conservation biological control and enemy diversity on a landscape scale” [*Biol. Control* 43 (2007) 294–309]. *Biological Control* 45, 238–253.
- Tschamntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E.A., Martínez-Salinas, A., Meehan, T.D., O’Rourke, M., Poveda, K., Rosenheim, J.A., Rusch, A., Schellhorn, N., Wanger, T.C., Wratten, S., Zhang, W., 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. *Biological Conservation* 204, 449–458. <https://doi.org/10.1016/j.biocon.2016.10.001>
- Tschamntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters* 8, 857–874.
- Tschamntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews* 87, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Van Emden, H.F., Harrington, R. (Eds.), 2017. *Aphids as crop pests*. CABI, Wallingford, UK.
- Vannier, C., Vasseur, C., Hubert-Moy, L., Baudry, J., 2011. Multiscale ecological assessment of remote sensing images. *Landscape ecology* 26, 1053–1069.
- Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.-M., Baudry, J., 2013. The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agriculture, ecosystems & environment* 166, 3–14.
- Ver Hoef, J.M., Boveng, P.L., 2007. Quasi-poisson vs. Negative binomial regression: how should we model overdispersed count data? *Ecology* 88, 2766–2772. <https://doi.org/10.1890/07-0043.1>

- Vermunt, B., Cuddington, K., Sobek-Swant, S., Crosthwaite, J.C., Lyons, D.B., Sinclair, B.J., 2012. Temperatures experienced by wood-boring beetles in the under-bark microclimate. *Forest Ecology and Management* 269, 149–157.
- Voeten, C.C., 2019. Using 'buildmer' to automatically find & compare maximal (mixed) models. <https://github.com/cvoeten/buildmer/>. v1.9.
- Welch, K.D., Harwood, J.D., 2014. Temporal dynamics of natural enemy–pest interactions in a changing environment. *Biological Control* 75, 18–27. <https://doi.org/10.1016/j.biocontrol.2014.01.004>
- Zalewski, M., Dudek, D., Tiunov, A.V., Godeau, J.-F., Okuzaki, Y., Ikeda, H., Sienkiewicz, P., Ulrich, W., 2014. High Niche Overlap in the Stable Isotope Space Of Ground Beetles. *Annales Zoologici Fennici* 51, 301–312. <https://doi.org/10.5735/086.051.0302>

Supplementary Material

Methods for meteorological data analyses

In time series regression analyses, it is common that the residual series are autocorrelated, implying that a correction for estimated regression parameters must be applied (Metcalf and Cowpertwait, 2009). The autocorrelation and partial autocorrelation functions were calculated for the regressions and we performed Durbin-Watson tests (*car* package, Fox and Weisberg, 2011) to visually and numerically estimate lag autocorrelation of residuals in our models, and to correct for it (Fox and Weisberg, 2011). Selection of best AR(p) structure was done on global models (*i.e.*, including all explanatory variables and interactions). For each GLS linear model, the date was specified as a quadratic time covariate and the sampling region as a grouping factor in the ARMA correlation structure. Finally, to analyse trends in DD4 cumulation, the same models as for mean temperatures were run with cumulated DD4 as a response variable, for both the winter period and the sampling period, except that the date as a quadratic covariate was removed.

During the winter period preceding sampling: For mean temperatures, incorporating eighth order autocorrelation had effectively eliminated the temporal autocorrelation in the residuals; the model that incorporates the AR(8) structure was a better fit than linear models with AR(1) or no AR structure according to AIC (2668, 2886, 3501, respectively for AR(8), AR(1) and AR(0)). For mean minimal temperatures, incorporating seventh order autocorrelation had eliminated the temporal autocorrelation in the residuals; the model that incorporates the AR(7) structure was a better fit than linear models with AR(1) or no AR structure according to AIC (3166, 3169, 3655, respectively for AR(7), AR(1) and AR(0)). Concerning daily rainfall data, a fourth order residual autocorrelation was found, but a GLS with AR(4) structure was not sufficient to completely remove autocorrelation in the residuals, and according to AIC, the Tobit regression model better fitted the data than an AR(4) GLS (3241 and 3509, respectively). To analyse trends in DD4 cumulation, the same parameters as for mean temperature models were used with cumulated DD4 as a response variable, for both the winter period and the sampling period.

During the sampling period: For mean temperatures, AR(5) GLS structure was the best fit according to AIC (2589, 2623, 3142, respectively for AR(5), AR(1), and AR(0)). For mean minimal temperatures, AR(1) structure was the best fit according to AIC (2850, 3124 respectively for AR(1) and AR(0)). For rainfall data a Tobit regression model again better fitted the data than an AR(1) GLS according to AIC (2723 and 3350, respectively).

Detailed results for meteorological data analyses

For the winter period (December 1st to March 21st), we found a quadratic effect of the date, showing that mean temperatures first decreased during the first phase of the winter and then increased. Mean temperatures were different among regions, with Brittany being on average warmer (6.12 ± 0.24 °C) than both Hauts-de-France (3.98 ± 0.25 °C, t-ratio = -3.8, $p < 0.01$) and Wallonia (4.14 ± 0.24 °C, t-ratio = -3.5, $p < 0.01$). As a consequence, and even though the mean temperature dynamic during the winter season was similar between regions, DD4 cumulated faster in Brittany than in both Wallonia and Hauts-de-France, for both years ($\chi^2 = 1.60$, $df = 2$, $p = 0.45$) (**Figure S4**, see **Table S3** for statistical results).

For the winter period, we found no difference in mean temperature between years, and the regional effect did not differ between years, or across the winter period (*i.e.*, no interaction effect with the date). However, change in temperatures did not occur at the same rate (*i.e.*, at the same date) between both years. Note that relatively severe cold snaps occurred in each region on 2016-12-31 (< -3.0 °C) and on 2017-01-20 (< -2.6 °C), while cold snaps occurred later for the second sampling year, on 2018-03-01 (< -4.3 °C in Wallonia, < -2.6 °C in other regions). Mean minimal temperatures followed the same trends as mean temperatures (means of 3.30 ± 0.28 , 1.42 ± 0.27 , and 1.24 ± 0.26 °C, for Brittany, Hauts-de-France and Wallonia, respectively). Daily precipitation rates differed between years; 2017 was dryer than 2018 (1.46 ± 0.16 and 2.80 ± 0.22 mm, respectively, all regions confounded), and precipitations occurred at different times during winter between both years. No regional effect was found on precipitation rates (**Table S3**).

For the sampling period (March 22nd to June 30th), mean temperatures significantly increased across the season (of on average of 0.12 ± 0.01 °C per day), there was no difference in mean temperature among years or regions. The increase rate of mean temperatures was not different among years and regions (*i.e.*, no interaction effect). DD4 did not cumulate faster in any of the regions ($\chi^2 = 1.22$, $df = 2$, $p = 0.54$) and cumulation was similar between years ($\chi^2 = 2.38$, $df = 2$, $p = 0.31$). Mean minimal temperatures were overall different between years, with 2017 having lower minimal temperatures than 2018 (8.32 ± 0.29 and 9.28 ± 0.24 °C, respectively), and this difference was consistent among regions and across the sampling season. Precipitation rates differed between years, with 2017 being dryer than 2018 (1.26 ± 0.19 and 1.90 ± 0.25 mm, respectively) (**Figure S4**), and precipitations occurred at different times between both years during the sampling period. No regional effect was found on precipitation rates (**Table S3**).

Supplementary Figure

Figure S1: Landscape variables correlogram. Pearson’s correlations were calculated between pairs of landscape metrics taken at the highest available buffer scale around sampling points, all regions, years and fields taken together.

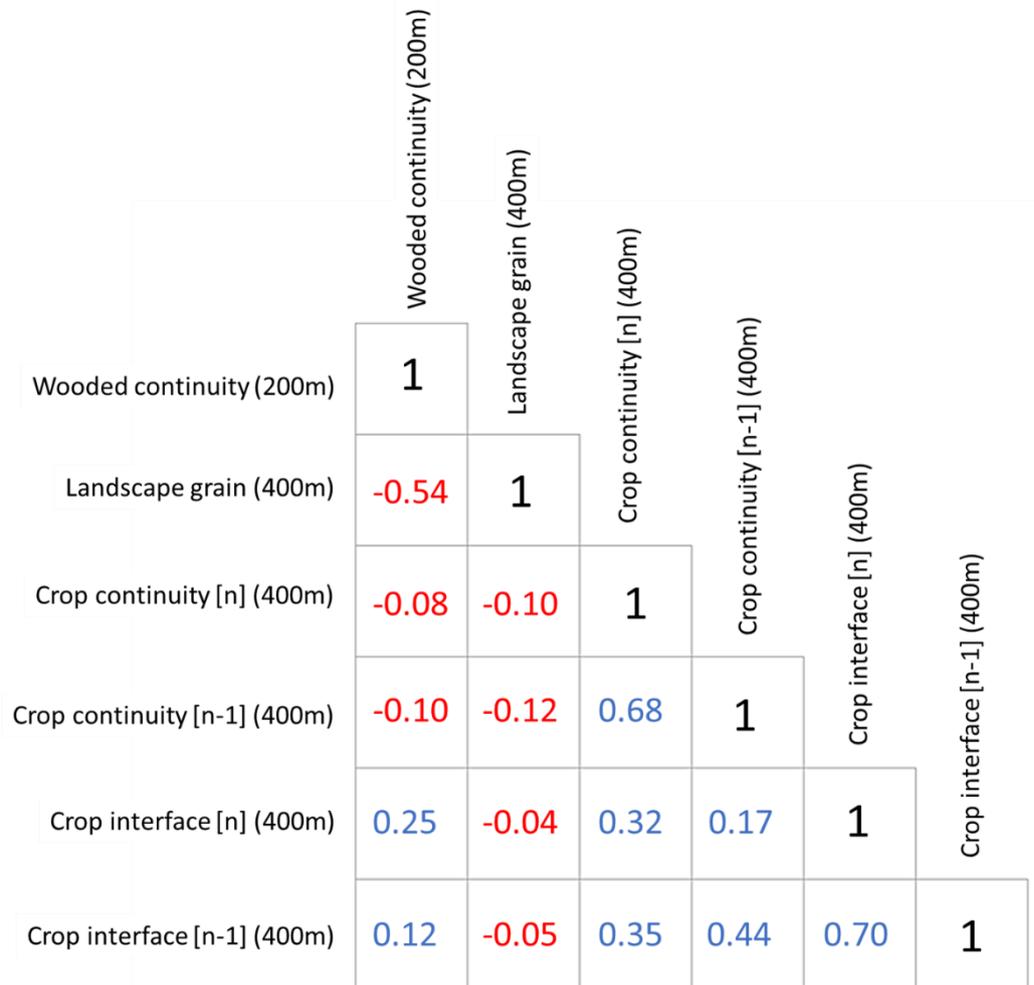


Figure S2: Landscape grain is used to characterize the landscape matrix from fine grain (many small elements) to coarse grain (fewer large elements) (Vannier et al., 2011). Networks with a high density of hedgerows are “fine grain”, i.e. the average mesh of the landscape is small, while “coarse grain” networks have a low density of hedgerows. This metric provides more information than just the hedgerow density because when the element is scarce, many spatial configurations of networks are possible. For instance, in a landscape with few hedgerows, they can be evenly distributed or clumped, which may create different ecological conditions. Few clumped hedgerows can maintain a high hedgerow influence in part of the considered landscape. The shape of fields also matters: rectangular fields have less area distant to hedgerows (limits) than square ones. This will change the effect of hedgerows on wind, heat, the microclimate of fields and hedgerows and the shape of the non-wooded matrix in the landscape. All of this enters in consideration in the calculation of the grain (calculated here using the CHLOE landscape software).

In a rectangular field (fine grain), there is less open land “far” from the surrounding hedgerow than in a square field (coarse grain). We consider that hedgerows have a windbreak effect to a distance up to 10 times their height. The average height is 10 m. We consider that beyond 100 m, all distances to hedgerow equal 100 m. In the example shown here, the area at >100 m from the hedgerow covers 14% of the total surface in the rectangular field, resulting in a small grain value, while it covers 25% in the rectangular field, resulting in a higher grain value. The red area in the right panel of the figure represents the grain at the landscape scale (the more “open” the landscape, the coarser the grain).

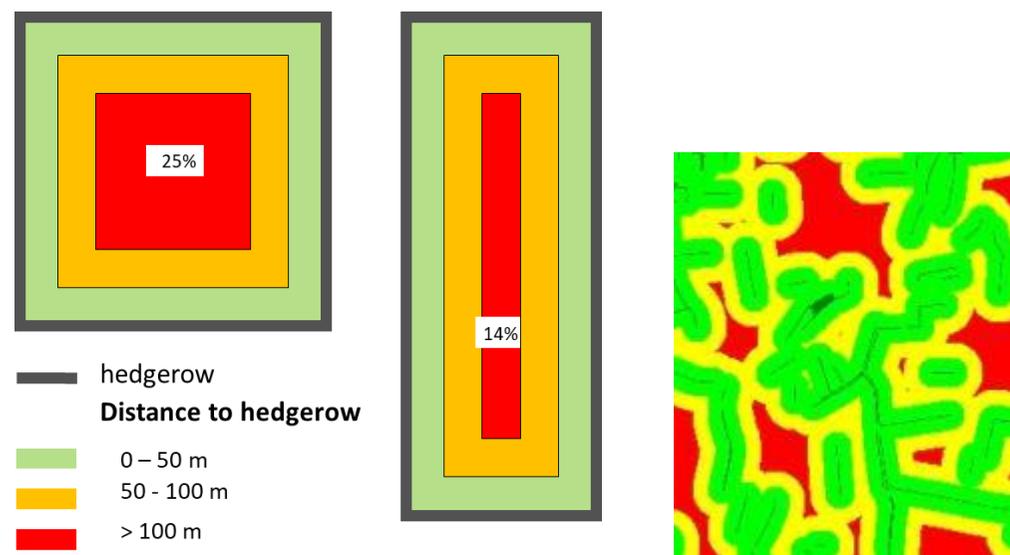
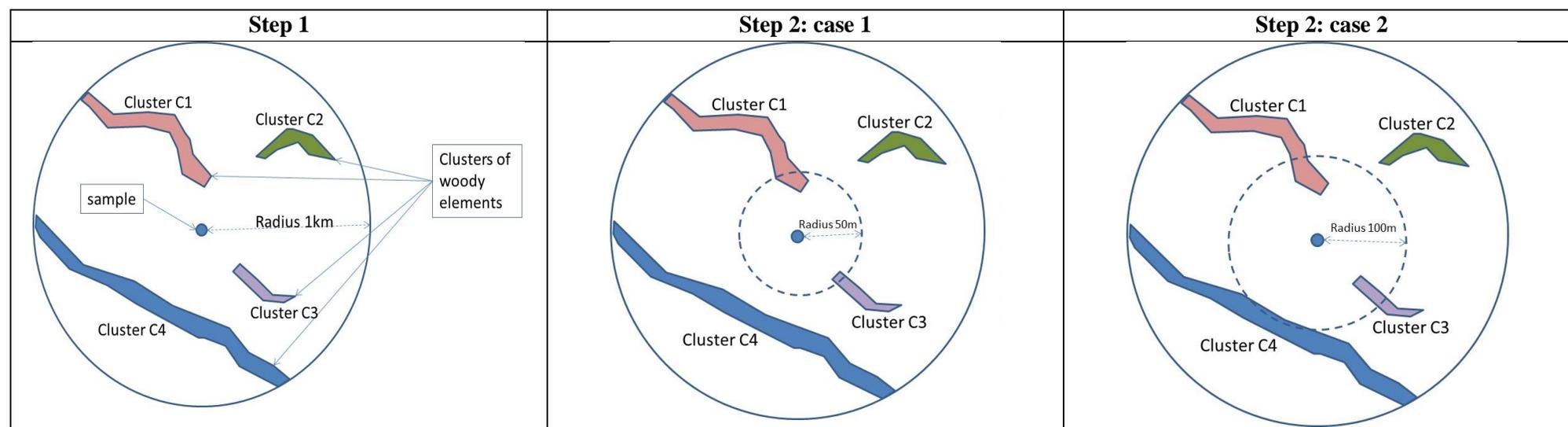


Figure S3: Calculation of the “continuity of wooded surface” metric. **Step 1: identification of the clusters** of interconnected wooded surfaces such as hedgerows and woodlots in a buffer of 1 km radius around the sampling point (large plain circle on the figure, not at scale). **Step 2:** Measure of the total area of the cluster overlapping concentric buffers of 50, 100, 150, and 200 m radius. Example: case 1, clusters C1 and C3 are included in the 50 m radius buffer, so the sum of their total surface (in hectare) in the 1 km radius gives the measure of the wooded continuity. Case 2, clusters C1, C3 and C4 are included in the 100 m radius buffer, so the sum of their total surface (in hectare) gives the measure of the wooded continuity. Similar method is used to measure the continuity of crop surfaces: it is calculated by adding the surface of interconnected winter crops to the surface of interconnected summer crops within the 1km radius circle.



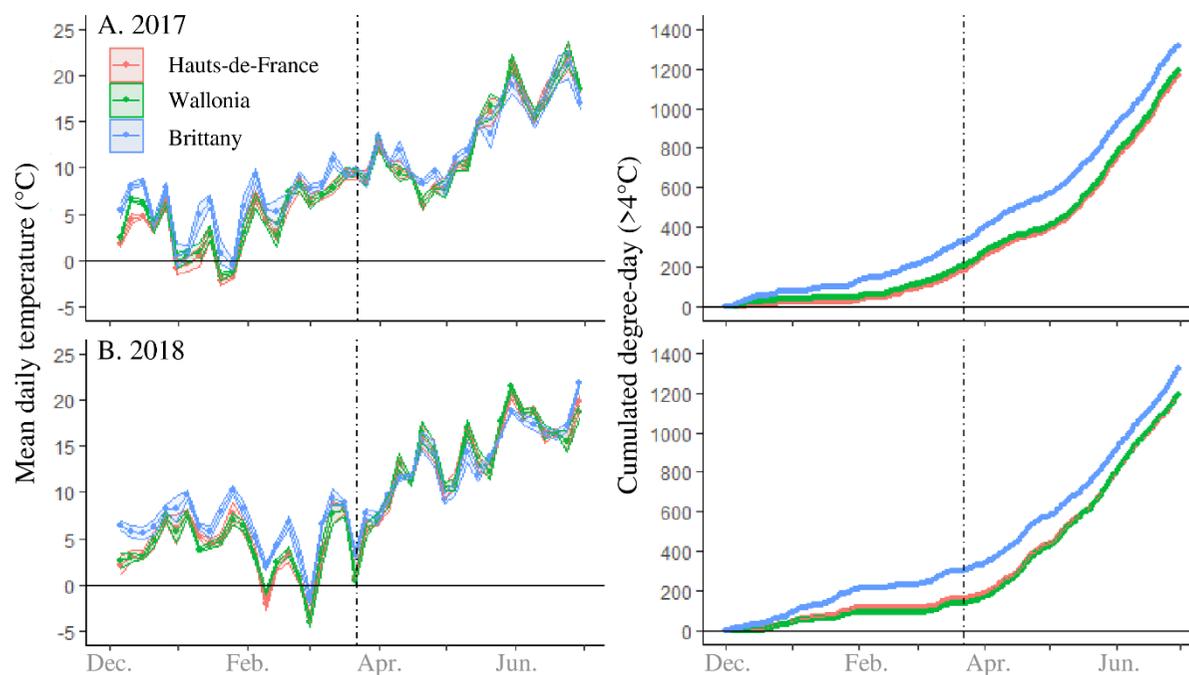


Figure S4: Five-day average temperatures and daily cumulated degree-day (>4 °C) for the three sampling regions (Hauts-de-France, Wallonia and Brittany), between December 1st and June 30th, and for **A.** 2017 and **B.** 2018. Dashed lines correspond to March 22nd of each year, separating the winter period and the sampling period. Smooth areas correspond to standard error on temperature averaged among the three to five weather stations of each region.

Supplementary Tables

Table S1: Names and coordinates of weather stations in the three study regions, from which meteorological data were obtained and averaged for statistical analyses. Each station is located within each of the study area, but distance between each station and each landscape window vary, hence the interest to use averaged data on all stations.

Region	Station location	Coordinates
Brittany	Broualan	48°29'N, 1°38'W
	Feins	48°19'N, 1°35'W
	Louvigné-du-Désert	48°28'N, 1°07'W
	Pontorson	48°34'N, 1°28'W
Haut-de-France	Aulnois-sous-Laon	49°35'N, 3°36'E
	Saint Quentin	49°49'N, 3°12'E
	Fontaine-lès-vervins	49°50'N, 3°52'E
	Origny-sainte-Beno	49°50'N, 3°28'E
	St-Hilaire-sur-Helpe	50°08'N, 3°55'E
Wallonia	Sivry	50°10'N, 4°10'E
	Beauvechain	50°75'N, 4°77'E
	Zulzeke	50°46'N, 3°34'E

Table S2: Selection of scales at which landscape variables were tested for each dependent variable and taxon based on Akaike's 'An Information Criterion' (AIC). AD (Activity-Density), SR (Species-Richness), AB (Abundance), PR (Parasitism Rate). Fitted generalized mixed linear models were of type *response variable ~ landscape explanatory variable (scale) + (1 | landscape_window_year)*, as described in the material and methods section. Selected scales based on smallest AIC are highlighted in bold. Given the high AIC values obtained, there is likely statistically no difference between two models with very close AIC values. More optimal solutions for model selection, such as model averaging, were impossible to perform due to restriction with available packages and methods, so the best option was to use the AIC as a standard measure of model goodness of fit and keep the lowest AIC value.

Taxon and response variable		Carabid AD	Carabid SR	Spider AD	Spider SR	Parasitoid PR	Slug AA	Aphid AB
Explanatory landscape variable	Scale (m)							
Landscape grain	100	12574.4	6463.9	6442.2	3863.5	4380.2	6627.7	8079.10
	200	12572.7	6462.5	6438.1	3860.7	4379.3	6632.3	8077.20
	300	12573.9	6461.9	6438.7	3861.1	4379.5	6632.2	8076.30
	400	12575.4	6462.8	6441.5	3862.1	4367.7	6632.9	8080.00
Crop continuity year n	50	12562.8	6463.9	6439.3	3865.4	4372.2	6634.2	8088.10
	100	12571.7	6463.9	6439.8	3865.4	4378.8	6632.9	8087.90
	200	12568.9	6462.8	6439.3	3863.9	4375.4	6634.2	8087.50
	300	12569.8	6463.9	6433.6	3865.1	4368.9	6634.2	8085.80
	400	12569.5	6464.2	6436.8	3865.7	4372.6	6631.9	8086.20
Crop continuity year n-1	50	12558.1	6462.9	6439.3	3864.9	4379.7	6633.1	8089.00
	100	12565.7	6462.4	6439.8	3861.7	4376.8	6634.2	8089.20
	200	12558.4	6460.6	6439.3	3862.8	4377.8	6632.2	8089.20
	300	12565.4	6463.2	6433.6	3959.1	4377.2	6634.1	8089.00
	400	12561.2	6463.0	6436.8	3861.8	4377.4	6634.0	8088.30
Crop interface year n	50	12549.5	6458.6	6445.6	3865.8	4382.0	6629.6	8089.20
	100	12539.1	6456.6	6445.6	3865.8	4382.1	6628.3	8089.10
	200	12532.7	6453.4	6445.4	3864.4	4378.8	6632.7	8088.90
	300	12546.5	6461.1	6445.5	3865.2	4373.3	6633.9	8089.10
	400	12554.7	6460.6	6445.5	3864.8	4378.9	6634.3	8088.60
Crop interface year n-1	50	12561.8	6464.2	6440.0	3861.9	4371.8	6633.3	8088.90
	100	12563.0	6462.9	6438.8	3860.2	4375.4	6634.2	8088.20
	200	12561.6	6464.2	6439.4	3860.3	4373.1	6633.2	8088.40
	300	12548.3	6463.6	6442.1	3862.1	4369.1	6633.6	8087.80
	400	12537.0	6460.3	6442.1	3861.3	4375.8	6631.4	8083.80
Wooded continuity	50	12572.4	6461.3	6445.6	3865.5	4367.70	6634.1	8083.30
	100	12569.2	6455.5	6436.6	3854.9	4371.10	6631.8	8088.20
	150	12572.0	6461.6	6438.9	3858.1	4367.20	6629.3	8087.20
	200	12561.5	6455.3	6438.1	3859.6	4353.00	6632.9	8088.70

Table S3: Statistical results of GLS linear models fit on mean daily temperature (°C), mean minimal temperature (°C), cumulated degree-day (> 4 °C), and Tobit linear models fit on mean

daily rainfall data (mm), for both the winter period (December 1st to March 21st) and the sampling period (March 22nd to June 30th). Explanatory variable selection was done based on best AIC fit. Significant variables and interactions based on type II Wald chi² statistics are highlighted in bold.

Dependent variable	Explanatory variable	χ^2	df	p(> χ^2)
Winter period				
Mean temperature	Date	2.6	1	0.11
	Date^2	5.5	1	<0.05
	Region	17.9	2	<0.001
	Year	0.2	1	0.67
	Year x Date	6.7	1	<0.01
	Year x Date^2	16.2	1	<0.001
Mean minimal temperature	Date	1.8	1	0.18
	Date^2	3.0	1	0.07
	Region	15.6	2	<0.001
	Year	0.01	1	0.94
	Year x Date	5.4	1	<0.05
	Year x Date^2	15.6	1	<0.001
Cumulated degree-day (> 4°C)	Date	333.4	1	<0.001
	Region	70.3	2	<0.001
	Year	0.63	1	0.43
	Year x Region	2.2	2	0.33
	Year x Date	1.6	1	0.20
	Date x Region	32.8	2	<0.001
Rainfall	Date	3.3	1	0.07
	Region	3.1	2	0.22
	Year	21.6	1	<0.001
	Year x Date	30.0	1	<0.001
Sampling period				
Mean temperature	Date	147.7	1	<0.001
	Year	0.86	1	0.35
Mean minimal temperature	Date	0.7	1	0.42
	Date^2	0.2	1	0.66
	Year	8.2	1	<0.01
	Year x Date	2.5	1	0.12
Cumulated degree-day (> 4°C)	Year x Date^2	3.0	1	0.09
	Date	494.8	1	<0.01
	Region	12.9	2	<0.01
Rainfall	Year	0.18	1	0.67
	Date	0.01	1	0.94
	Region	4.1	2	0.13
	Year	8.9	1	<0.01
	Year x Date	4.8	1	<0.05

Table S4: Statistical results of full generalized linear mixed models (*i.e.*, all terms and interactions included), either binomial (parasitism rates, logit link function) or negative binomial (all other taxa, log link function). See Table S2 for selection of the scale at which landscape metrics were tested, for each dependent variable. For each predictor, estimates on the response scale (incidence rate ratios or odds ratios) and 95% confidence intervals (CI) are presented. (*) Models concerning spiders were done for 2018 data only. DF = 1 except for the regional effect where DF = 2. Carabids (abundances = 49,381 and 104 species), spiders (abundances = 26,661 and 156 species), parasitoids (abundances = 1,693), aphids (abundances = 13,173) and slugs (abundances = 9,049). Sample sizes are provided in the material and methods section.

Predictors	CARABID abundance			CARABID species richness			SPIDER abundance			SPIDER species richness			PARASITISM rate			APHID abundance			SLUG abundance		
	Incidence Rate Ratios	CI	p	Incidence Rate Ratios	CI	p	Incidence Rate Ratios	CI	p	Incidence Rate Ratios	CI	p	Odds Ratios	CI	p	Incidence Rate Ratios	CI	p	Incidence Rate Ratios	CI	p
(Intercept)	37.04	24.15 – 56.80	<0.001	4.9	3.60 – 6.67	<0.001	47.55	33.23 – 68.06	<0.001	12.28	10.40 – 14.50	<0.001	0.12	0.07 – 0.21	<0.001	14.36	10.54 – 19.57	<0.001	6.25	2.80 – 13.96	<0.001
year [2018]	0.98	0.64 – 1.50	0.915	0.98	0.71 – 1.34	0.877	NA	NA	NA	NA	NA	NA	1.16	0.65 – 2.05	0.617	0.39	0.29 – 0.52	<0.001	0.61	0.28 – 1.34	0.22
region [Hauts-de-France]	1.52	0.80 – 2.89	0.198	1.02	0.66 – 1.58	0.934	0.39	0.22 – 0.69	0.001	0.46	0.35 – 0.60	<0.001	0.08	0.04 – 0.19	<0.001	0.35	0.21 – 0.58	<0.001	1.25	0.41 – 3.81	0.693
region [Wallonia]	0.27	0.16 – 0.48	<0.001	0.68	0.46 – 1.00	0.047	0.66	0.38 – 1.14	0.138	0.59	0.45 – 0.76	<0.001	0.15	0.07 – 0.30	<0.001	0.61	0.39 – 0.96	0.032	0.72	0.26 – 1.96	0.515
DD4c	1.38	1.26 – 1.52	<0.001	0.96	0.92 – 1.00	0.052	1.03	0.96 – 1.11	0.385	0.93	0.89 – 0.97	<0.001	2.76	2.46 – 3.10	<0.001	2.76	2.37 – 3.23	<0.001	1.25	1.05 – 1.49	0.011
boundary [strip]	1.17	1.04 – 1.31	0.007	1.03	0.97 – 1.09	0.322	1.12	1.00 – 1.25	0.06	1.07	1.01 – 1.14	0.031	0.81	0.69 – 0.96	0.013	0.89	0.75 – 1.05	0.172	0.75	0.59 – 0.96	0.023
position	1.38	1.27 – 1.51	<0.001	1.09	1.05 – 1.13	<0.001	1.08	1.00 – 1.18	0.06	1.02	0.98 – 1.07	0.342	1.52	1.37 – 1.69	<0.001	0.83	0.74 – 0.93	0.002	0.61	0.52 – 0.70	<0.001
grain	1.25	1.05 – 1.49	0.014	1.06	0.97 – 1.16	0.179	1.08	0.92 – 1.27	0.361	1.02	0.94 – 1.11	0.586	0.68	0.54 – 0.86	0.001	0.74	0.60 – 0.93	0.008	0.98	0.80 – 1.21	0.857
wooded continuity	0.8	0.72 – 0.90	<0.001	0.91	0.86 – 0.97	0.003	0.9	0.80 – 1.02	0.089	0.91	0.86 – 0.97	0.005	0.8	0.73 – 0.88	<0.001	1.13	1.00 – 1.28	0.044	1.18	0.96 – 1.44	0.121
crop continuity n	0.8	0.70 – 0.91	0.001	1	0.94 – 1.06	0.924	0.88	0.79 – 0.99	0.03	0.94	0.88 – 1.01	0.082	1.11	0.98 – 1.27	0.104	0.93	0.80 – 1.07	0.305	0.99	0.81 – 1.22	0.947
crop continuity n-1	0.87	0.80 – 0.96	0.005	0.97	0.93 – 1.02	0.273	1.15	1.04 – 1.28	0.007	1.03	0.97 – 1.09	0.29	0.99	0.89 – 1.10	0.826	0.94	0.82 – 1.09	0.434	1.16	0.95 – 1.42	0.143
crop interface n	0.86	0.78 – 0.94	0.002	0.94	0.90 – 0.98	0.003	0.94	0.86 – 1.04	0.238	0.94	0.89 – 0.99	0.025	1.02	0.94 – 1.11	0.586	0.91	0.79 – 1.06	0.235	1.31	1.13 – 1.51	<0.001
crop interface n-1	1	0.91 – 1.09	0.917	0.99	0.94 – 1.04	0.581	1.01	0.91 – 1.13	0.803	1.01	0.96 – 1.07	0.675	1.06	0.97 – 1.16	0.171	1.23	1.05 – 1.44	0.012	0.7	0.56 – 0.88	0.002
DD4c * boundary [strip]	0.99	0.88 – 1.12	0.927	0.94	0.89 – 1.00	0.046	0.99	0.89 – 1.09	0.785	0.99	0.93 – 1.04	0.639	1.17	0.99 – 1.37	0.067	1.02	0.83 – 1.25	0.848	1	0.79 – 1.25	0.978
DD4c * position	1.06	0.97 – 1.16	0.221	0.95	0.92 – 0.99	0.017	1.13	1.05 – 1.22	0.001	0.98	0.95 – 1.02	0.436	0.9	0.81 – 1.00	0.046	1.01	0.88 – 1.16	0.906	1.11	0.95 – 1.30	0.184
boundary [strip] * position	0.93	0.83 – 1.05	0.232	0.94	0.89 – 0.99	0.026	0.82	0.73 – 0.92	0.001	0.86	0.81 – 0.92	<0.001	1.11	0.95 – 1.30	0.178	0.99	0.84 – 1.16	0.855	1.21	0.99 – 1.48	0.066
(DD4c * boundary [strip]) *	1.2	1.06 – 1.37	0.004	1.09	1.03 – 1.15	0.004	1.02	0.92 – 1.13	0.66	1.02	0.96 – 1.08	0.502	0.94	0.80 – 1.09	0.399	1.07	0.88 – 1.31	0.501	0.89	0.71 – 1.10	0.277
Random Effects																					
σ^2	0.77			0.25			0.44			0.15			3.29			1.22			1.54		
τ_{00}	0.17	windwregionyear		0.10	windwregionyear		0.08	windwregion		0.02	windwregion		0.28	windwregionyear		0.05	windwregionyear		0.59	windwregionyear	
ICC	0.18			0.28			0.15			0.1			0.08			0.04			0.28		
N	16	windwregionyear		16	windwregionyear		8	windwregion		8	windwregion		16	windwregionyear		16	windwregionyear		16	windwregionyear	
Observations	1417			1417			714			714			1422			1422			1421		
Marginal R ² / Conditional R ²	0.288 / 0.419			0.060 / 0.325			0.270 / 0.381			0.351 / 0.413			0.466 / 0.508			0.560 / 0.577			0.188 / 0.414		