Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats

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ARTICLE INFO

ABSTRACT

Semi-natural habitats (SNH) play key roles for arthropod natural enemy communities in agricultural landscapes. Positive relationship between landscape complexity and biological pest control is now well known and is assumed to mainly come from the fact that natural enemies use semi-natural habitats for overwintering. However, the respective role of each type of semi-natural habitats in the landscape in shaping natural enemy communities and pest control remains poorly studied. Moreover, the relative importance of environmental variables in structuring these communities remains largely unexplored. The main purpose of this study was to provide an insight into the types of SNH natural enemies use for overwintering as well as the effects of local and landscape characteristics in structuring their overwintering communities. Overwintering natural enemy communities were sampled in 7 types of SNH (i.e., forest interior (FI), South-facing forest edge (FES), North-facing forest edge (FEN), dry unmanaged grassland (UGD), wet unmanaged grassland (UGW), managed grass strip (CAP grass strip) either dominated by monocotyledonous plants (MGM) or by dicotyledonous plants (MGD)). Abundance, species richness as well as community composition of each group of enemies were then explained by local and landscape parameters to assess their relative importance. In our study, overwintering natural enemy communities differed markedly among types of SNH. Explanatory variables proved to have a decreasing influence in shaping natural enemy community compositions from the local (i.e. in the emergence trap perimeter, in 3 m- and 15 m-radius circular zones around it) to the immediat landscape (within 30 m- and 60 m-radius circular zones) and then the mid-distant one (within 120 m-, 250 m- and 500 m-radius circular zones). We particularly found that management intensity and vegetation height were very strong drivers of natural enemy diversity at the local scale. Managed CAP grass strips turned out as the main source habitat of beneficials in the spring while forests acted quite negatively on local abundances of most of the beneficials studied. On the opposite, medium arable land and grassland surface areas proved to be favourable for them as a whole in the immediat landscape, while in the mid-distant landscape, fallows favoured aphidophagous hoverflies and arable lands did so for spiders. Our results highlight the need for a more precise description of SNH in the landscape if we are to mechanistically understand the role of compositional landscape heterogeneity on zoophagous arthropod populations and to give relevant guidelines to design landscapes favouring natural biological pest control.

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1. Introduction

Agricultural intensification, characterized by monocrops supplied with high amounts of agrochemical inputs, homogeneous landscapes and high fragmentation of semi-natural habitats, has been recognized as a main driver of biodiversity and ecosystem

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services losses (Robinson and Sutherland, 2002; Tscharntke et al., 2005). For instance, the harmful effects of pesticides on second pest outbreaks and biological control are well documented (Geiger et al., 2010; Jonsson et al., 2012). There is therefore a need to design a more ecologically sound form of agriculture relying on ecological functions and processes if we are to simultaneously secure food production while minimizing environmental impacts (Bommarco et al., 2013). There is a growing body of evidence suggesting strong positive relationships between landscape complexity (i.e., proportion of semi-natural habitats in the landscape) and biological pest control (Chaplin-Kramer et al., 2011; Veres et al., 2013). Semi-natural habitats (SNH) such as hedgerows, moors, natural grasslands, forests or field margins, display key ecological functions for natural enemies during the whole year because they are more stable and less disturbed habitats than cultivated ones. Indeed, overwintering arthropods are much more abundant and diversified in SNH than in arable fields (Pfiffner and Luka, 2000).

Several hypotheses have been formulated to explain the underlying mechanisms explaining their positive effects on natural enemies. SNH may provide alternative hosts or prey, pollen or nectar (Landis et al., 2000). They may also be overwintering habitats and refuges from disturbance (Pfiffner and Luka, 2000), allowing natural enemy populations to build-up and therefore enhance their impact on pest populations (Landis et al., 2000). Yet, very few studies have tested these hypotheses especially from a community perspective. Moreover, the majority of studies examining the effects of landscape complexity on biodiversity and associated ecosystem services, considered non-crop habitats as the same land use class assuming similar functions within and between SNH types (Chaplin-Kramer et al., 2011; Woltz et al., 2012). However, SNH can strongly differ over time and space due to variations in plant species richness, soil characteristics, vegetation structure or microclimate and can thus have different effects on natural enemy communities (Landis et al., 2000; Pywell et al., 2005). Moreover, the role of SNH types on overwintering natural enemies and the main local and landscape drivers of natural enemies distribution during the winter have been little explored (Schmidt et al., 2005; Griffiths et al., 2008; Geiger et al., 2009). Thus, refining categorization of land covers and gaining information about the role of SNH types on natural enemies and about the main local and landscape drivers of natural enemies distribution, would allow a better mechanistic understanding of ecological processes behind the patterns observed at both the farm and landscape scales (Veres et al., 2013). This is even more critical when considering the overwintering phase of natural enemies for which the majority is assumed to depend on SNH for overwintering (Häni et al., 1998). Thus, given that majority of arthropod pests are active as early as the spring, the spatial distribution of these overwintering habitats within the landscape is of major importance for early control of crop pests (Chiverton, 1986; Tenhumberg and Poehling, 1995). Knowing the exact role of well described overwintering habitats on population dynamics and community structure of natural enemies would allow to manipulate, at the farm level, SNH in agricultural landscapes to increase and optimize natural pest control services (Gardiner et al., 2009; Rusch et al., 2012).

The main purpose of our study was to provide an insight into the role of several SNH types considered at the farm scale, as reservoirs of overwintering natural enemies, and to investigate the effects of local and landscape characteristics on these communities. Particularly, we addressed the following questions:

(i) Does the structure of natural enemy communities differ among habitat types?
(ii) Are there key habitat types which can be considered as major providers of natural enemies on farmland?

(iii) Which local and landscape characteristics mainly drive natural enemy assemblages and diversity?

To do so, we conducted a study based on emergence data collected in various SNH in an agricultural landscape of South-Western France, with highly variable management intensity, soil characteristics and plant composition according to the different SNH types.

2. Materials and methods

2.1. Study area

The study was conducted from January to July 2006 in South-Western France (43°N, 1°E), in the "Gascony Hills and Valleys" site, straddling Gers and Haute-Garonne Departments, which is one of the long term observation sites of the European LTER Network (LTER-Europe). The study region is a hilly area (200–400 m alt.) within a sub-Atlantic climate exposed to Mediterranean and mountain influences. Thus, the area is characterized by hot summers (monthly means for May to July 2006 of 21 °C, maximum temperature 27.3 °C, minimum temperature 12.8 °C and precipitation 144 mm) and cool winters (monthly means for January and February 2006 of 3.7 °C, maximum temperature 9.7 °C, minimum temperature −1.8 °C and precipitation 59 mm). The landscape is mainly composed with crop fields (winter wheat, winter barley, sunflower, sorghum, oilseed rape) and grasslands either natural or sown. Scattered fragmented oak forests represent the minor part (less than 20%) of the landscape.

2.2. Sampling sites and study design

All sampling sites were located on three adjoining hilly farms, within a 1 km-radius, in order to assess the respective influence of both local and landscape characteristics. Local parameters concerned the trap scale: both inside the trap perimeter and within its immediat surroundings, i.e. in 3 m- and 15 m-radius circular zones. Landscape parameters were evaluated within 30 m- and 60 m-radius circular zones for the immediat landscape ones, and within 120 m-, 250 m- and 500 m-radius circular zones for the mid-distant landscape ones. By doing so, we could grasp the hierarchy of environmental conditions upon which farmers can have a hold over in their management. All the SNH we studied were included into four main categories of the level 2 of CORINE Land Cover (CLC) classification (Bossard et al., 2000): (i) pastures, (ii) heterogeneous agricultural areas (i.e. Annual crops associated with permanent crops, Complex cultivation patterns, Land principally occupied by agriculture with significant areas of natural vegetation, of level 3 of CLC classification), (iii) shrub and/or herbaceous vegetation associations (i.e. Natural grasslands, Sclerophyllous vegetation, Transitional woodland-shrub, of level 3 of CLC classification), and (iv) forests (i.e. Broad-leaved forests, of level 3 of CLC classification). A fifth category was present in the landscape but not studied, the arable land category (i.e. Non-irrigated arable land, of level 3 of CLC classification).

Seven types of SNH were studied: forest interior (FI), South-facing forest edge (FES), North-facing forest edge (FEN), dry unmanaged grassland (UGD), wet unmanaged grassland (UGW), managed grass strip (CAP grass strip) either dominated by mono-cotyledonous plants (MGM) or by dicotyledonous plants (MGD). Therefore they were representative of the great majority of the SNH that occur on farms of this LTER site. Apart forest-copse patches under 15 to 50 year-rotation management for fire wood, natural grasslands were the sole sampling sites under regular and direct management activities (lightly grazed by cattle) but they were unsown and unfertilized. Each of the 7 types of SNH was repeated 7

Table 1
Descriptive variables used for each study site and their scales. Many of them have been based and adapted from the BioHab methodology for monitoring European habitats (Bunce et al., 2008).

Category	Criteria	Scale
Relative altitude	Altitude.	m.
Coverage	Soil coverage within the emergence traps	1–4 (bared soil to >75% of coverage)
	Degree of openness within a 3 m-radius circle around the em. traps ("enclose 3 m")	1–4 (open to close)
	Degree of openness within a 15 m-radius circle around the em. traps ("enclose 15 m")	1–4 (open to close)
Phytosociology	Abundance of dicotyledons within the em. traps (% of dicotyledons/monocotyledons)	1 (0–25%), 2 (25–50%), 3 (50–75%), 4 (75–100%)
	Species richness of monocotyledons within the em. traps	Number of species
	Species richness of dicotyledons within the em. traps	Number of species
	Vegetation height within the em. traps	1 = at least 2/3 of the vegetation < 40 cm; 2 = at least 2/3 of the vegetation between 40 and 90 cm; 3 = at least 2/3 of the vegetation > 90 cm
Management	Management index within and around the em. traps	1 = abandoned; 2 = unmanaged; 3 = neglected; 4 = intensively managed
Soil	Litter thickness.	cm.
	Moisture regime within the em. traps	1–4 (xeric to wet)
	Soil hardness within the em. traps	N/m^2
	Five fraction granulometry, within the em. traps: Clay (<2 μm), Fine and coarse silt (2–20 μm and 20–50 μm), Fine and coarse sand (0.05–0.2 mm and 0.2–2 mm)	g/kg
	Organic matter, within the em. traps = volatile matter at 550 °C	g/100 g
Landscape context	Woodland	% in a 250 m-radius
	Arable land	% in a 250 m-radius
	Grassland	% in a 250 m-radius
	Fallow	% in a 250 m-radius

times in order to get the widest range of ecological (light, temperature, air humidity, soil dampness) and anthropogenic (managed or neglected state) conditions, due to agricultural activities, in each CLC category of SHN. Thus, 49 sampling sites were selected in total, chosen in such a way that besides the fact that they had to represent the widest array of environmental conditions potentially existing on Gascony farms, the distance between two sites belonging to the same SNH type was over 202 m. Indeed, for two 250 m-radius overlapping circular zones, it is the distance beyond which there is less than 50% of overlap between both.

2.3. Environmental description

Field inspections were made to precisely characterize the SNH studied. Each sampling site was described according to 18 criteria that dealt with soil coverage, plant community composition, management and soil (Table 1). Most of the criteria have been based and adapted from the BioHab methodology for monitoring European habitats (Bunce et al., 2008). Vegetation within the emergence traps (see below) was characterized through four variables presented in Table 1. Plant richness and abundance were measured by recording the number of monocotyledonous and dicotyledonous species and assessing their relative abundance within the trap based on a cover-abundance scale derived from the Braun-Blanquet methodology. Plant height of the herb layer was characterized using three height intervals: 0–40 cm, 40–90 cm and >90 cm. Within each trap, we visually estimated the percentage of total soil coverage by the herb layer and measured the thickness of the litter layer. Management intensity was also recorded from the farmers as it is an essential parameter which strongly influences vegetation cover. Soil hardness was an unconfined compression strength determined as the mean value of five measures taken inside the trap perimeter just after trap removal, using a hand-held penetrometer with a 1 cm² probe. This sampling gave fairly homogeneous data for each trap

and very different values between traps (from 30 to 1000 N/m²). All these compression strength measurements were made by the same person over a single afternoon in order to avoid potential bias due to operator and temporal variations in soil humidity. Soil analyses were done by the national Soil Analysis Laboratory of INRA (http://www.arras.inra.fr/; Arras, France). The five fractions of granulometric analyses and the soil content in organic matter were determined based on 400–500 g samples of dry soil collected from 0 to 20 cm deep at random from two points inside the trap perimeter just after trap removal. Given that all these environmental features could not be recorded in all directions and at different distances around the traps, we described the immediat surroundings on the base of the main vegetation structure in a 3 m- and a 15 m-radius circular zone in order to evaluate the degree of openness of each habitat at these two scales. Considering that beyond the distance of 15 m, the habitat type is generally another one, we decided to characterize the landscape context around each site, using four main categories of land occupancy: forest, arable land, grassland, fallow. Based on aerial photographs (BD ORTHO®, IGN, France; pixel size: 0.5 m) and intensive field surveys, the studied zone was digitized using a geographical information system (ArcGIS, version 9, ESRI©, Redlands, California) and the four main categories of land occupancy calculated at the five different radii described above (30 and 60 m for the immediat landscape and 120, 250 and 500 m for the mid-distant one). At each radius, landscape heterogeneity was represented by the ecotone length and variability was measured in number of habitat plots per hectare (fragmentation). To represent the landscape habitat diversity and evenness, a Shannon diversity index was calculated using land occupancy proportions.

2.4. Emergence survey and functional groups of natural enemies

Arthropods were sampled using macro-emergence traps (a modified Malaise trap to the design of M.C.D. Speight; B&S

Entomological Services, Co. Armagh, N. Ireland, UK) set up in the field for 7 months, from the beginning of January to the end of July 2006. Each emergence trap covered a 1.8 m^2 surface area and was set up in such a way that walls were tightly fit to the ground. Emerging arthropods were collected at the top of the trap within a bottle filled with 70% ethanol (vol./vol.), and all the bottles were replaced every three weeks and organisms sorted in the lab. Natural enemies were identified either at the species level for the main aphidophagous or polyphagous insect families (Carabidae, Chrysopidae, Coccinellidae, Hemerobiidae, Syrphidae, Anthocoridae), or at the genus or even family level for the Hymenopteran parasitoids and Staphylinidae respectively. Therefore, only zoophagous taxa were taken into account, in order to address whether particular SNH in particular landscape contexts can harbour natural enemies of crop pests in winter. It is assumed that a large part if not the great majority of the ground dwelling predators and parasitoids which had emerged within the emergence traps, have been caught in the bottles situated at more than 1.8 m above the soil. Indeed, with an overall average density of 150 individuals caught/m^2, it is highly likely that even if living on the ground surface, being shut in in a very little space, they walked or flew all around the traps to finally try to escape through the opening leading to the collecting bottle.

2.5. Data analysis

To examine the effect of habitat type on abundance and species richness of each taxonomic group, we used one-way analysis of variance with Tukey's HSD post hoc tests. Normality and homoscedasticity of the residuals were carefully checked using the Shapiro–Wilk test and the Levene's test, respectively. Where transformations of the data did not address normality, we applied a Kruskal–Wallis test followed by pairwise comparisons. We performed the same approach on total abundance of natural enemies to explore the relative importance of each habitat type as sources of natural enemies in the landscape.

To assess the question of environmental variables effects on the taxonomic richness of natural enemies, we selected the most influent variables by performing linear model for each variable separately and comparing them using Akaike Information Criterion (AIC). We used generalized linear model with Gaussian (link identity) or Poisson (link log) family when transformation were needed to achieve normality. When two strongly correlated ($r > 0.5$) variables were selected, we excluded the less influent (in term of explained deviance). To select influent variables on the whole natural enemies community, we performed the same analysis on weighted sum of richness of each taxon.

Species composition of each taxonomic group was analyzed in relation to the two environmental data sets (i.e., local conditions and adjacent landscape context at each scale) using redundancy analyses (RDA). For each taxonomic group and environmental variable set, we performed a forward selection to identify the explanatory variables which significantly affected each assemblage ($P < 0.05$ after 999 Monte Carlo permutations). We reduced risks associated with the forward selection by following the procedure proposed by Blanchet et al. (2008): (i) we prevented problem of inflation of the overall type I error by only performing forward selection on models for which a global test with all explanatory variables was significant; (ii) then, to reduce the risk of incorporating too many variables into the model, we used the adjusted coefficient of multiple determination as a stopping criterion in addition to the traditional significance level α (Borcard et al., 2011).

Variation partitioning was then conducted to determine the unique and joint fractions of variation explained by the local and the adjacent landscape data sets. Only the significant variables previously selected by the forward selection for each data set were used. We reported the variation explained by each RDA model

as the adjusted R^2 which is an unbiased estimate of the contributions of each explanatory variable, taking into account the number of predictor variables and sample size (Peres-Neto et al., 2006). Following Peres-Neto et al. (2006), we interpreted negative adjusted R^2 as a zero value. Species that appeared in less than five traps were excluded from the analyses. Abundance data were Hellinger-transformed to make them appropriate for linear analyses (Legendre and Gallagher, 2001) and qualitative variables were treated as dummy variables.

Because landscape buffers partially overlapped, we examined spatial autocorrelation in species composition of each group using a Mantel test (based on Pearson correlations and 999 permutations). We tested for correlations between assemblage dissimilarity (Bray–Curtis) of each group and geographic coordinates dissimilarity (Euclidian). We found no spatial autocorrelation in species assemblages of each group (Araneae: $P = 0.12$, $R = 0.06$; Carabidae: $P = 0.09$, $R = 0.07$; Coccinellidae: $P = 0.94$, $R = -0.06$; Syrphidae: $P = 0.65$, $R = -0.02$; Neuroptera: $P = 0.32$, $R = 0.01$; Hemiptera: $P = 0.50$, $R = -0.005$; Hymenopteran parasitoids: $P = -0.04$, $R = 0.65$).

Differences in beta diversity, as a measure of variation in community structure (Anderson et al., 2011) among habitat types, were examined using a test of homogeneity of multivariate dispersion based on the Gower dissimilarity matrix (Anderson et al., 2006). Differences among groups were tested using pairwise permutations of distance to centroid values.

All analyses were performed using the statistical software R 3.0.2 (R Development Core Team, 2013), the "vegan" package (Oksanen et al., 2013) and the "packfor" package (Dray et al., 2013).

3. Results

In total, 15,133 invertebrates were recorded from the emergence traps (Table 2). They were identified as belonging to:

- 211 species of the taxonomic groups Araneae (118 spp.), Carabidae (Coleoptera) (27 spp), Coccinellidae (Coleoptera) (25 spp), Neuroptera (24 spp) and Syrphidae (Diptera) (17 spp.);
- 4 genera of Hymenopteran parasitoids (*Aphidius*, *Diaeretiella*, *Ephedrus*, *Praon*);
- 3 families of Hemiptera (Anthocoridae, Miridae, Nabidae)
- the family of Staphylinidae (Coleoptera).

3.1. Effects of SNH types, local and landscape variables on abundance and species richness of natural enemy communities

3.1.1. Effects of SNH types

The total abundance of natural enemies was extremely variable between traps (min.: 60 ind m^{-2}; max.: 1270 ind m^{-2}). On the whole, we found a significant effect of habitat types on total abundance of natural enemies ($F = 10.94$, df = 6, $P < 0.001$) (Fig. 3). Per taxonomic group, significant effects of habitat types have been found on: (i) Carabidae abundance ($\chi^2 = 32.65$, df = 6, $P < 0.001$) and their species richness ($\chi^2 = 23.38$, df = 6, $P < 0.001$), (ii) Syrphidae abundance ($\chi^2 = 13.65$, df = 6, $P = 0.03$) but not their species richness ($\chi^2 = 11.89$, df = 6, $P = 0.06$), (iii) Neuroptera abundance ($F = 3.33$, df = 6, $P = 0.008$) but not their species richness ($F = 1.33$, df = 6, $P = 0.26$), (iv) Hemiptera abundance ($F = 2.42$, df = 6, $P = 0.04$) and family richness ($F = 2.76$, df = 6, $P = 0.023$), (v) Staphylinidae abundance ($F = 12.44$, df = 6, $P < 0.001$), and (vi) Hymenopteran parasitoid abundance ($F = 9.71$, df = 6, $P < 0.001$) and their genus richness ($F = 6.86$, df = 6, $P < 0.001$) (Figs. 1 and 2). In contrast, there were no significant effects of habitat types on abundance ($\chi^2 = 12.11$, df = 6, $P = 0.059$) and species richness ($F = 1.66$, df = 6, $P = 0.15$) of Araneae and on abundance ($F = 1.78$, df = 6, $P = 0.12$) and species richness ($F = 2.04$, df = 6, $P = 0.08$) of Coccinellidae (Figs. 1 and 2).

Table 2
Number of individuals and species (or other taxonomic levels) of the different groups studied, and their sampling period.

Groups	Total number of individuals	Total richness	Sampling period[e]
Araneae	2215	117[a]	04/02/2006–05/04/2006
Carabidae	994	27[a]	04/02/2006–05/04/2006
Coccinellidae	427	25[a]	04/02/2006–21/07/2006
Syrphidae	240	17[a]	04/02/2006–21/07/2006
Neuroptera	355	24[a]	04/02/2006–18/07/2006
Hemiptera	366	3[b]	04/02/2006–05/04/2006
Staphylinidae	10,162	_[c]	04/02/2006–05/04/2006
Parasitoid	374	4[d]	04/02/2006–25/04/2006

[a] Species richness.
[b] Family richness.
[c] Not sorted.
[d] Genus richness.
[e] dd/mm/yyyy–dd/mm/yyyy.

MGD gave shelter to the highest abundances of Neuroptera, Hemiptera, Staphylinids and provided the highest abundance and genus richness of Hymenopteran parasitoids. They also showed high abundances of Syrphids and Carabids together with MGM. The highest abundances of these two taxa occurred on FEN and UGW respectively. The highest species richness of ground beetles was recorded on MGM, followed by MGD and UGW. At last, MGM were the second best habitats for abundance and genus richness of Hymenopteran parasitoids. In contrast, FI have proven to harbour the lowest abundances of Syrphids, Neuroptera, Staphylinids, Carabids and Hymenopteran parasitoids, closely followed by UGD for the very same taxa and FES for the two latter and Hemiptera. FI also displayed the lowest species richness of Carabids, whereas they harboured the non significant but very informative highest species richness of Coccinellids (Fig. 2).

3.1.2. Effects of environmental variables

Two to five variables were selected as significantly influential for each taxonomic group. Deviance explained by these variables ranged from 15.59% (Araneae) to 55.98% (Carabidae). Local variables, i.e. inside the trap perimeters and within their immediat surroundings at 3 m- and 15 m-radius around, together with immediat landscape variables at 30 m- and 60 m-radius circular zones,

proved to be more influent on taxonomic richness than mid-distant landscape parameters at 120 m-, 250 m- and 500 m-radius circular zones (Table 3). Management showed up as the major local variable. Taxonomic richness of Carabidae, Hymenopteran parasitoids, Hemiptera (slightly) and the overall natural enemies community increased in traps located in both neglected and intensively managed habitats (CAP grass strips). Enclosure within both 3 m- and 15 m-radius circular zones (highly correlated: $r = 0.74$) shaped different groups non-linearly. Coccinellid diversity was favoured by an enclosed area while Carabids and Hymenopteran parasitoids were more diverse in open areas. Syrphids favoured medium openness. Many soil parameters influenced a group: soil hardness limited Carabid species richness while fine sand improved it, Hemiptera were more diverse in soils with low organic matter content, Neuroptera diversity increased within thick litter and Coccinellidae and Syrphidae species richness increased with fine and coarse silt respectively. Phytosociologic characteristics such as vegetation height and species richness of monocotyledons within the traps, improved Syrphidae and the whole community richness for the former, and limited Coccinellidae diversity for the latter. Soil coverage increased Neuroptera species richness.

Concerning landscape parameters, arable land and forest surface areas within different radii appeared to be the most influent.
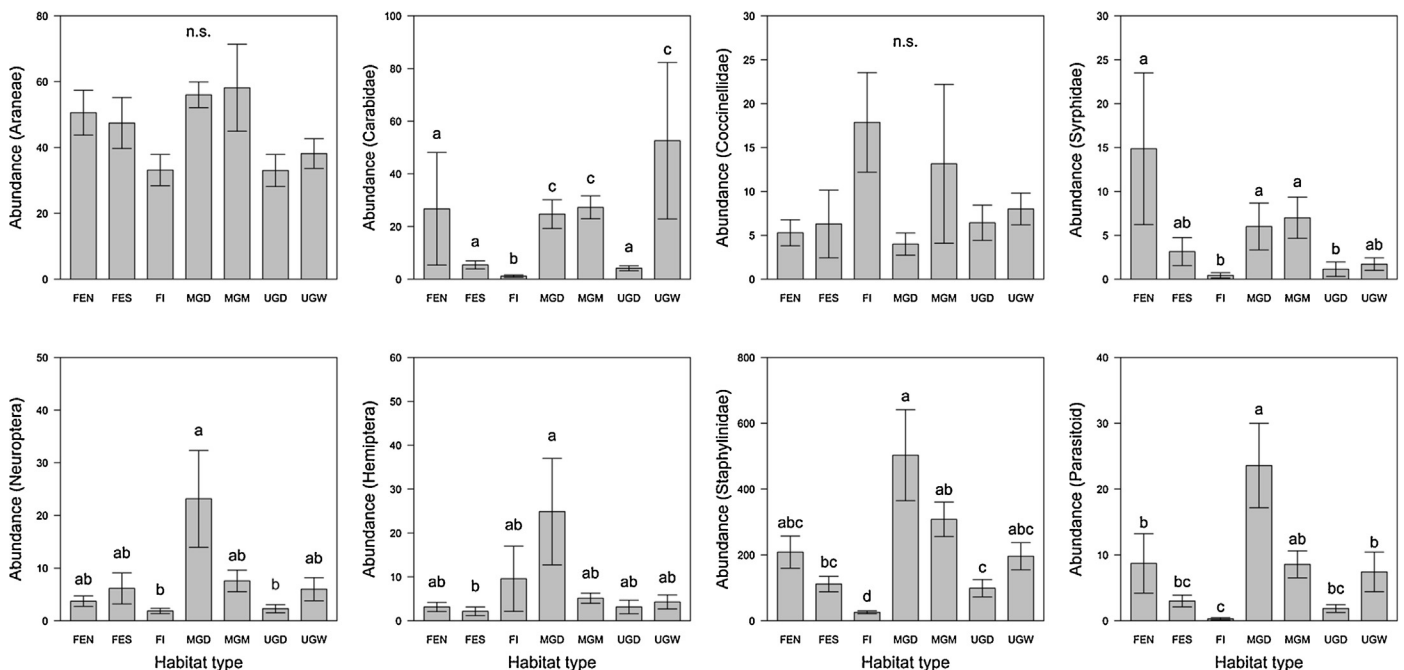

Fig. 1. Total abundance of the different groups studied, per habitat type.
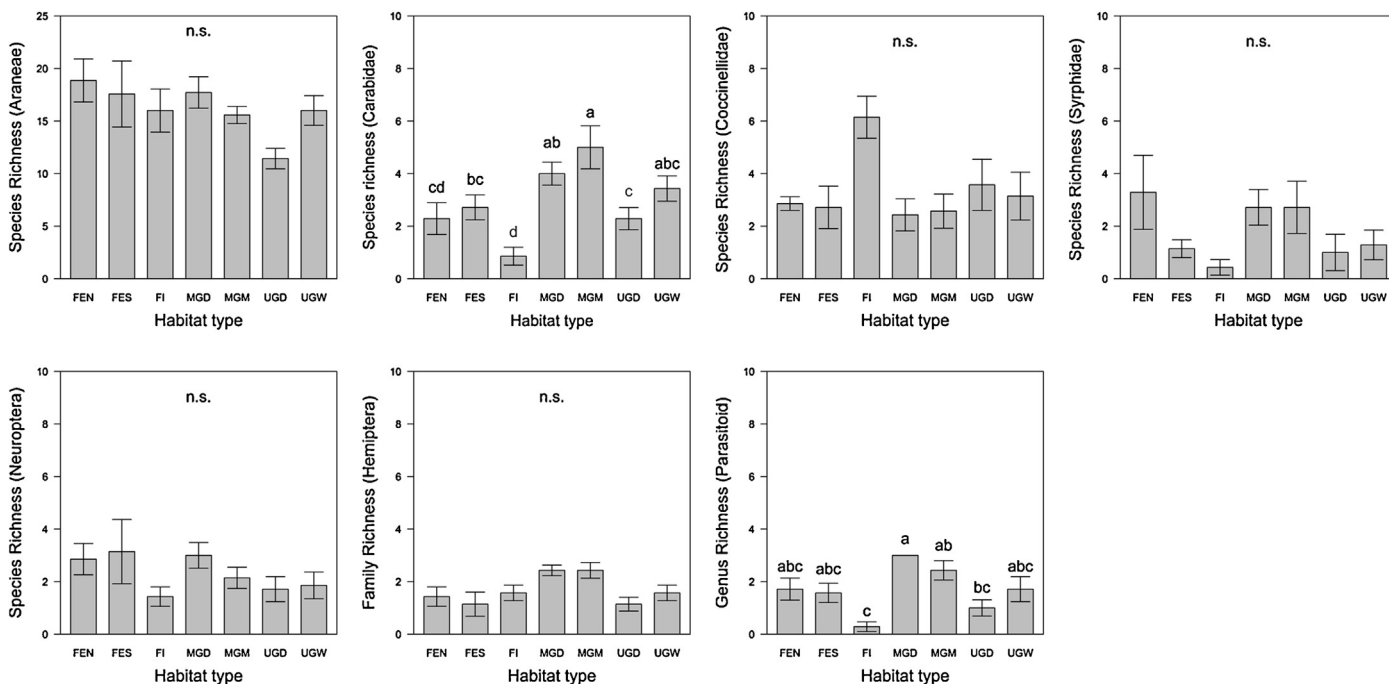
Fig. 2. Species (or other taxonomic level) richness of the different groups studied, per habitat type. Staphylinids do not appear because not identified at the species level.

Increasing forest surface area within 60 m- and 120 m-radii (correlated, $r = 0.53$) around the traps tended to reduce taxonomic richness of Hemiptera, Neuroptera, Syrphidae, Carabidae and Hymenopteran parasitoids and therefore the whole community. Only Coccinellidae diversity was favoured by high forest surface area (within 60 m-radius). Medium surface areas of arable land and grassland within 30 m around the traps improved taxonomic richness of Araneae, Hymenopteran parasitoids and the whole community for the former and Hemiptera for the latter. Habitat diversity in the immediat landscape (30 m) favoured Hymenopteran parasitoid richness but limited the Coccinellid's one. Few landscapes descriptors at higher radii were selected. Within 120 m, medium arable land surface areas disfavoured

Hemiptera while medium fallow surface areas improved Syrphidae richness. Finally, within a 250 m-radius around the traps, Araneae were favoured by highly arable landscapes while Neuroptera exhibited higher family richness in average diversified landscapes and the whole natural enemies community was more diverse in moderately diverse ones.

3.2. Effects of SNH types, local and landscape variables on natural enemy assemblages

Except for Neuroptera whose community differs significantly in both MGM and MGD ($F = 3.18$, $P = 0.012$), no differences in variation in community structure (β diversity) were found between SNH types for the other taxa (spiders: $F = 1.10$, $P = 0.376$; ground beetles: $F = 1.83$, $P = 0.118$; Coccinellidae: $F = 0.70$, $P = 0.651$; Syrphid: $F = 0.94$, $P = 0.484$; Hymenopteran parasitoids: $F = 2.35$, $P = 0.053$; Hemiptera: $F = 0.75$, $P = 0.609$).

Using forward selection and variance partitioning, we were able to highlight the explanatory variables which significantly explained a part of variation in the assemblages of each taxonomic group. The relative importance, for each group, of variables linked to local conditions (SNH types, ecological parameters inside the trap perimeters and in the 3 m- and 15 m-radius circular zones around them) on the one hand, and to landscape contexts (in the range of radii, from 30 m to 500 m circular zone) on the other hand, differed significantly. Few landscape descriptors were selected as significant variables shaping natural enemy communities (Table 4). Proportion of forests proved to shape only Araneae and Carabidae in the 30 m- and 250 m-radius circular zones respectively. Neuroptera community was structured by grasslands in the immediat landscape (30 m) and by fallows in the mid-distant one (120 m). Arable land in a 120 m-radius circular zone (i.e. in the mid-distant landscape) affected Hemiptera community. Finally, fragmentation of the immediat landscape around the trap (30 m) proved to shape Coccinellidae. In contrast, numerous descriptors of local conditions were selected by the forward selection procedure in explaining overwintering natural enemy assemblages (Table 4). Some SNH types proved to structure species assemblages during winter: UGD
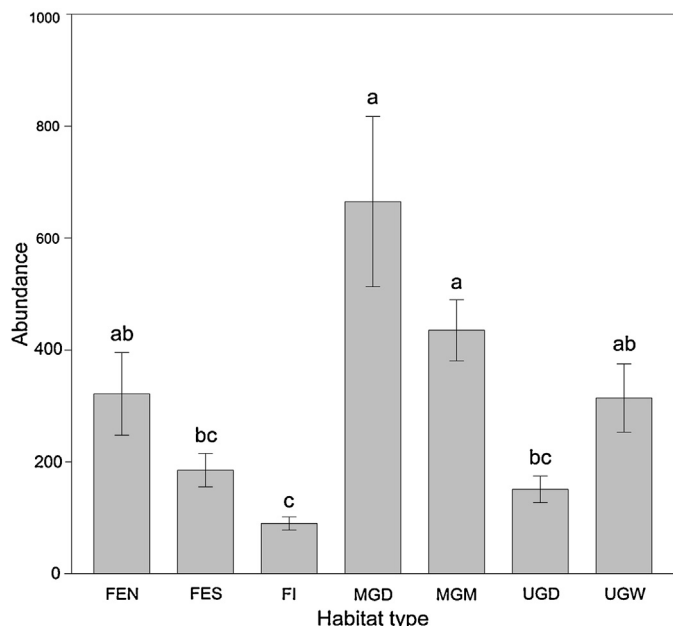

Fig. 3. Total abundance of natural enemies per habitat type.

Table 3
Selected local (bold) and landscape variables significantly influent on species richness of each taxon, ordered according to the model AIC score. The selected models are expressed as Richness – Intercept + c_1*variable + c_2*variable^2, after log transformation for Coccinellidae and using a log-link function for the marked (*) taxa. Explained deviance is expressed as D^2 (see Section 2.5 for details on the method).

	Variable	Scale (m)	Intercept	C_1	C_2	Chi^2	F-value	D^2
Araneae	Arable land	30	15.03***	0.15*	−1.97E−03*		3.22**	0.12
	Arable land	250	9.86**	0.10*			4.09**	0.08
Carabidae (*)	**Management**		0.22	0.32***		20.61***		0.35
	Enclosure 3 m		0.37	1.04*	−0.27**	19.09***		0.32
	Woodland	60	1.45***	−1.42E−02***		16.09***		0.27
	Soil hardness		1.55***	−1.41E−03***		15.31***		0.26
	Fine sand		0.15	7.10E−03***		12.02***		0.20
Coccinelidae (log transformed)	**Enclosure 15 m**		2.11**	−0.85	0.20*		7.46***	0.24
	Habitat diversity	30	1.80***	−0.47**			8.28***	0.15
	Fine silt		0.53	3.82E−03**			8.10***	0.15
	Woodland	60	1.26***	6.91E−03**			7.78***	0.14
	Monocot. species rich		1.84***	−0.19**			7.75***	0.14
Hemiptera (*)	Arable land	120	0.92	−3.23E−02	3.96E−04	7.25***		0.22
	Woodland	120	0.84***	−1.68E−02*		4.83**		0.15
	Organic matter		2.30**	−0.23*	4.52E−03	6.61**		0.20
	Management		1.05	−0.80	0.19	6.05**		0.19
	Grassland	30	0.27	3.29E−02*	−4.37E−04	6.04**		0.19
Neuroptera (*)	**Soil coverage**		4.74***	−2.93***	0.49***	17.30***		0.31
	Fragmentation	250	−2.55	7.18**	−3.57***	10.29***		0.18
	Woodland	120	0.88***	1.68E−02	−6.52E−04	7.39**		0.13
	Litter thickness		0.54***	0.11*		4.69**		0.08
Parasitoid (*)	**Management**		−0.51	0.38***		16.13***		0.30
	Woodland	60	0.97***	−1.78E−02***		13.70***		0.26
	Habitat diversity	30	−0.33	1.10***		12.93***		0.24
	Arable land	30	−0.11	0.04**	−3.47E−04**	13.07***		0.25
	Enclosure 15 m		−1.34	2.09	−0.48*	12.63***		0.24
Syrphidae (*)	**Vegetation height**		−1.16**	0.81***		23.84***		0.20
	Fallow	120	2.02E−03	0.10***	−2.10E−03***	20.92***		0.17
	Enclosure 3 m		−1.11	1.89**	−0.43***	16.28***		0.14
	Woodland	120	1.06***	−2.63E−02**		11.49***		0.10
	Coarse silt		−1.20*	1.53E−02**		9.74***		0.08
Whole community	**Vegetation height**		1.24***	0.71***			29.50***	0.39
	Management		2.51***	−0.40	0.15		13.91***	0.38
	Arable land	30	2.12***	0.04***	−4.04E−04		11.62***	0.34
	Woodland	120	3.15***	−0.02***			16.76***	0.26
	Habitat diversity	250	1.83**	2.79**	−1.55		6.49**	0.22

 * <0.1.
 ** <0.05.
 *** <0.01.

and UGW proved to structure Carabid communities; FEN were selected as significant variable shaping both Neuroptera and Coccinellidae communities while FI proved to shape both Coccinellid and spider communities.

Some ecological traits from inside the trap perimeters also proved to structure species assemblages during winter: management intensity had influence on Araneae, Neuroptera and Hymenopteran parasitoids; soil coverage proved to shape both ground beetle and hoverfly communities; dicotyledons abundance together with organic matter content influenced Hemiptera community; moisture regime proved to shape Araneae community.

Finally, openness in immediat surroundings of the traps (15 m) and relative altitude, structured overwintering species assemblages of ground beetles and Hemiptera respectively.

On the whole, variance partitioning revealed that all the significant local and to a lesser extent landscape variables, explained a part of the total variation in the assemblages of the different natural enemies groups (Table 5). They ranged from 2.12% for hoverflies to 28.92% for ground beetles with local descriptors and from 2.16% for ladybirds to 10.37% for Hemiptera with landscape descriptors.

Ordination biplots for each taxon with the selected habitat types and/or environmental variables are found in supplementary materials.

4. Discussion

In this study, we found that natural enemies communities overwintering in non-crop habitats differed markedly between SNH types and that explanatory variables related to both local and landscape characteristics explained their diversity and structured their assemblages. However, local variables proved to account for higher proportions of the total variance in community structure of all natural enemies groups than did landscape variables (18 vs. 6 variables respectively). Among local variables, SNH types appeared to be of high importance, and managed grass strips, both those dominated by monocotyledonous (MGM) or dicotyledonous (MGD) plants, proved to support the highest abundances of most natural enemies and delivered the highest taxonomic richness of Carabids and Hymenopteran parasitoids. These results most probably reveal their higher prey and host availability compared to other SNH. A lesser winter mortality in managed grass strips compared to other habitats could also explain at least partly the results, since it has been demonstrated that insects have developed various strategies for the selection of favourable overwintering habitats in order to limit this mortality (Danks, 1996). However, this phenomenon is unlikely since the driest habitats (UGD and FES), where entomopathogenic fungi *Metarhizium anisopliae* and *Beauveria bassiana* are very prone to be much less present, displayed very low or

Table 4

Results of the forward selection procedure on local and adjacent landscape variables for each taxonomic group. Only significant variables for explaining community composition of each taxonomic group are presented in the table. % of variation is indicated here by the R^2 of the respective variable. See Table 1 for explanations about the explanatory variables.

Taxa	Araneae			Carabidae			Coccinellidae			Syrphidae		
Variables	F-value	P-value	% of variation	F-value	P-value	% of variation	F-value	P-value	% of variation	F-value	P-value	% of variation
Local												
Managed grassland dicot.												
Managed grassland monocot.												
Unmanaged grassland wet				3.53448394	0.0063	4.15						
Unmanaged grassland dry				3.18637806	0.0105	3.37						
Forest edge S												
Forest edge N							4.8947	0.0001	7.50			
Forest interior												
Altitude												
Enclose 3 m												
Enclose 15 m				3.55449957	0.0054	4.04						
Soil coverage				8.4040034	0.0001	13.36				2.04087	0.0463	2.12
Vegetation height												
Species richness monocot.												
Species richness dicot.												
Dicot. abundance												
Management	4.81703854	0.0001	7.37									
Moisture regime	3.84438766	0.0001	5.29									
Soil hardness												
Litter thickness												
Clay												
Fine silt												
Coarse silt												
Fine sand												
Coarse sand												
Organic matter												
Landscape												
30 m												
Woodland	2.39166709	0.0002	2.56									
Arable land												
Grassland												
Fallow												
Fragmentation							2.123	0.0286	2.16			
Ecotone length												
Habitat diversity												
60 m												
Woodland												
Arable land												
Grassland												
Fallow												
Fragmentation												
Ecotone length												
habitat Diversity												
120 m												
Woodland												
Arable land												
Grassland												
Fallow												
Fragmentation												
Ecotone length												
Habitat diversity												

250 m
Woodland
Arable land
Grassland
Fallow
Fragmentation
Ecotone length
Habitat diversity

	5.2880084	0.0005	7.24

500 m
Woodland
Arable land
Grassland
Fallow
Fragmentation
Ecotone length
Habitat diversity

Neuroptera			Hemiptera			Parasitoid		
F-value	*P*-value	% of variation	*F*-value	*P*-value	% of variation	*F*-value	*P*-value	% of variation
4.33863	0.0045	0.058						
			2.83787	0.0428	3.01			
			4.09641	0.0105	5.17			
7.54544	0.0006	0.12	6.02253	0.0004	8.75	9.19784	0.0001	14.59
3.20083	0.0146	0.038						
			5.94617	0.0022	9.34			
2.66431	0.0337	0.028						

Table 5
Results of the variance partitioning performed by RDA between local conditions and adjacent landscape contexts for each taxonomic group. The proportion of variation explained is given by the adjusted R^2, following Peres-Neto et al. (2006).

Data set	Araneae	Carabidae	Coccinellidae	Syrphidae	Neuroptera	Hemiptera	Parasitoid
Explained variance adjusted R^2							
Local (%)	9.67[***]	28.92[***]	7.77[***]	2.12[*]	12.38[**]	16.93[***]	14.59[***]
Landscape (%)	2.57[***]	4.10[***]	2.16[*]	ns	6.55[**]	10.37[**]	ns
Local ∩ landscape (%)	2.98			. . .	5.46		. . .

"∩" indicates that the variation explained is the shared variation between the two components.
No significant variables in a data set were reported as "ns". ". . ." indicates that shared component is not available as no significant variables were selected in one of the data set.
Cells are left blanked when the adjusted R^2 value was not interpretable (see Methods).

[*] <0.1.
[**] <0.05.
[***] <0.01.

even the lowest abundances of most of the natural enemies. The highest diversity of polyphagous ground dwelling predators in managed grass strips (MGM and MGD) is consistent with several published works (e.g. Sotherton, 1984; Collins et al., 2002; Thomas et al., 2002) and is at the base of the interest of beetle banks for conservation biological control (MacLeod et al., 2004). However, little or non-managed habitats, except if too dry, with high spontaneous vegetation, played also an important role as reservoirs for zoophagous arthropod taxonomic richness, provided that they were not too closed at 3 m and 15 m. On the opposite, the lowest densities of natural enemies, recorded within forest habitats (FI), at their South-facing edge (FES) and in very dry unmanaged grasslands (UGD), suggest that these SNH have the lowest prey and host availability. Geiger et al. (2009) already mentioned that forest habitats supported much lower densities of overwintering predatory arthropods than open agricultural habitats did. On the other hand, North-facing edges (FEN) displayed the highest abundances of aphidophagous hoverflies and forest edges as a whole structured both ladybirds and Neuropteran communities, what proves that forest habitats have both a quantitative and qualitative impact on natural enemies. Furthermore, this strong effect of the types of the SNH on abundance and species richness of overwintering natural enemies, could provide a good explanation for the variable results found in studies examining relationships between SNH or non-crop habitats at the landscape scale and natural enemy diversity and/or biological control (Bianchi et al., 2006; Chaplin-Kramer et al., 2011).

Soil coverage inside the trap perimeters proved to structure both hoverfly and ground beetle communities, what is in accordance with Maudsley et al. (2002) for the latter, and tall plants significantly increased species richness of the former and appeared as pre-requisites for larval development for these aphidophagous beneficial species (Speight, 2012). The fact that carabid and Hemiptera (only zoophagous species) together with Neuroptera and spider communities, and in a lesser extent hoverflies, Hymenopteran parasitoids and ladybirds, were much more structured by local than landscape features, suggests that a wealth of habitats at the group-of-fields level, with dry or wet, managed or unmanaged, open or closed habitats sheltering both monocotyledonous and dicotyledonous plants, is important to maintain a high level of biodiversity, functional or not (Pywell et al., 2005; Griffiths et al., 2007). Among landscape variables, forests proved to take the greatest part in structuring those predator communities, acting negatively on local abundances of most of the invertebrates studied (ground beetles, aphidophagous hoverflies, Neuroptera, Hemiptera and Hymenopteran parasitoids) and positively only on ladybirds. In the immediat landscape, medium arable land and grassland surfaces proved to be favourable for the beneficials as a whole and for several individual groups (Hemiptera, Hymenopteran parasitoids, spiders) while in the mid-distant landscape, fallows favoured aphidophagous hoverflies and arable lands did so for spiders whereas they were detrimental for Hemiptera. These results are

consistent with several publications such as Tscharntke et al. (2002) for Hymenopteran parasitoids, Sarthou et al. (2005) as well as Meyer et al. (2009) for hoverflies, and Batary et al. (2008) and Schmidt et al. (2008) for spiders. All these studies emphasized the importance of heterogeneous landscapes with arable fields intermingled with various and well represented SNH to enhance diversity and abundances of those taxa. Concerning hoverflies for instance, it has been demonstrated that fallow land was favourable to *Episyrphus balteatus* (the main syrphid species we caught in our study) populations at the landscape level, mainly when associated with close South-forest edges for improving overwintering conditions of this species (Sarthou et al., 2005).

Our study emphasizes the greater importance of local parameters over the landscape ones for the overwintering natural enemies we studied. However, the relative small spatial scale of our study, i.e. the 'farm scale', extending nevertheless up to 500 m around the traps, may underestimate wide landscape effects in structuring overwintering communities especially considering the variable dispersal abilities of the studied taxonomic groups. For instance, it has been shown for spiders that the spatial scales with the highest explanatory power ranged from 95 m- to 3 km-radii around sampling sites depending on the species (Schmidt et al., 2008). In any case, these results at our immediat and mid-distant landscape scale (without any spatial autocorrelation for any taxonomic group) are in accordance with those we found at the local one but also with those found by Raymond et al. (2014) relative to spring emergence of aphidophagous hoverfly species in crop fields. Thus, the wealth of SNH at the group-of-fields scale or at the farm scale must not be ignored and farmers' actions on SNH are thus to be considered as potentially very efficient way to improve their capacity to give shelter to a large variability of natural enemies. Different amount of organic matter, variable litter thickness, soil coverage, vegetation height, in various more or less open, more or less dry or wet SHN intermingled among crop fields, grassland, fallow land and little woodlots, should lead to the conservation of highly diversified natural enemy communities. This point appears to be of the utmost importance in the current context of global change, as it refers to the insurance hypothesis (Loreau et al., 2003; Tscharntke et al., 2012).

One other very important result of this study, which highlights the potential role of farm habitats, is the evidence that CAP grass strips, mainly those dominated by dicotyledonous plants, proved to strongly benefit to most of the major overwintering natural enemies in agricultural landscapes. Indeed, ground beetles, Neuroptera, Hemiptera, rove beetles and Hymenopteran parasitoids, showed either their maximum abundance or their maximum taxonomic richness, in CAP grass strips. These latter also significantly favoured high hoverfly abundances, which were the highest in FEN. In that, arable land adjacent to managed grass strips and other farmed and non-farmed habitats harbouring diverse overwintering natural enemies, are likely to benefit from high emigration rates of natural enemies and therefore high levels of natural pest control in

the spring (Blitzer et al., 2012, but see Wamser et al., 2011). One of the best known examples is the one of ground beetles which play a major role in pest control thanks to many polyphagous species which can feed both on little invertebrates and weed seeds (Kromp, 1999; Symondson et al., 2002). Several authors demonstrated that setting up grassy field margins around crop fields improves their overwintering conditions and thus enhances their populations and the biological control service they provide in the crop (Collins et al., 2002; MacLeod et al., 2004; Holland et al., 2009), thanks to the spillover effect (Thies and Tscharntke, 1999). Hence, CAP grass strips particularly favoured beneficials which are known to respond at relatively small spatial scales (Maisonhaute et al., 2010; Jonsson et al., 2012), and this feature fits very well with the European CAP measures and the current political willing to encourage European crop production systems towards less pesticides-dependent systems.

Moreover, the pre-eminence of farm-level over landscape-level phenomena driving diversity and structure of natural enemy communities, highlights the farmers' prerogatives in strengthening populations of natural enemies on their own farms thanks to appropriate habitat management. Indeed, it is the first time to our knowledge that these really innovative results, ensuing from comparison between precisely described local and landscape features, are pushed forward in explaining local densities, taxonomic richness and community structures of several groups of beneficial arthropods. In addition, our results highlight the need for a more precise description of SNH in studies at the landscape scale, as asked for by several authors (Griffiths et al., 2007, 2008; Veres et al., 2013), if we are to mechanistically understand the role of compositional landscape heterogeneity on exchanges of populations between compartments in the landscape and if we are to give relevant guidelines to design multifunctional landscapes. It is for instance of the utmost and increasing importance to combine at the very best agricultural production and biodiversity conservation for provision of ecosystem services (Macfadyen et al., 2012) on the same management unit (i.e. the farm).

5. Conclusions and perspectives

In our study, we found that habitat types and local, more than landscape variables determined natural enemy communities in overwintering habitats. We particularly found that managed grass strips (CAP ones in this study) were the main source of rich and diverse natural enemy communities on farmland, thus giving strong prerogative back to farmers from a conservation biological control perspective. Indeed, farmers have with grass strips an efficient way to improve the biological control potential on their farm by setting up grass strips (other than the CAP ones) near each crop field, and by favouring their spontaneous wild dicotyledonous plant species. Nevertheless, if in fact forest interior habitats seem to not be the key habitat-type for natural enemy conservation in general, what is a widespread and deeply held conviction nowadays, they take special importance in contributing to maintain high biological control on farmland through high densities or particular community structures of overwintering aphidophagous and other zoophagous beneficial insects, along their edges. Quite the same picture came up with unmanaged wet or dry habitats. Finally, the heterogeneity of habitats at the farm level, as a result of an extensive or even non-existent management of uncultivated areas, may be the key for abundant and diverse communities of natural enemies on farmland, hence for reaching the insurance hypothesis.

Further similar researches including measures of pest control services in adjacent crop fields, temporal dynamics in natural enemy populations and roles of SNHs for other service-providing communities such as pollinators or other wild biological groups, would allow a better understanding of the relationships between land use, biodiversity and ecosystem services. Finally, such multi-functional landscapes could provide more stability, resilience and adaptability to agricultural productions in a globally changing world.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2014.04.018.

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