



## Impacts of agricultural intensification on arable plants in extensive mixed crop-livestock systems



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### ABSTRACT

Populations of segetal species are facing sharp declines in Europe due to agricultural intensification. To better conserve them, it is important to assess the effect of intensification in extensive mixed crop-livestock systems, which are considered hotspots for segetal species. The aim of this study was to evaluate how certain key farming practices and land-use intensity affect the composition, species richness and abundance of segetal species, taking into account spatial heterogeneity within the studied fields. To do this, we sampled 94 winter cereal fields - 41 farmed organically and 53 farmed conventionally - along a gradient of land-use intensity. At field scale, we found that both the species richness and the abundance of segetal taxa decreased with an increase in land-use intensity. The results also showed significant differences in segetal taxa composition, species richness and abundance between the edges and the inner-fields location and these differences significantly increased with land-use intensity. The species richness and abundance of both common and threatened segetal taxa were significantly higher at the edges of fields than within them. Herbicide treatments had a significant negative impact on segetal taxa species richness and abundance, while mechanical weeding had a positive impact on abundance. Nitrogen inputs had a significant detrimental effect only on the abundance of common segetal taxa. Crop seed origin and the ratio of cereal crops in the rotational cycle had no effect on segetal taxa species richness and abundance. Despite these impacts, we found that segetal species richness and abundance were better explained by farm identity (random factor) than by current management (fixed factors). Variation in segetal species richness and abundance between fields of the same farm and between farms reflect the long-term effects of farming practices and the history of seed transfer between farms more than by current management practices. In our study area, the production of cereals is destined for the consumption of the farm's sheep and the fact the cereals are not marketed makes it possible to tolerate the presence of segetal species in higher proportions than in intensive farming systems.

### 1. Introduction

Agricultural intensification has been already identified as a major driver of rapid and negative trends in arable plant species in many European countries over recent decades (Cirujeda et al., 2011; Fried et al., 2008; Meyer et al., 2013). At both field and landscape scales, agricultural intensification involves increasing field size, mechanization, and the use of agrochemical inputs, as well as changing from spring to winter cereal crops and shortening crop rotation cycles (Robinson and Sutherland, 2002). These modifications have

considerably increased cereal crop yields in European countries over the last decades (Donald et al., 2001).

In agro-ecosystems, increasing yields requires strictly controlling the abundance of arable plants, as cereals compete with most of these plants for the same limited nutrients and light resources (Poffenbarger et al., 2015). The most common farming practices used on European farms to control arable plants are herbicides and ploughing. Another factor negatively affecting arable plants is that the high mineral nitrogen level, associated with agricultural intensification, disadvantages this species with a low competitive capacity by reducing essential

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factors like the availability of others nutrients (Storkey et al., 2010). Moreover, mineral fertilization input leads to a crop canopy that casts more shade, reducing light penetration and thus arable plant growth (Kleijn and van der Voort, 1997). Lastly, agricultural intensification impacts arable plant abundance by reducing (i) the germination of seeds from the seedbank, (ii) plant survival and (iii) the number of seeds per arable plant returning to the soil seedbank (Albrecht, 2003; Robinson and Sutherland, 2002). In most intensive agro-ecosystems, arable plant populations thus only survive around field edges (Cirujeda et al., 2019; Fried et al., 2009), where farming practices and fertilization are less thorough at controlling them (Kleijn and Verbeek, 2000).

Agricultural intensification has led many European arable plant species to become rare, and a number are included in the IUCN Red List (Storkey et al., 2011). Various rare and threatened European arable plant species survived in highland agro-ecosystems, which provide a higher landscape heterogeneity and smaller field sizes due to the more uneven topography and more extreme soil conditions (Albrecht et al., 2016). Therefore, agricultural production in most mountain agro-ecosystems, maintained by traditional extensive farming methods and characterized by low agrochemical input, little mechanization and landscapes dominated by permanent grasslands and perennial habitats, are areas of high conservation value for biodiversity (e.g. Albrecht et al., 2016; Fonderflick et al., 2010a). However, in recent years, many of these crop-livestock agro-ecosystems have undergone arable field intensification to increase forage autonomy and productivity (Fonderflick et al., 2010b; Mottet et al., 2006). As agricultural intensification has potentially more pronounced effects on biodiversity in less intensively managed agro-ecosystems (Kleijn et al., 2011), implementing conservation measures to protect biodiversity that depends directly on farming practices can be more effective in extensively than in intensively farmed systems (Batáry et al., 2015; Kleijn et al., 2009). Then, several measures have been proposed to conserve arable plant species, such as favouring organic farming or preserving field edges in the context of agri-environment schemes (Walker et al., 2007). To develop effective conservation strategies for arable plants in traditionally managed areas, it is first crucial to identify and to assess the negative or positive impacts of certain farming practices on both threatened and unthreatened arable plant species (Richner et al., 2015).

Most threatened arable plants are segetal (Albrecht et al., 2016; Rotchés-Ribalta et al., 2016), i.e. species whose mainly inhabit winter cereal fields (Albrecht, 2003). Populations of segetal species have severely declined in many European countries due to agricultural intensification (Chamorro et al., 2016; Fried et al., 2009; Robinson and Sutherland, 2002). Compared to generalist arable plants, these species are strongly affected by changes in land use and intensification, as their persistence in winter cereal fields almost exclusively depends on extensive farming practices. Despite many studies have focused the impact of agricultural intensification on the species diversity and composition of arable communities (e.g. Fried et al., 2008; Pinke et al., 2009), few have focused segetal species in detail (but see Rotchés-Ribalta et al., 2015a).

Thus, our study aimed to assess the effect of agricultural intensification on the composition and diversity of segetal species in low-intensity farming systems, characterized by semi-natural landscape, to provide basics knowledge for future conservation strategies. We hypothesized that land-use intensity would have a stronger effect on threatened than on common segetal species. More specifically, we aimed to better understand the impacts of land-use intensity and farming practices on segetal species composition, species richness and abundance, considering spatial heterogeneity within a field. The ultimate objective was to derive strategies to maintain segetal species in an area considered a segetal hotspot in France. To this end, the study assessed: (1) the impact of land-use intensity on segetal species composition, species richness and abundance at the edge and the inner of winter cereal fields and (2) the relative contribution of different farming practices on variations in segetal species richness and

abundance. We studied the responses to these two questions of the total segetal species in the study area as well as of three subsets: threatened, near-threatened and common (identified according to their conservation status in France).

## 2. Materials and methods

### 2.1. Study area

The study was conducted in 2014 and 2015 on the Causse Méjean and the Causse de Sauveterre, limestone plateaus at the southern edge of France's Massif Central (44°24'N, 03°28'E). These high plateaus (850–1247 m a.s.l.) host the largest steppe-like grasslands in France. They are typical karst systems with poor limestone soils and more fertile colluvia accumulated in depressions. The climate is mountain Mediterranean type with highly variable rainfall, peaking in September and April. Annual precipitation ranges from 900 to 1200 mm, and the average daily temperature varies from about  $-3^{\circ}\text{C}$  (mean January minimum) to  $24^{\circ}\text{C}$  (mean July–August maximum); the mean annual temperature is about  $7^{\circ}\text{C}$ .

At the beginning of the 20th century, agriculture in this area was almost entirely dedicated to sheep farming for meat or milk production (Jaudon et al., 2010). Today, agricultural use in the study area is still characterized by extensive livestock farming, with 300–600 sheep grazing rangelands of 230–720 ha. Their farmland included between 5 and 15 arable fields, which are usually less than 5 ha each. The landscapes have a low percentage of arable fields (10–20 %) surrounded by steppe-like grasslands, shrublands and pine forests. The arable fields are cultivated with forage and cereal crops which are exclusively used for feeding sheep. The crop rotation pattern is 2–3 years of cereals followed by 3–5 years of a forage crop, including legumes. After harvest, fields are usually grazed by sheep. In recent decades, the total surface area of arable fields has increased and farming practices have been intensified in order to achieve fodder autonomy (Fonderflick et al., 2010b).

Of the hundreds of farms in the study area, we sampled 20 that differed in farming intensity, 9 of which were farmed organically and 11 were managed conventionally. At each of these 20 farms, between 3 and 5 fields of winter cereals (wheat, triticale, barley, spelt and meslin) were selected. From all winter cereal fields available at each farm, fields were selected in order to minimize the differences between organic and conventional methods on field characteristics (area, perimeter, area/perimeter ratio; Table 1) and the surface area of arable land in the surrounding landscape (Table 1), because segetal species diversity is correlated to the length of field boundaries and the surrounding landscape, which could act as a retreat area and source of seed dispersal into the fields (e.g. Armengot et al., 2011b; Solé-Senan et al., 2014). For this reason, we calculated the area and the perimeter of a field and the area of arable land within a circle with a 1-km radius around the barycentre of each field using a Geographic Information System (QGIS 2.6 software). We mapped the arable land in the 1-km-radius circle using aerial photographs from 2008. The proportion of arable land was considered as a landscape descriptor, inversely proportional to the surface area of natural areas in the agricultural landscape (Gabriel et al., 2006).

Our dataset consisted of 94 fields, including 41 that were organically farmed (18 sampled in 2014 and 23 in 2015) and 53 under conventional use (30 sampled in 2014 and 23 in 2015). For each field, we collected information on specific farming practices by individually interviewing farmers. We selected farming practices (Table 1) for their potential importance in explaining variation in segetal species composition, species richness and abundance (Armengot et al., 2011a; Rotchés-Ribalta et al., 2016): these included the mean annual inputs of exogenous nitrogen (organic and mineral) per ha, the frequency of applications of mechanical weeding per year, the number of herbicide treatments per year, seed origin (three types: certified, farmer-produced and cleaned, farmer-produced and not cleaned), cereal ratio (percentage of years within a rotational cycle that the field was sown with

**Table 1**

Characteristics of fields, landscapes, the type of winter cereal crops and farming practices in the 94 sampled winter cereal fields (53 conventional and 41 organic). The significance of the difference in mean data ( $\pm$  Standard Deviation) between conventional and organic fields was tested using Anova or Chi-square tests (n.s. not significant, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ). The data for the following was obtained through interviews with individual farmers: seeding (kg ha<sup>-1</sup>), cereal ratio (percentage of years within a rotational cycle that the field was sown with cereal), crop diversity (number of different families of crop sown within the last five years), number of herbicide treatments (per year), number of applications of mechanical weeding (per year), total annual inputs of exogenous nitrogen (sum of organic and mineral exogenous nitrogen) in kg ha<sup>-1</sup>, and seed origin (certified: seeds purchased commercially; farmer-produced and sorted: re-use of own cereal seeds and sorted; farmer-produced and not sorted: re-use of own cereal seeds and not sorted).

|   | Conventional<br>(N = 53) | Organic<br>(N = 41) | p-value (test)         |
|---|--------------------------|---------------------|------------------------|
| Field and landscape characteristics                     |                          |                     |                        |
| Field area (ha)   | 2.3 $\pm$ 1.9            | 1.9 $\pm$ 1.5       | n.s. (Anova test)      |
| Field perimeter (m)                                     | 748 $\pm$ 322            | 695 $\pm$ 342       | n.s. (Anova test)      |
| Area/perimeter ratio                                    | 27.9 $\pm$ 10.4          | 25.7 $\pm$ 9.9      | n.s. (Anova test)      |
| Arable land surrounding landscape (ha)                  | 49.4 $\pm$ 22.3          | 44 $\pm$ 15.4       | n.s. (Anova test)      |
| Winter cereals  |                          |                     |                        |
| Spelt   | 1                        | 2                   | n.s. (Chi-square test) |
| Meslin  | 5                        | 21                  | *** (Chi-square test)  |
| Barley  | 21                       | 2                   | *** (Chi-square test)  |
| Triticale   | 17                       | 9                   | n.s. (Chi-square test) |
| Wheat   | 9                        | 7                   | n.s. (Chi-square test) |
| Farming practices                                       |                          |                     |                        |
| Seed origin (certified/farmer sorted/farmer not sorted) | 14/33/6                  | 8/27/6              | n.s. (Chi-square test) |
| Cereal ratio (%)  | 32 $\pm$ 6               | 29 $\pm$ 4          | ** (Anova test)        |
| Crop diversity  | 2 $\pm$ 0                | 2.2 $\pm$ 0.4       | *** (Anova test)       |
| Number of herbicide treatments                          | 0.3 $\pm$ 0.5            | 0                   | *** (Anova test)       |
| Number of applications of mechanical weeding            | 0.4 $\pm$ 0.6            | 0.4 $\pm$ 0.7       | n.s. (Anova test)      |
| Total nitrogen inputs (kg ha <sup>-1</sup> )            | 134 $\pm$ 66.1           | 80 $\pm$ 50.5       | *** (Anova test)       |
| Mineral nitrogen inputs (kg ha <sup>-1</sup> )          | 73 $\pm$ 40.6            | 0                   | *** (Anova test)       |
| Organic nitrogen inputs (kg ha <sup>-1</sup> )          | 61 $\pm$ 55.9            | 80 $\pm$ 50.5       | n.s. (Anova test)      |

cereal), and crop diversity (number of different families of crop sown during the last five years). Organic fields received no mineral nitrogen and no herbicide treatment.

## 2.2. Plant survey

Plant surveys were carried out at the peak of segetal species diversity in this region, i.e. between mid-May and early July. For each of the 94 selected cereal fields, we sampled two different locations: at the edge of the field (defined as the first cultivated metre adjacent to the field boundary) and the inner-field. At each location, we surveyed a 50m-long by 1 m-wide transect, parallel to the rows of crops. The transect at the edge was randomly positioned somewhere on the field perimeter. The inner-transect was at least 10 m from all edges (more for the larger fields) to avoid any edge effect, parallel to the edge transect. Each transect was divided into five sections. In each section, we sampled four contiguous 1 m x 1 m quadrats; these groups of contiguous quadrats were separated by 6 m. In total, 40 quadrats of 1 m<sup>2</sup> were sampled per field, including 20 quadrats in the inner field transect and 20 in the field edge transect.

For each quadrat, we recorded the presence or absence of all arable plant species. We also visually estimated the percentage of coverage of cultivated plants in each quadrat by visual comparison with a cover chart (0 %, 1 %, 3 %, 5 %, 10 %, 15 %, 20 %, etc. to 90 %, 100 %). Species inventories were carried out principally on segetal species that appear on the French segetal species national conservation programme list, which includes 102 species (Aboucaya et al., 2000; Cambecèdes et al., 2012) and seven species from lists which cover the regional flora. Of the resulting 109 segetal species (target species list), 56 have been previously detected in our study area (Cévennes National Park, unpublished data). We grouped together species that are difficult to differentiate at the beginning and the end of the field season: *Viola arvensis* Murray and *Viola tricolor* L. were recorded as *Viola* sp.; *Legousia hybrida* (L.) Delabre and *Legousia speculum-veneris* (L.) Durande ex Vill. were recorded as *Legousia* sp. We used The Plant List (2013) for species nomenclature.

## 2.3. Statistical analysis

### 2.3.1. Land-use intensity analysis

Rather than the standard organic/conventional dichotomy, which is considered less pronounced in extensive farming systems, we used an index of land-use intensity (LUI index; Armengot et al., 2011a) based on five farming practices to assess agricultural intensity for each sampled field (Supplementary data). According to this index, the number of applications of mechanical weeding and the number of herbicide treatments (0, 1 or 2 treatments per year) were grouped as arable plant control methods with three possibilities (0 = no arable plant control; 1 = harrowing of arable plants; 2 = application of herbicide) and seed origin was grouped with two possibilities (0 = farmer-produced and 1 = certified). The three other farming practices we assessed were: the total annual nitrogen input (kg ha<sup>-1</sup>), cereal ratio (percentage of years within a rotational cycle that the field was sown with cereal), and crop diversity (number of different families of crop sown within the last five years).

The LUI index was obtained by using each field's scores on the first axis of a Principal Coordinates Analysis (PCoA) based on these five farming practices (matrix of 94 sampled fields x 5 farming practices). We used PCoA, instead of PCA proposed by Armengot et al. (2011a), in relation with our dataset based on quantitative and discrete variables. Each field's scores on the first axis of the PCoA were then used as a continuous linear variable describing variation in land-use intensity between fields.

### 2.3.2. Segetal species diversity analysis

Segetal species richness and relative abundance were calculated separately at both field level and for the two locations in the field (edge and inner field). The species richness was the number of segetal species from the target species list, found at least once in the 40 sampled quadrats at field level or in the 20 sampled quadrats for each field location. The positive number of quadrats for each species was summed over all segetal species to obtain an index of relative abundance. It was calculated at field level and at the two locations for each field. Species richness and relative abundance at field level and for the two field

**Table 2**

Occurrence of segetal species (or taxa) recorded at the quadrat level for the two farming systems (organic and conventional) and the two field locations. Occurrence frequency was the sum of sampled quadrats with a positive identification of a species divided by all sampled quadrats in farming systems or field locations. The significance of the difference in occurrence frequency between conventional vs. organic quadrats and edge vs. inner quadrats was provided by Chi-square tests when counts were > 5, otherwise by Fisher's test (n.s. not significant, \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001).

| Species or taxon   | Conservation status | Org.<br>n = 1640 | Conv.<br>n = 2120 | p-value | Edge<br>n = 1880 | Inner<br>n = 1880 | p-value |
|--|---------------------|------------------|-------------------|---------|------------------|-------------------|---------|
| <i>Adonis flammea</i> Jacq.  | Threatened          | 0.106            | 0.078             | **      | 0.087            | 0.093             | n.s.    |
| <i>Agrostemma githago</i> L.                                       | Threatened          | 0.054            | 0.001             | ***     | 0.023            | 0.025             | n.s.    |
| <i>Androsace maxima</i> L.   | Threatened          | 0.145            | 0.087             | ***     | 0.111            | 0.113             | n.s.    |
| <i>Asperula arvensis</i> L.  | Threatened          | 0.049            | 0                 | ***     | 0.0282           | 0.015             | **      |
| <i>Bupleurum rotundifolium</i> L.                                  | Threatened          | 0.013            | 0                 | ***     | 0.007            | 0.005             | n.s.    |
| <i>Camelina microcarpa</i> Andr. ex DC.                            | Threatened          | 0.001            | 0.009             | **      | 0.006            | 0.005             | n.s.    |
| <i>Camelina sativa</i> (L.) Crantz                                 | Threatened          | 0.016            | 0.001             | ***     | 0.012            | 0.003             | **      |
| <i>Ceratocephala falcata</i> (L.) Pers.                            | Threatened          | 0.018            | 0                 | ***     | 0.011            | 0.005             | n.s.    |
| <i>Conringia orientalis</i> (L.) Dumort.                           | Threatened          | 0.001            | 0.001             | n.s.    | 0.001            | 0                 | n.s.    |
| <i>Consolida regalis</i> Gray                                      | Threatened          | 0.001            | 0                 | n.s.    | 0                | 0.001             | n.s.    |
| <i>Myagrum perfoliatum</i> L.                                      | Threatened          | 0.006            | 0.001             | **      | 0.003            | 0.003             | n.s.    |
| <i>Neslia paniculata</i> (L.) Desv.                                | Threatened          | 0                | 0.002             | n.s.    | 0.002            | 0.001             | n.s.    |
| <i>Polycnemum majus</i> A. Braun                                   | Threatened          | 0.005            | 0.001             | *       | 0.005            | 0                 | **      |
| <i>Valerianella echinata</i> (L.) DC.                              | Threatened          | 0                | 0.009             | ***     | 0                | 0.011             | ***     |
| <i>Ajuga chamaepitys</i> (L.) Schreb.                              | Near-threatened     | 0.001            | 0.004             | n.s.    | 0.005            | 0                 | **      |
| <i>Anthemis arvensis</i> L.  | Near-threatened     | 0.022            | 0.004             | ***     | 0.019            | 0.004             | ***     |
| <i>Anthemis cotula</i> L.  | Near-threatened     | 0.076            | 0.027             | ***     | 0.060            | 0.037             | **      |
| <i>Bromus arvensis</i> L.  | Near-threatened     | 0.018            | 0.027             | n.s.    | 0.033            | 0.014             | ***     |
| <i>Bunium bulbocastanum</i> L.                                     | Near-threatened     | 0.170            | 0.047             | ***     | 0.100            | 0.103             | n.s.    |
| <i>Calepina irregularis</i> (Asso) Thell.                          | Near-threatened     | 0.002            | 0.009             | *       | 0.007            | 0.005             | n.s.    |
| <i>Caucalis platycarpus</i> L.                                     | Near-threatened     | 0.265            | 0.123             | ***     | 0.303            | 0.112             | ***     |
| <i>Cyanus segetum</i> Hill   | Near-threatened     | 0.098            | 0.088             | n.s.    | 0.111            | 0.073             | ***     |
| <i>Euphorbia falcata</i> L.  | Near-threatened     | 0                | 0.001             | n.s.    | 0.001            | 0                 | n.s.    |
| <i>Fumaria vaillantii</i> Loisel.                                  | Near-threatened     | 0.002            | 0.007             | n.s.    | 0.009            | 0                 | ***     |
| <i>Galium tricoratum</i> Dandy                                     | Near-threatened     | 0.152            | 0.095             | ***     | 0.110            | 0.130             | n.s.    |
| <i>Iberis pinnata</i> L.   | Near-threatened     | 0.004            | 0.028             | ***     | 0.032            | 0.003             | ***     |
| <i>Legousia</i> sp.  | Near-threatened     | 0.317            | 0.226             | ***     | 0.315            | 0.215             | ***     |
| <i>Lolium rigidum</i> Gaudin                                       | Near-threatened     | 0.008            | 0.012             | n.s.    | 0.010            | 0.010             | n.s.    |
| <i>Lycopsis arvensis</i> subsp. <i>occidentalis</i> (Kusn.) Nordh. | Near-threatened     | 0.001            | 0.001             | n.s.    | 0.002            | 0.001             | n.s.    |
| <i>Papaver argemone</i> L.   | Near-threatened     | 0.013            | 0.021             | n.s.    | 0.022            | 0.012             | *       |
| <i>Ranunculus arvensis</i> L.                                      | Near-threatened     | 0.084            | 0.059             | **      | 0.073            | 0.067             | n.s.    |
| <i>Thlaspi arvense</i> L.  | Near-threatened     | 0.009            | 0.036             | ***     | 0.033            | 0.015             | ***     |
| <i>Torilis leptophylla</i> (L.) Rchb. f.                           | Near-threatened     | 0.003            | 0.006             | n.s.    | 0.009            | 0.001             | **      |
| <i>Valerianella coronata</i> (L.) DC.                              | Near-threatened     | 0.005            | 0                 | **      | 0.001            | 0.003             | n.s.    |
| <i>Valerianella dentata</i> (L.) Pollich                           | Near-threatened     | 0.082            | 0.126             | ***     | 0.119            | 0.095             | **      |
| <i>Valerianella eriocarpa</i> Desv.                                | Near-threatened     | 0.084            | 0.040             | ***     | 0.069            | 0.050             | *       |
| <i>Aphanes arvensis</i> L.   | Common              | 0.160            | 0.146             | n.s.    | 0.158            | 0.146             | n.s.    |
| <i>Buglossoides arvensis</i> (L.) I.M.Johnst.                      | Common              | 0.117            | 0.079             | ***     | 0.111            | 0.079             | **      |
| <i>Papaver dubium</i> L.   | Common              | 0.030            | 0.050             | **      | 0.048            | 0.035             | *       |
| <i>Papaver rhoeas</i> L.   | Common              | 0.331            | 0.204             | ***     | 0.261            | 0.257             | n.s.    |
| <i>Scandix pecten-veneris</i> L.                                   | Common              | 0.113            | 0.067             | ***     | 0.135            | 0.038             | ***     |
| <i>Sinapis arvensis</i> L.   | Common              | 0.018            | 0.017             | n.s.    | 0.013            | 0.022             | n.s.    |
| <i>Valerianella locusta</i> (L.) Laterr.                           | Common              | 0.301            | 0.292             | n.s.    | 0.324            | 0.267             | ***     |
| <i>Viola</i> sp.   | Common              | 0.496            | 0.452             | **      | 0.494            | 0.449             | **      |

locations were calculated for all segetal species together and for the three subsets of segetal species (threatened, near-threatened and common) according to their conservation status in France (Aboucaya et al., 2000) or, for the seven additional species from new regional lists, according to expert judgement (Table 2).

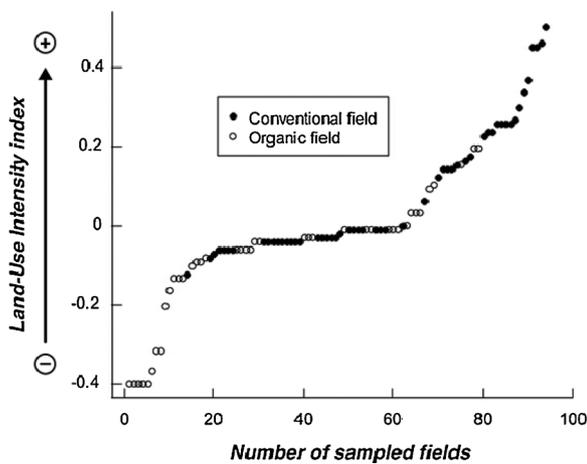
In a first step, we compared the occurrence frequency at quadrat level of each segetal species recorded in the 94 field sampling for the two farming systems (organic versus conventional) and the two field locations. Occurrence frequency was the sum of sampled quadrats with a positive observation of a species divided by all quadrats sampled in the two farming systems or the two field locations. The occurrence frequency of each segetal species was compared between the two farming systems and between the two field locations using a Chi-square test when occurrences were > 5, otherwise a Fisher's exact test was used.

In a second step, variation in segetal species richness and relative abundance between the two field locations in each the 94 fields was modelled using Generalized Linear Mixed Models (GLMM hereafter). We used a Poisson distribution with a log-link function to model variation in segetal species richness and a negative binomial distribution

with a log-link function to model variation in relative abundance. Negative binomial distribution was used to deal with overdispersion in the abundance count data (Payne et al., 2015). We tested the effect of land-use intensification (LUI index), the field location (edge and inner), and of their interactions as fixed factors. The year of sampling (2014 or 2015) was included as a fixed factor in order to test for differences between years. 'Farm identity' was added as a random factor to account for the nested design of fields in the farms (repeated measurements at the farm level) and reflects the historical and current nature of all farmer's farming practices. This analysis was separately conducted for all segetal species together and for the three subsets of segetal species according to their conservation status.

### 2.3.3. Segetal species composition analysis

We conducted four separate permutational multivariate analyses of variance (Anderson, 2001), using a distance matrix based on the Gower dissimilarity index (Anderson et al., 2006), to analyse how the LUI index affected segetal species composition in each of the 94 fields, 94 inner-field locations, 94 field-edge locations, and between the two field locations. Segetal species composition was analysed separately using



**Fig. 1.** Ordination of the 94 sampled fields (x-axis) on a gradient of land-use intensity (y-axis: low LUI index = negative values and high LUI index = positive values). Organically farmed fields are represented by white circles and conventionally farmed fields by black circles. The LUI index corresponds to the score of each field on the first axis of a Principal Coordinates Analysis (PCoA) that included five farming practices (total nitrogen input, weed control, cereal ratio, crop diversity and seed origin; see [Armengot et al., 2011a](#) for more details).

presence/absence of the segetal species recorded at the field level and for the two locations within the fields. Segetal species found in only one out of the 94 sampled fields were removed from the composition analysis. The significance of the LUI index was obtained by means of *F*-tests based on sequential sums of quadrats from 999 permutations of the raw data, restricting permutations within each farm so as to take into account the nested design of fields in the farm ([Anderson, 2001](#)).

#### 2.3.4. Effect of farming practices on segetal diversity

We used GLMMs with a backward selection procedure to determine which of six farming practices (type of winter cereal fields, total nitrogen input, number of herbicide applications, number of mechanical weeding applications, seed origin and cereal crop ratio) contributed most to the variation in segetal species richness and relative abundance at the field level. We checked the correlation structure between these six farming practices to avoid multicollinearity in the models. We used Anova to test the difference in the LUI index score between categorical variables (type of winter cereal fields and seed origin). We used Pearson's correlation coefficient to explore correlation between continuous variables (total nitrogen, number of herbicide applications, number of mechanical weeding applications and cereal crop ratio). We only found a significant difference in the LUI index for spelt and meslin fields in comparison with the three other types of winter cereal fields, likely because spelt and meslin were more present in the organic sampled fields than in the conventional fields ([Table 1](#)). All correlation coefficients between the four continuous variables were below 0.5.

The full model for explaining variations in segetal species richness and relative abundance at the field level included the six farming practices as fixed factors and the farm identity as a random factor to account for the nested design of fields in the farms. We used a Poisson distribution with a log-link function to model variations in segetal species richness and a negative binomial distribution with a log-link function to model variation in relative abundance. Negative binomial distribution was used to deal with overdispersion in abundance count data. From this full model, we removed all the factors that were not significant one by one until all the remaining factors were significant ( $p < 0.05$ ). Backward selection procedures were used to model variation in species richness and relative abundance for all the segetal species together and for the three subsets of segetal species according to their conservation status.

After the backward selection procedure, we assessed the goodness-of-fit of the best models by computing their coefficients of determination (pseudo- $R^2$ ). Two types were computed ([Nakagawa and Schielzeth, 2013](#)): the marginal  $R^2$  ( $R^2_{GLMM(m)}$ ), accounting for the variance explained by fixed factors after backward selection, and the conditional  $R^2$  ( $R^2_{GLMM(c)}$ ), accounting for the variance explained by both the fixed factors selected and the random factor (farm identity). Because coefficients of determination ( $R^2$ ) were not accessible with a negative binomial, segetal species abundance was log transformed and we used a Gaussian distribution to compute coefficients of determination ( $R^2$ ) for this last analysis.

All analyses were carried out with R 3.2.3 software ([R Core Team, 2015](#)). Composition analyses were conducted using the 'vegan' package ([Oksanen et al., 2009](#)). All GLMMs were fitted using the glmer or glmer.nb functions in the 'lme4' package ([Bates et al., 2015](#)) and the 'MuMIn' package was used for the  $R^2$  calculation ([Bartoń, 2013](#)).

### 3. Results

#### 3.1. Landscape and field characteristics, farming practices and land-use intensity

In our study area, the landscape is largely dominated by natural areas; arable land represented only  $15.2\% \pm 6.4$  ( $\pm$  SD) within the 1km-radius circles around field. Our sampling design found no significant differences between organic and conventional fields or landscape characteristics, but revealed some significant differences between farming practices ([Table 1](#)). Total annual nitrogen input was significantly higher in conventionally farmed fields than in organic fields (Anova test,  $F_{(1, 92)} = 18.84$ ,  $p < 0.001$ , [Table 1](#)), but varied greatly between both farms and fields. Less than half of the conventional fields sampled received one herbicide treatment per year (16 out of 53 sampled) and only one received two treatments per year. Organic fields had significantly more complex crop rotations with cereal crops occurring less frequently during the cycle (Anova test,  $F_{(1, 92)} = 8.67$ ,  $p < 0.01$ ). No significant difference was observed for seed origin (Chi-square test,  $X^2 = 0.29$ ,  $p = 0.59$ ) or the number of applications of mechanical weeding (Anova test,  $F_{(1, 92)} = 0.19$ ,  $p = 0.67$ , [Table 1](#)).

The PCoA based on the five farming practices showed that the first axis was negatively correlated to crop diversity and positively to the four other practices. The score of each field on the first axis thus described a gradient from agricultural intensification ([Fig. 1](#)), from low intensity (negative values) to high intensity (positive values) and was thus interpreted as a land-use intensity index (LUI index). There was considerable variation within the two farming systems field scores, with a little more variability for conventional than for organic fields (standard deviation: 0.17 for conventional fields and 0.15 for organic fields). There was a significant difference in the LUI index between organic and conventional fields (Mann-Whitney test,  $W = 557$ ,  $p < 0.0001$ ), with most organic fields corresponding to lower LUI index values than conventional fields. However, the ordination of each field on the LUI index showed that some conventional fields have lower LUI index values than some organic fields ([Fig. 1](#)).

#### 3.2. Effect of farming systems and locations within a field on segetal species diversity and composition

A total of 44 segetal taxa were found in the 94 fields sampled, with 42 taxa occurring at the field edge and 39 in the inner field ([Table 2](#)). Four segetal taxa (*Consolida regalis* Gray, *Euphorbia falcata* L., *Valerianella coronata* (L.) DC. and *Valerianella echinata* (L.) DC.) were found in one field only. Of the 44 segetal taxa, 14 taxa are classified as threatened, 22 as near-threatened and 8 as common ([Table 1](#)).

We found on average ( $\pm$  SD)  $20.6 \pm 3.7$  segetal taxa per farm,  $11.3 \pm 4.2$  segetal taxa per field (min. = 2, max. = 20), with  $11.9 \pm 3.9$  segetal taxa (min. = 5, max. = 20) in organic fields and

10.9 ± 3.9 segetal taxa (min. = 2, max. = 17) in conventional fields, and 2.9 ± 2.2 segetal taxa per quadrat (min. = 0, max. = 11), with 3.4 ± 2.2 segetal taxa in organic quadrats and 2.9 ± 2.2 segetal taxa in conventional quadrats. Of the 29 segetal taxa with a significantly different occurrence frequency between the two farming systems, 23 had higher occurrence frequency in organic than in conventional fields (Table 2). Of these 23 segetal taxa, 22 had higher occurrence frequency at the edge of a field than in the inner-field location (Table 2).

At quadrat level, there was a highly significant correlation between the number of segetal taxa and the number of other arable plants (Pearson coefficient; n = 3760, r = 0.81, p < 0.001), both for inner field quadrats (Pearson coefficient; n = 1880, r = 0.81, p < 0.001) and quadrats at the edge (Pearson coefficient; n = 1880, r = 0.80, p < 0.001). Quadrats at the edge contributed on average to 84.7 % ± 14 of the total segetal species richness found in all quadrats sampled in the field. Moreover, we observed that the percentage of cultivated plant cover in sampled inner field quadrats was significantly higher than in quadrats at the edge (Wilcoxon signed-rank test, N = 1880, p < 0.001; average ± SD for inner field quadrats: 48.4 % ± 19.5, for field edge quadrats: 33.6 % ± 15.5).

The GLMMs showed that the species richness and relative abundance of total segetal taxa decreased at the field level when the LUI index increased, but not significantly (Fig. 2, Table 3). Total segetal species richness and relative abundance were significantly higher at the field edge than at the inner-field location and this difference significantly increased when the LUI index increased (Fig. 2, Table 3). For threatened segetal taxa, relative abundance significantly decreased at the field level when the LUI index increased. However, this was not the case for species richness. For near-threatened segetal taxa, variation in species richness and relative abundance were significantly correlated to land-use intensity in interaction with the location in the field, but not with the LUI index alone. Species richness and relative abundance of near-threatened segetal taxa were significantly higher at the edge than at the inner-field location and this difference significantly increased when the LUI index increased (Table 3). For common segetal taxa, the LUI index had no significant correlation with species richness and relative abundance at the field level. However, we found that species richness and relative abundance of common segetal taxa were significantly higher at the edge than at the inner-field location. The year had no significant effect on segetal species richness and relative

abundance.

The permutational multivariate analysis of variance showed that land-use intensity had a significant effect only on segetal taxa composition in interaction with field location (Table 4); this composition was significantly different between field edge and inner field locations ( $F_{(1, 186)} = 59.75, p < 0.001$ , Table 4). The LUI index alone did not significantly impact segetal taxa composition between fields or between locations within the field. No difference in segetal taxa composition was found between the two years.

### 3.3. Effects of farming practices on segetal taxa diversity

The backward selection procedure showed that only the number of herbicide treatments and the number of applications of mechanical weeding were significantly correlated with segetal species richness and relative abundance at field level (Table 5). For total segetal taxa, the number of herbicide treatments was significantly negatively correlated with both species richness and relative abundance, and the number of applications of mechanical weeding was positively correlated with relative abundance. For threatened segetal taxa, species richness increased significantly with the frequency of mechanical weeding, while the relative abundance decreased significantly with the number of herbicide treatments. For near-threatened segetal taxa, relative abundance increased significantly with the number of mechanical weeding applications and decreased significantly with the number of herbicide treatments. Wheat had significantly lower relative abundance of near-threatened segetal taxa than spelt and barley. Relative abundance of common segetal taxa decreased significantly with the number of herbicide treatments and increased significantly with exogenous nitrogen inputs. In all models, seed origin and the percentage of years within a rotational cycle that the field was sown with cereal (cereal ratio) had no significant correlation with species richness or relative abundance of segetal taxa in our study area.

In the best models selected after backward selection, the random factor (farm identity) showed a strong influence on the species richness and relative abundance of total segetal taxa as well as of the three subsets of segetal taxa according to their conservation status (Table 5). The conditional  $R^2$  was stronger than the marginal  $R^2$  in explaining the variation in species richness and relative abundance of segetal taxa at field level. Fixed factors (marginal  $R^2$ ) explained only 11 % of variance

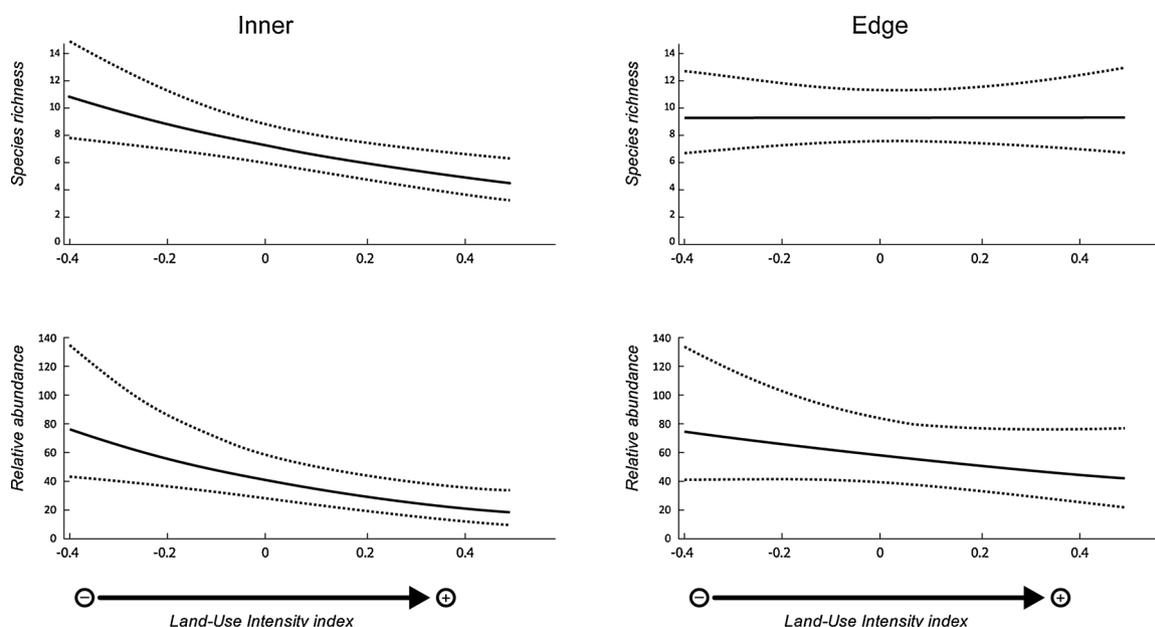


Fig. 2. Variation in the species richness and relative abundance of segetal taxa between two locations within a field (inner and edge) on a gradient of land-use intensity (x-axis: low LUI index = negative values and high LUI index = positive values) modelled with Generalized Linear Mixed Models.

**Table 3**

Generalized Linear Mixed Model used to model the variation in species richness and relative abundance of total segetal taxa and the three subsets of segetal taxa according to their conservation status (see Table 2) in relation to: land-use intensification (LUI index), two field locations (edge or inner) and the year (2014 or 2015). Significance of statistical analyses: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

|                              | Variables                    | Estimated parameter | Standard error | Z or t-value | p-value |
|------------------------------|------------------------------|---------------------|----------------|--------------|---------|
| <b>Species richness</b>      |                              |                     |                |              |         |
| Total segetal taxa           | (Intercept)                  | 2.221               | 0.106          | 20.994       | ***     |
|                              | Year (2015)                  | 0.019               | 0.147          | 0.128        | 0.90    |
|                              | LUI index                    | 0.002               | 0.299          | 0.005        | 0.99    |
|                              | Location (inner)             | -0.263              | 0.051          | -5.187       | ***     |
|                              | LUI index x Location (inner) | -1.079              | 0.290          | -3.723       | ***     |
| Threatened segetal taxa      | (Intercept)                  | 0.096               | 0.205          | 0.469        | 0.64    |
|                              | Year (2015)                  | -0.295              | 0.284          | -1.039       | 0.30    |
|                              | LUI index                    | -0.787              | 0.775          | -1.015       | 0.31    |
|                              | Location (inner)             | -0.183              | 0.148          | -1.236       | 0.22    |
|                              | LUI index x Location (inner) | -1.209              | 0.848          | -1.425       | 0.15    |
| Near-threatened segetal taxa | (Intercept)                  | 1.430               | 0.132          | 10.862       | ***     |
|                              | Year (2015)                  | 0.043               | 0.182          | 0.237        | 0.81    |
|                              | LUI index                    | 0.336               | 0.412          | 0.816        | 0.42    |
|                              | Location (inner)             | -0.354              | 0.076          | -4.647       | ***     |
|                              | LUI index x Location (inner) | -1.395              | 0.423          | -3.296       | ***     |
| Common segetal taxa          | (Intercept)                  | 1.342               | 0.093          | 14.510       | ***     |
|                              | Year (2015)                  | 0.078               | 0.122          | 0.636        | 0.53    |
|                              | LUI index                    | -0.141              | 0.363          | -0.389       | 0.70    |
|                              | Location (inner)             | -0.193              | 0.076          | -2.525       | *       |
|                              | LUI index x Location (inner) | -0.633              | 0.436          | -1.451       | 0.15    |
| <b>Relative abundance</b>    |                              |                     |                |              |         |
| Total segetal taxa           | (Intercept)                  | 4.090               | 0.180          | 22.744       | ***     |
|                              | Year (2015)                  | 0.040               | 0.248          | 0.160        | 0.87    |
|                              | LUI index                    | -0.610              | 0.506          | -1.206       | 0.23    |
|                              | Location (inner)             | -0.374              | 0.086          | -4.334       | ***     |
|                              | LUI index x Location (inner) | -0.951              | 0.477          | -1.993       | *       |
| Threatened segetal taxa      | (Intercept)                  | 1.581               | 0.307          | 5.158        | ***     |
|                              | Year (2015)                  | -0.479              | 0.413          | -1.160       | 0.25    |
|                              | LUI index                    | -2.664              | 1.178          | -2.262       | *       |
|                              | Location (inner)             | 0.027               | 0.239          | 0.114        | 0.91    |
|                              | LUI index x Location (inner) | 0.418               | 1.324          | 0.316        | 0.75    |
| Near-threatened segetal taxa | (Intercept)                  | 3.165               | 0.226          | 13.996       | ***     |
|                              | Year (2015)                  | 0.185               | 0.311          | 0.596        | 0.55    |
|                              | LUI index                    | 0.274               | 0.689          | 0.397        | 0.69    |
|                              | Location (inner)             | -0.579              | 0.122          | -4.753       | ***     |
|                              | LUI index x Location (inner) | -1.468              | 0.675          | -2.176       | *       |
| Common segetal taxa          | (Intercept)                  | 3.318               | 0.189          | 17.568       | ***     |
|                              | Year (2015)                  | 0.068               | 0.259          | 0.264        | 0.79    |
|                              | LUI index                    | -0.893              | 0.576          | -1.552       | 0.12    |
|                              | Location (inner)             | -0.283              | 0.101          | -2.813       | **      |
|                              | LUI index x Location (inner) | -0.779              | 0.565          | -1.377       | 0.17    |

in species richness and 14 % of variance in relative abundance of total segetal taxa in the best models, while 44 % and 55 % of the respective variance was explained when the farm identity was integrated as a random factor (Table 5).

## 4. Discussion

### 4.1. Impact of location in the field on segetal species

In our study area, which is characterized by extensive mixed crop–livestock systems, our results reveal significant differences in the composition, species richness and total abundance of segetal species between edge and inner-field locations and these differences became stronger with increasing land-use intensity. Species richness and abundance of threatened, near-threatened and common segetal species were significantly higher at field edges than in inner field locations (Table 2, Fig. 2). These results are consistent with those obtained in several previous studies on arable plants (e.g. Fried et al., 2009) as well as on segetal species (José-María et al., 2010; Romero et al., 2008; Solé-

Senan et al., 2014) and show the importance of cereal field edges for the conservation of segetal species (Cirujeda et al., 2019; Romero et al., 2008), even in extensive farming systems. The different patterns of segetal species distribution within a field are directly related to the efficiency of the agricultural practices carried out both to limit the development of arable plants (herbicide treatment and mechanical weeding) and to increase yields (nitrogen supply), which are more thorough at the interior than at the edge of a cereal field. In our case study, the smallest percentage of cereal cover occurred at the field edges (33.6 % on average) compared with inner fields (48.4 % on average), reducing competition for resources between cereals and segetal species (Rotchés-Ribalta et al., 2016), and thus conferring more favourable development conditions for segetal species at field edges (Solé-Senan et al., 2014). This indicates that small fields with an important length of boundary could provide local refuges for arable plants and segetal species.

**Table 4**

Results from the four separate permutational multivariate analyses of variance in segetal species composition in relation to the LUI index: between fields, between inner field locations, between field edge locations and between the two field locations. Degree of freedom (d.f.), sums of quadrats (SS), F statistic and p-value: \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001.

|                                  | d.f. | SS    | F      | p-value |
|----------------------------------|------|-------|--------|---------|
| <b>Between fields</b>            |      |       |        |         |
| LUI index                        | 1    | 0.052 | 1.392  | 0.47    |
| Residual                         | 92   | 3.417 |        |         |
| Total                            | 93   | 3.469 |        |         |
| <b>Between inner locations</b>   |      |       |        |         |
| LUI index                        | 1    | 0.093 | 3.431  | 0.22    |
| Residual                         | 92   | 2.494 |        |         |
| Total                            | 93   | 2.587 |        |         |
| <b>Between edge locations</b>    |      |       |        |         |
| LUI index                        | 1    | 0.067 | 2.374  | 0.18    |
| Residual                         | 92   | 2.587 |        |         |
| Total                            | 93   | 2.654 |        |         |
| <b>Between the two locations</b> |      |       |        |         |
| Locations                        | 1    | 1.665 | 59.750 | ***     |
| LUI index                        | 1    | 0.046 | 1.661  | 0.13    |
| Location * LUI index             | 1    | 0.068 | 2.430  | *       |
| Residual                         | 184  | 5.127 |        |         |
| Total                            | 187  | 6.905 |        |         |

**4.2. The impact of land-use intensity and farming practices on segetal species composition and diversity**

At the field scale, the results show that land-use intensification tends

**Table 5**

Generalized Linear Mixed Models that best explained the variation in species richness and relative abundance of total segetal taxa and the three subsets of segetal taxa according to their conservation status (see Table 2) after a backward selection procedure. The full model included six farming practices: the type of winter cereals (see Table 1), total annual inputs of exogenous nitrogen (Nitrogen input), number of herbicide treatments per year (Herbicide), number of applications of mechanical weeding (Mechanical weeding), seed origin and ratio of cereal crops in a rotational cycle (cereal ratio). Non-significant variables were removed one by one after multiple regressions (p-to-enter < 0.05, p-to-remove > 0.05). Statistical analyses: \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001. For the model selected after the backward selection procedure, we computed the marginal R2 (R2 GLMM (m)), accounting for the variance explained by the fixed factors selected, and the conditional R2 (R2 GLMM (c)), accounting for the variance explained by both the fixed factors selected and the random factor (fields in the same farm).

|                              | Variables          | Estimated parameter | Standard error | Z or t-value | p-value | R2 GLMM (m) | R2 GLMM (c) |
|------------------------------|--------------------|---------------------|----------------|--------------|---------|-------------|-------------|
| <b>Species richness</b>      |                    |                     |                |              |         |             |             |
| Total segetal taxa           | (Intercept)        | 2.460               | 0.062          | 39.60        | ***     | 0.11        | 0.44        |
|                              | Herbicide          | -0.303              | 0.108          | -2.81        | **      |             |             |
| Threatened segetal taxa      | (Intercept)        | 0.133               | 0.147          | 0.902        | 0.37    | 0.08        | 0.25        |
|                              | Mechanical weeding | 0.326               | 0.159          | 2.057        | *       |             |             |
| Near-threatened segetal taxa | (Intercept)        | 1.688               | 0.075          | 22.505       | ***     | 0.04        | 0.28        |
|                              | Herbicide          | -0.249              | 0.144          | -1.721       | 0.09    |             |             |
| Common segetal taxa          | (Intercept)        | 1.567               | 0.052          | 30.217       | ***     | 0.04        | 0.04        |
|                              | Herbicide          | -0.216              | 0.125          | -1.725       | 0.09    |             |             |
| <b>Relative abundance</b>    |                    |                     |                |              |         |             |             |
| Total segetal taxa           | (Intercept)        | 4.626               | 0.125          | 37.020       | ***     | 0.14        | 0.55        |
|                              | Herbicide          | -0.540              | 0.174          | -3.100       | **      |             |             |
|                              | Mechanical weeding | 0.261               | 0.130          | 2.000        | *       |             |             |
| Threatened segetal taxa      | (Intercept)        | 2.465               | 0.301          | 8.192        | ***     | 0.07        | 0.35        |
|                              | Herbicide          | -1.190              | 0.458          | -2.601       | **      |             |             |
| Near-threatened segetal taxa | (Intercept)        | 4.055               | 0.238          | 17.014       | ***     | 0.25        | 0.50        |
|                              | Spelt              | -0.436              | 0.106          | -4.109       | ***     |             |             |
|                              | Meslin             | 0.0345              | 0.464          | -0.742       | 0.46    |             |             |
|                              | Barley             | -0.794              | 0.259          | -3.064       | **      |             |             |
|                              | Triticale          | -0.382              | 0.272          | -1.407       | 0.16    |             |             |
|                              | Herbicide          | -0.724              | 0.257          | -2.818       | **      |             |             |
|                              | Mechanical weeding | 0.357               | 0.174          | 2.058        | *       |             |             |
| Common segetal taxa          | (Intercept)        | 4.379               | 0.214          | 20.461       | ***     | 0.15        | 0.50        |
|                              | Nitrogen input     | -0.004              | 0.002          | -2.196       | *       |             |             |
|                              | Herbicide          | -0.434              | 0.199          | -2.178       | *       |             |             |

to modify segetal species composition (Table 4), and to decrease segetal species richness and relative abundance (Table 3), as has been shown in northeastern Spain (José-María et al., 2010; Romero et al., 2008) and in Central Europe (Albrecht, 2003). However, this modification trend was not significant in our case study. The very high contribution of field edges to segetal species richness in a field (on average 84.7 % of the total specific richness of a field), even in the fields with the highest land-use intensity, certainly attenuated the decrease in richness generated by agricultural intensity, for both common and threatened segetal species. Variation in segetal species abundance according to land-use intensity in fact depended on their conservation status. In line with Storkey et al. (2010), our results show that intensification further decreased the abundance of the most threatened segetal species compared to common segetal species (Table 3), probably due to differences in eco-physiological traits between these two groups of plants (Storkey, 2006). Threatened segetal species are expected to possess a smaller specific leaf area than common segetal species. For example, the threatened species *Adonis flammea* Jacq. (small specific leaf area, heavy seeds, late flowering) is less competitive for light than common segetal species such as *Sinapis arvensis* L., especially when nitrogen inputs increase (Storkey et al., 2010). Increased nitrogen input favours cereal growth, increasing the competition for light for other plants underneath them (Storkey et al., 2010) and decreasing the fitness of segetal species. As a follow-up to this study, an approach assessing functional traits would be particularly useful to better understand changes in the diversity and composition of segetal species in relation to agricultural intensification (Storkey et al., 2010; Solé-Senan et al., 2017).

Our findings also show that only a few types of farming practices

had a significant effect on explaining variations in segetal species richness and abundance. According to José-María et al. (2011), the use of herbicides – even a single herbicide treatment – is clearly the farming practice that most explains the decline in threatened and common segetal species richness and abundance, even though these treatments are more targeted towards arable plants such as *Elytrigia repens* Desv. than segetal species. In fact, cereal fields favourable to the development of arable plants are also favourable to segetal species (Rotchés-Ribalta et al., 2015a), explaining the strong correlation between the number of segetal species and other arable plants in our case study. On the other hand, the increase in species richness of threatened segetal species and the total abundance of segetal species in line with an increase in mechanical weeding is more surprising, since this practice is most often used, especially in organic farming (Benaragama and Shirliffe, 2013), to limit the development of arable plants. These results may be partly explained by the fact that segetal species have evolved for centuries in soils regularly disturbed by cultivation practices. Superficial soil tillage, by modifying the vertical distribution of the seeds of segetal species in the soil profile, may also generate very favourable conditions for the emergence of seeds from dormancy (Gruber and Claupein, 2009).

Overall, the contribution of nitrogen inputs, seed origin and the ratio of cereal crops in the rotation cycle seemed to play a minor role in explaining the variations in the species richness and abundance of segetal species. However, an increase in nitrogen inputs had a significant negative impact on the abundance of common segetal species (but not on threatened and near-threatened segetal species) (Table 5). This effect has also been observed in Spain (Rotchés-Ribalta et al., 2015a). In mixed crop–livestock systems, unlike intensive systems, a significant proportion of the nitrogen inputs to cereal crops comes from manure application, even for conventionally farmed fields (62 % of total nitrogen inputs in our case study, Table 1). In these systems, the cereals produced are self-consumed and serve as food for the farm's sheep flocks in addition to forage rations. The straw is used as litter or sometimes as food. The mixture of animal manure and straw spread as fertilizer thus contains seeds of segetal species: unfortunately, existing literature does not describe in what proportion. It is possible that the increase in nitrogen, favouring the production of cereal plants at the expense of more oligotrophic segetal species, is partly offset by a flow of seeds from the manure. Similarly, it is also highly probable that epizoochorous seed dispersal of segetal species is carried out when sheep graze the fields after harvest. Fischer et al. (1996) found over 8500 seeds in the fleece of only one sheep and this seeds dispersal mechanism is often underestimated.

In mixed crop–livestock systems, farmers often use their own cereal seeds, so when they reseed each year, a considerable proportion of seeds may come from segetal species harvested with cereals. In the information obtained in our interviews, only 5 out of 20 farmers stated that they do not systematically clean their seeds, and even these farmers used methods provide only uncertain efficiency due to varying duration of cleaning (Gasc et al., 2010). Loddo et al. (2009) estimated that cleaning could eliminate 93 % of segetal seeds and more than half of the species. In our case, the impact of cleaning is unknown and merits further investigation. In any event, for many segetal species, some seeds fall to the soil before harvest and thus contribute to the field's seedbank. Additionally, species of low height such as *Androsace maxima* L. and *Viola arvensis* L. are not affected by combine harvesters. The historical composition of seedlings in a field, beyond the cleaning practices and the type of cereals grown, is likely to partly explain the composition of the segetal community in any given growing season.

Concerning the ratio of cereal crops in the rotation cycle, our findings indicate that this was more or less identical for all the fields sampled. The short duration of forage crops such as legumes in crop rotation does not seem to affect the viability of the segetal seedbank in the soil, as opposed to the introduction of longer-duration prairie crops (Dutoit et al., 2003).

#### 4.3. What explains the diversity in segetal species?

Field-to-field variation in arable plants is common, even within an individual farm (Marshall and Arnold, 1994). The variance shown by the coefficient of determination (marginal  $R^2$  and conditional  $R^2$ ) clearly indicates that a large part of the variation in segetal species richness and abundance between fields is explained by farm identity (random factor) rather than current farming practices (fixed factors). This important result is consistent with that recently observed by Rotchés-Ribalta et al. (2015a) in Spain. It indicates that factors other than those taken into account in our study explain the diversity of segetal species observed between fields. Determining these factors seems essential to better understand the flow of segetal seeds between fields on the one hand, and to better take into account the segetal seedbank in the soil and its temporal persistence on the other. This would allow a more comprehensive view of the diversity and the dynamics of the segetal species in a field. In mixed crop–livestock systems, measuring the seed flow of segetal species between fields requires assessing how effectively farmer-produced seeds are cleaned, the scale of seed exchanges between farmers, and the share of seeds input into a field by spreading manure or through epizoochorous dispersal by sheep (Dutoit et al., 2003; Fischer et al., 1996). All these practices contribute to maintaining high spatial dispersion of segetal seeds within a farm and between farms in the same area (Dutoit et al., 2003). Variation in segetal species richness and abundance is also related to the stock of the seedbank in the soil from past farming practices (Armengot et al., 2011b), as the number of individual arable plants at the soil surface represents only 1–10 % of the total number of arable plants in the soil (Albrecht and Pilgram, 1997). Due to the constraints imposed by the topography and the low soil fertility of highland farms, agricultural intensification in these systems is more recent (Fonderflick et al., 2010a; Mottet et al., 2006) than in lowland farming systems. It is therefore possible that in our case study there is a discrepancy between current farming practices and the observed segetal species, originating partly from a seedbank benefitting from old, more favourable, farming practices (Albrecht, 2005). It should be noted, however, that the survival of seeds in the soil is a few years for most segetal species (Dutoit et al., 2003; Saatkamp et al., 2011, 2009).

#### 4.4. Conservation issues

Most of the segetal taxa inventoried in our study area was found threatened in France (Aboucaya et al., 2000; Cambecèdes et al., 2012). Many of them, such as *Agrostemma githago*, *Neslia paniculata* and *Papaver argemone*, have almost disappeared from most other parts of France over the last decades (Fried et al., 2009; Pointereau et al., 2010) and have strongly declined in Catalonia (Chamorro et al., 2016). As a very illustrative example, the French survey *Biovigilance Flore*, a large-scale national weed survey, concluded that 78 % of the surveyed fields did not contain any segetal species (out of 3,323 fields surveyed between 2002 and 2007; Pointereau et al., 2010). The high frequency of threatened segetal species found in our study area confirms its status as a hotspot for segetal species. With an average of  $20.6 \pm 3.7$  segetal taxa per farm and  $11.3 \pm 4.2$  segetal taxa per field (per 40 m<sup>2</sup> sampled), only certain limestone areas in southern France, such as the Embrunais and the Luberon, have more segetal taxa, with respectively 14.7 and 16.7 species per field (Pointereau et al., 2010).

Our study confirms the importance of mixed crop–livestock systems in highlands with a limestone substrate for the conservation of segetal species. In these extensive farming systems, the production of cereals is destined for intrafarm consumption and yields are lower than in the plains. The fact the cereals are not sold makes it easier to tolerate higher proportions of arable plants and segetal species than in more intensive farming systems. If the local production specializes, as seen at a European scale (van Vliet et al., 2015v), the cereal crops on which segetal species depend may be abandoned and replaced exclusively by

forage crops, with the cereals required for feeding the sheep purchased elsewhere. The conservation of segetal species in extensive mixed crop–livestock systems therefore requires the maintenance of the production of self-consumed cereals on the farm.

Our results regarding the impact of herbicides on the diversity of segetal species suggest that their use should be prohibited in areas considered as hotspots for these plants. Even at low doses, herbicides affect the development and reproduction of both common and threatened segetal species (Rotchés-Ribalta et al., 2015b) and contribute to their decline. As a majority of farmers in these extensive systems already employ other techniques to limit the development of arable plants, avoiding herbicides does not appear to be a major technical hurdle.

## 5. Conclusion

In extensive mixed crop–livestock systems, field edges play an important role in the conservation of both threatened and common segetal species. We found that a higher proportion of variation in segetal species richness and abundance between fields was explained by farm identity than by farming practices in the growing season. This heterogeneity in segetal species diversity between fields of the same farm and between farms with similar farming practices is likely linked to the cumulative effects of past farming practices in a field and the history of seed exchange practices between farms within the same area. These temporal and spatial seed flows complicate the understanding of the interactions between farming practices and the composition and diversity of segetal species in extensive farming systems and deserve further study. Since land-use intensity is relatively recent in these extensive systems, its impact over time also needs to be monitored to measure its long-term effects.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2019.106778>.

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