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Major field margin vegetation types in France and their relationships with climate, agricultural landscapes and management intensity

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ABSTRACT

Arable field margins are an important semi-natural habitat providing multiple functions in agroecosystems. Despite three decades of research, analyses of species assemblage and functional traits are lacking. Leveraging a national monitoring network in metropolitan France, we aim to provide a comprehensive taxonomic and functional synthesis of field margin flora, outline main field margin types and explore their associations with management practices, climate, and agricultural landscapes. We analysed data from 532 field margins surveyed between 2013 and 2017, using both uni- and multivariate analyses. Field margins exhibited great diversity with 711 distinct taxa (12% of all flora in mainland France) at the national scale and an average of 16 species per 10 m^2 locally. While field margins contained few species of conservation value, they offered a refuge for many declining species as well as rare arable weed species. We identified seven main field margin types, each linked to distinct conditions of climate, soil, landscape and agricultural practices. Mediterranean field margins notably differed from all others. In the main cluster, vineyard margins also stood out as distinct from annual crop margins. Additionally, field margins in landscapes with a high proportion of grassland differed from those within intensively cultivated field crop plains in conventional agriculture. Overall, our study highlights the high botanical diversity of field margins and their interest for plant conservation in agricultural landscapes. Promoting the installation and/or maintenance of field margins through agri-environmental schemes should thus favour biodiversity conservation and associated ecosystem provision.

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1. Introduction

Semi-natural elements bordering crop fields, hereafter referred to as field margins, have become important in agroecology over the last 30 years (Greaves and Marshall 1987; Le Coeur et al. 1997; Marshall 2002; Mkenda et al. 2019), and are now a study area in themselves (i.e. field margin ecology). Field margins are studied by different disciplines for various purposes. Ecologists and conservation biologists consider field margins as a suitable habitat for a range of wildlife including birds (Vickery et al. 2009; Zollinger et al. 2013) and arthropods (Dennis and Fry 1992; Landis et al. 2000). Bordering crop fields, field margins have also caught the attention of weed scientists. Indeed, field margins may act as a potential source of weeds colonising fields (Cordeau et al. 2011, 2012; Cirujeda et al. 2019), but also as a refuge for rare weed species that are threatened within arable fields (Kleijn and Van Der Voort 1997; Fried et al. 2009). At larger spatial scale, landscape ecologists consider field margins as corridors, and their spatial arrangement in the landscape is used as a metric (i.e. configurational landscape heterogeneity) that can explain biological diversity patterns through improved connectivity between populations (Fahrig et al. 2011; Alignier et al. 2020).

Despite this abundant literature, field margins represent a complex habitat whose vegetation *per se* has not received a great deal of attention. Some studies have investigated the relative effects of agricultural practices and/or landscape factors on the diversity and composition of field margin vegetation (Tarmi et al. 2009; Aavik and Liira 2010; Chaudron et al. 2016; Fried et al. 2018; Boinot and Alignier 2023). Others aimed to manage field margins to optimise multiple ecosystem services at the field scale (Smith et al. 2008; Ramsden et al. 2015; Chaudron et al. 2020), such as by adjusting plant composition through the addition of nectar-producing plants to favour both endangered birds and auxiliary insects (Olson and Wäckers 2007). Ecotoxicological studies on the other hand have been carried out to mimic the effect of herbicide drift, and to understand how pesticides can impact field margin vegetation (Egan et al. 2014; Bohnenblust et al. 2016). Those examples show that

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beyond their diversity (often approximated by simple species richness), it is essential to describe and understand the nature and composition of the vegetation of field margins as a preliminary step to evaluate and even improve their functionalities. From a conservation perspective, this knowledge is essential for preserving rare or endangered species and avoiding field colonisation by invasive species. Before proposing to introduce new plant species to optimise field margin functions, it is important to identify and describe the baseline species pool of field margins, the major types of field margin communities occurring, and their associations with environmental and agricultural conditions.

Field margins are strips of vegetation immediately adjacent to a cultivated plot (Marshall 2002). As such, their botanical composition is a mixture of (i) arable weed species from the neighbouring crop, (ii) spontaneous species from the local environment, and (iii) sown species in the case of sown field margin strips. To assess the quality of field margins, Aavik and Liira (2009) proposed to distinguish indicator species groups, opposing common agrotolerant species (i.e. common arable weeds) and nature-value species. Nature-value species encompass hemerophobic species, which are sensitive to agricultural disturbances and, as a result, are predominantly found in natural and semi-natural habitats (e.g. *Filipendula vulgaris*, *Succisa pratensis*), as well as rare weeds that have significantly declined in abundance within fields due to intensive agricultural practices (e.g. *Glebionis segetum*, *Ranunculus arvensis*). Besides, using life history traits to understand what distinguishes agrotolerant and nature-value species, and more generally to distinguish broad types of field margin vegetation, can also help to position these plant species and communities more broadly within the well-known typologies used in functional ecology, such as acquisitive versus conservative strategies (Reich et al. 1992) or the Grime's CSR strategies (Grime 1977).

Here, we analysed the vegetation of a broad spectrum of field margins using the 500 ENI (for "Non-Intended Effects") network. This national network set up by the French Ministry of Agriculture aims to monitor the state of biodiversity in agroecosystems over the long term. In particular, it aims to measure the impact of agricultural practices (including pesticides) on species not targeted by treatments (Andrade et al. 2021).

We specifically ask i) how diverse is the flora field margin, taxonomically, chorologically and functionally, and does it include conservation issues (protected plant species)? and ii) whether it is possible to group plant communities of field margins into a few major types that differ in a consistent way according to regions (soil and climate), landscapes and broad agricultural practices? Our objectives are therefore to 1) describe the field margin vegetation of France, including diversity patterns, taxonomic affiliations, biological spectrum (i.e. percent representation of the number of species belonging to each life-form), species chorology (including native/alien status) and conservation value of species (i.e. red-listed and protected species); 2) deepen the approach opposing agrotolerant species and species with natural value (Aavik and Liira 2009) by analysing their functional differences; and 3) analyse large-scale geographical patterns in the composition of field margin vegetation and outline the main types of field margin communities and their relationships with climate, agricultural landscapes and management intensity.

2. Material & methods

2.1. Study sites and choice of crops

The 500 ENI survey covers the whole of metropolitan France (including Corsica) with 532 field margins sampled between 2013 and 2017 (Andrade et al. 2021; Figure S1). While the original goal was to sample 500 fields per year, the annual sample size is slightly below the target (2013, 487 fields; 2014, 476; 2015, 444; 2016, 478; 2017, 468) due to various constraints inherent to a network of this size (see Andrade et al. 2021). The network aims to be representative of the main climatic (Atlantic, continental and Mediterranean) and edaphic conditions, as well as the main cropping systems in the different regions of France. The largest part of the network follows the field margins of two reference annual crops: winter wheat (main crop sown in autumn in France) and maize (main crop sown in spring). Due to rotations, other crops are grown on the monitored sites, but the wheat and maize reference sites represent different cropping systems. A perennial crop (grape vine) was also included to take into account a variety of agricultural practices, that are different from those observed in annual crops (e.g. greater use of fungicides, generally smaller plot sizes and greater proportion of non-crop area in the surroundings). In a same way, part of the network covers market gardening crops, where more than one crop is grown during the growing season. The location of these four reference crops was proportional to their importance in each of the 22 administrative units of France in 2012. Therefore, 156 maize fields, 189 wheat fields, 100 vineyards and 57 lettuce fields were sampled in 2013, the first year of the ENI survey. We selected 80% of fields under conventional farming and 20% under organic farming in each region.

2.2. Vegetation survey protocol

The area surveyed in this study focused on the *field margin strip*, which is the area of herbaceous vegetation between the cultivated strip and the adjacent landscape element (Figure 1), the latter being either another cultivated field (Figure 1(b)), a road or a track (Figure 1(c)), another habitat (grassland, forest) or a field boundary (hedge, fence). Wild plant species were identified in 10 quadrats (each 1 m^2) located in the field margin strip. Quadrats were divided into two sets separated by 30 m, each consisting of five contiguous quadrats of $0.5\,m \times 2\,m$ (Figure 1(a)). Quadrats were placed in the centre of the field margin strip (i.e. equidistant from the field and the adjacent habitat). Their position should ideally be maintained in the same field margin strip throughout the study, but their precise location may differ slightly from year to year. Only the presence or absence of plant species was recorded for the 10 quadrats; each species present is thus characterised by a frequency of occurrence ranging between 1 and 10. In subsequent analysis, we used this frequency of occurrence as a proxy for the local abundance of species. Surveys were performed at the peak of the flowering season for the majority of species; April-May is advised for Mediterranean regions, mid-May to June in regions with oceanic to continental climates, and July-August for mountain areas above 1000 m.

2.3. Functional traits and other species features

In order to distinguish between common agrotolerant and nature-value species, and to characterise the main types of field margins, we used seven traits and five ecological indicators. Traits included those of the Leaf-Height-Seed (LHS) scheme of Westoby (1998). These three axes cover proxies of (i) relative growth rate with Specific Leaf Area (SLA) taken from the TRY trait database (Kattge et al. 2011); (ii) competition for light with maximum plant height taken from *Flora Gallica* (Tison and de Foucault 2014); and (iii) the trade-off between establishment success (high seed mass, low seed output) and the capacity to colonise growth opportunities at a distance (low seed mass, high seed output), with seed mass taken from the Seed Information database (Society for Ecological Restoration, International Network for Seed Based Restoration, Kew RBG 2023). We also used flowering onset and flowering duration (Tison and de Foucault 2014), pollination mode and dispersal syndromes (Julve 1998). Four modes of pollination have been distinguished: anemogamous species (pollinated by the wind), autogamous and apogamous species (whose reproduction does not depend on an external agent), obligatory entomogamous species and facultative

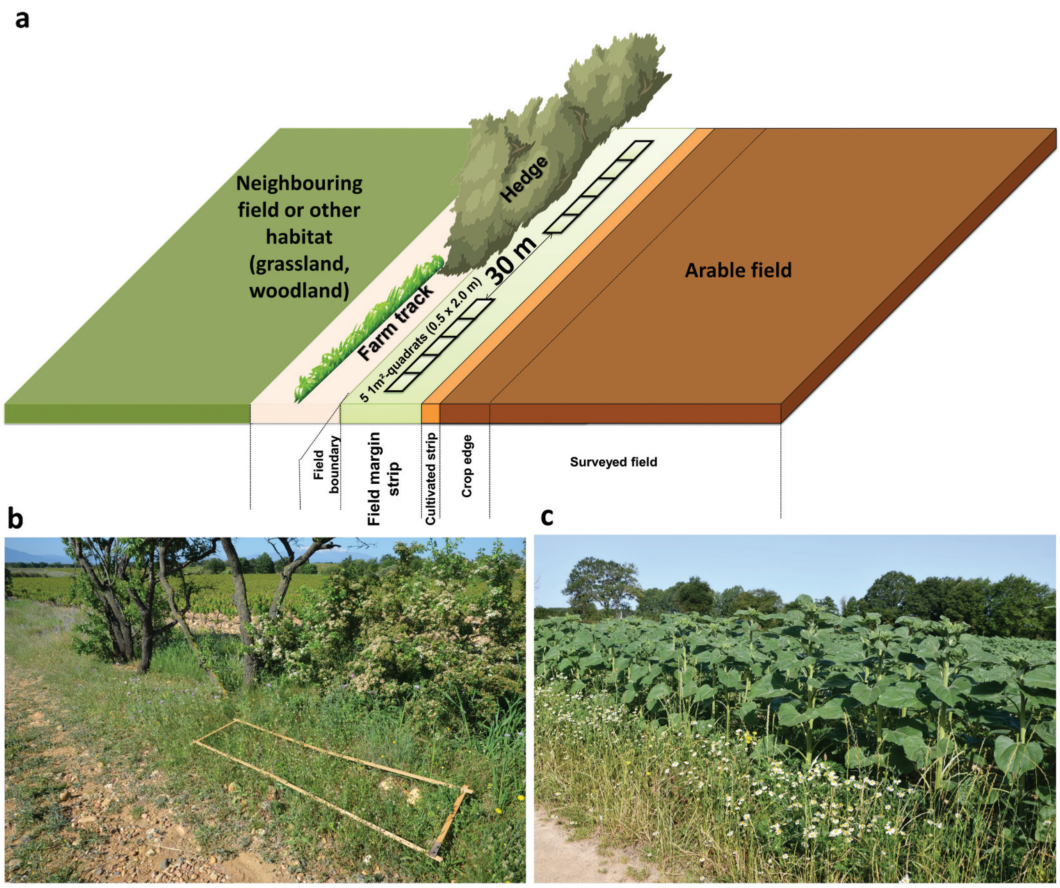

Figure 1. (a) Diagram representing the different elements of an agricultural field, in particular the elements in the external border of the plot, and the sampling protocol of the vegetation of the field margins in the 500 ENI network. (b) example of a sampled field margin (with a 2×0.5 m quadrat) located between a hedge and a tilled vineyard edge. (c) field margin of a sunflower crop next to a farm track.

entomogamous species (which can be pollinated by insects but also according to another mode). Dispersal syndromes distinguish species spread by wind, gravity or animals, the latter being divided into endozoochory and epizoochory (myrmecochory has been merged with the latter category). In addition to traits, we used Ellenberg Indicator Values for light (EIV-L), temperature (EIV-T), soil moisture (EIV-F), continentality (EIV-K), soil reaction (EIV-R) and soil nutrients (EIV-N) (Tichý et al. 2023) and Raunkiaer's life forms.

We also recorded for each species its native status (native versus alien) and its residence time distinguishing between archaeophytes (introduced before 1500) and neophytes (introduced after 1500) according to *Flora Gallica* (Tison and de Foucault 2014). We specified the chorology of the species (Atlantic, circumboreal, cosmopolitan, thermo-cosmopolitan, European, Eurasiatic, Holarctic, Mediterranean and subtropical) according to the baseflor database (Julve 1998), and their conservation status by taking into account species protected at the national level (INPN 2023), species evaluated on the Red List of the vascular flora of France (UICN France, FCBN, AFB, MNHN 2018) and species listed by the "*Plan national d'actions en faveur des plantes messicoles*", dedicated to the conservation of rare and threatened arable weeds (Cambecèdes et al. 2012). In addition to their IUCN (International Union for Conservation of Nature) status, we also used the population trend (decreasing, stable, increasing) of species evaluated on the Red List based on expert judgement.

2.4. Environmental data

In order to characterise the main types of field margin, we used climatic, landscape and agronomic data. Climate was summarised by four bioclimatic variables: mean annual temperature, minimum temperature, total annual precipitation, and precipitation of the driest quarter using the Worldclim dataset averaged for the years 1970–2000 at 2.5 min resolution (i.e. ~21 km^2 at the equator) (Fick and Hijmans 2017). For soil, we used soil pH and texture (percentages of sand, silt and clay) retrieved from the SoilGrids dataset at 250 m resolution (Hengl et al. 2017).

Landscape composition was described based on the proportion of land cover types within 250 m and 500 m radii buffer centred on the field margin. For that purpose, we used two landscape databases of land cover and land use in France: BD Topo (topographic database) and BD Parcellaire (administrative field database) from the IGN (National Institute for Geographical and forest information) as well as the "Registre Parcellaire Graphique" database which provides information on the identity of the crops cultivated (see Andrade et al. 2021 for further details). We used the percentage of crop, grassland and vineyard as well as the Shannon Diversity Index (SHDI) as metrics of landscape composition. We also used the High Natural Value (HNV) farmland indicator which is computed at the "municipality" scale (representing typically landscape of a few km^2) and relies on crop diversity, degree of intensification of farming practices in the 2010s (based on the level of pesticide use and the amount of fertilisation according to the French Agricultural Statistical Service), and the presence of landscape elements (proportion of semi-natural habitats, including hedges) considered beneficial to biodiversity (see Pointereau et al. (2010) for further details on the methodology). The higher the HNV indicator, the higher the expected level of biodiversity. Preliminary analyses showed that landscape metrics at 250 m and 500 m were highly correlated (Andrade et al. 2021). We thus selected metrics at the intermediate scale of 250 m.

Field margins were characterised by (i) the diversity of adjacent habitats by summing the number of distinct elements (by distinguishing copses and small woods, hedges, ditches, wetlands, natural grasslands, croplands and wastelands, and roads and tracks); (ii) sun exposure (full light versus semi-shaded); (iii) margin width (in meters); and (iv) margin management (number of management events per year regardless of the nature of the management). Mowing was the dominant management, followed by grazing ($n = 11$ margins) and herbicides ($n = 12$ margins). In these two cases, grazing and chemical weed control are not the only methods used, but are used in addition to management by mowing. The main features of field margins are summarized in Table S1. Farming practices in the neighbouring crop field were obtained based on interviews with the farmers and were summarised by the main crop type (wheat, maize, market garden, vineyard), the mode of production (organic versus conventional), the Treatment Frequency Index (TFI) of herbicides, and the dose of nitrogen fertilisation (averaged between 2013 and 2017). TFI is calculated as the cumulative ratio of the dose applied versus the recommended dose, for all treatments applied during the growing season (Halberg 1999). We also used geographical coordinates (longitude, latitude), altitude and the biogeographic French regions ($N = 11$) from the Végétal Local map (Office Français de la Biodiversité 2021). Pearson correlations between quantitative environmental variables are shown in Figure S2. Correlations between quantitative and qualitative environmental variables were visualized using a Hill & Smith multivariate analysis (Hill and Smith 1976; Figure S3) and correlations between community characteristics are shown in Figure S4.

2.5. Data analysis

Herein, we focused on the first five years of the 500ENI monitoring that covered 532 field margins between 2013 and 2017.

2.5.1. Species diversity

First, we computed gamma diversity (γ), the total species richness at the scale of the whole network in France during the first 5 years. Second, we calculated the mean species richness per field margin and per year (α-diversity). We then assessed possible inter-annual variability using a Kruskal-Wallis test followed by a Dunn test for post-hoc comparisons. We also provided α-diversity for the field margins of the four reference crop types (wheat, maize, market gardening crops and vineyards).

Next, in order to understand how diversity was organised within field margins and between years, we developed a diversity partitioning analysis. Diversity partitioning provides the structure with which diversity can be measured at different levels of nested organisation. We followed the diversity partitioning approach developed by Lande (1996). This model defines diversity β as the difference between total diversity (γ) and diversity within communities (α) according to the equation $\beta = \gamma - \alpha$. The analysis was computed for $n = 372$ field margins with comprehensive data between 2013 and 2017 (i.e. we excluded all field margins for which data for 1 or more year was lacking). We distinguished several levels of organisation: (1) 1 m^2 quadrat in field margin (α); (2) five quadrats of 1 m^2 in the same block (β_{Block}); (3) 10 quadrats of 1 m^2 regrouping the two blocks of five contiguous 1 m^2 quadrats in the same field margin ($\beta_{Field\ margin}$); (4) addition of species in the same field margin over the different years of the survey between 2013 and 2017 ($\beta_{Multiyear}$); (5) gamma diversity at the scale of the field margin over 5 years. Partitioning of diversity was thus calculated using the following equation $\gamma = \alpha + \beta_{Block} + \beta_{Field\ margin} + \beta_{Multiyear}$.

2.5.2. Taxonomic affiliations and life forms

To describe taxonomic affiliations of field margin flora, we compared the number of species belonging to different families with the proportion expected from the whole flora in France according to the baseflor database (Julve 1998). Using Chi-square tests, we determined whether certain families were over- or underrepresented in field margins. This corresponds to the difference between the *sensu lato* or unfiltered species pool (here the flora of France) and the *sensu stricto* species pool or filtered pool (i.e. the set of species found in field margins at the scale of France based on the specificities of the dataset). This approach makes it possible to measure filtering by habitat at this scale (Zobel and Scheiner 2016).

The biological spectrum represents the proportion of each life form that makes up the vegetation cover, a way to understand the physiognomy and structure of field margin vegetation, and to compare it with other nearby habitats (arable fields, grasslands). We computed the biological spectrum at the level of the whole 500 ENI network (i.e. the species pool level) and at the level of the field margin (i.e. the community level). At the species pool level, the biological spectrum is the percentage of species of each Raunkiaer's life form (phanerophytes, nanophanerophytes, chamaephytes, geophytes, hemicryptophytes, therophytes). At the community level, the biological spectrum is the mean relative abundance of each life form. In addition to Raunkiaer's life forms, we analysed the relative proportion and abundance of graminoids (regrouping Poaceae, Cyperaceae and Juncaceae) versus forbs (including all other Angiosperms). Ferns ($n = 5$ species) were not included in this analysis.

2.5.3. Agrotolerant species and their related trait value

To identify common agrotolerant species sensu Aavik and Liira (2009), we used the Biovigilance Flore survey (Fried et al. 2008, 2019) that monitored arable weeds in annual crops and vineyards in France between 2002 and 2012. To better understand this classification, we sought to identify trait values specific to common agrotolerant species. For this purpose, we compared trait values of common agrotolerant versus nature-value species with a Wilcoxon test for quantitative traits and Fisher's exact test for qualitative traits (see 2.3. for the list of traits).

2.5.4. Field margin vegetation classification

In order to identify the main types of field margin vegetation, we used the cumulative species composition of each field margin between 2013 and 2017. To reduce the influence of the number of years of sampling, we removed field margins that were only monitored once or twice, and focused on plots that were monitored at least 3 years ($n = 484$ plots). A species is considered present in a field margin when first observed during this period. We used the maximum abundance score (1–10) of a species between 2013 and 2017 as its abundance in the aggregated community. As we wanted our classification to take abundance into account, we computed a distance between samples (i.e. the aggregated communities) based on the Bray-Curtis dissimilarity index, a widely used index recognized as having good properties for reflecting ecological dissimilarities between samples (Ricotta and Podani 2017). We then performed a hierarchical ascending classification with Ward's algorithm, an average linkage method, most often used in ecology as it produces more compact clusters (particularly compared to simple linkage or complete linkage methods). Optimal classification yielded three groups. However, we chose a finer resolution tree with seven groups, representing the most balanced solution with both a sufficiently high number of groups allowing a detailed distinction of different groups of field margins, and a sufficient number of samples per group allowing statistical comparison.

In order to interpret the seven types of field margins, we identified agroecological variables (climate, soil, landscape, agricultural practices) and community characteristics (diversity index, community-weighted means [CWMs] of the main traits) associated with each type. For community characteristics, we computed community-weighted means of the traits mentioned above (SLA, plant height, seed mass, flowering onset, flowering duration, pollination mode, dispersal syndrome), and of the Ellenberg indicator values for light, soil moisture, continentality, soil reaction, temperature and nutrients, the relative abundance of agrotolerant versus nature-value species, and graminoid versus forbs. For qualitative traits (e.g. pollination mode), CWM corresponded to the percentage of each trait attributes. We also compared the mean species richness (S), Shannon's diversity (H'), Piélou's evenness (J) and the abundance of field margin communities for each type. In order to identify indicator species of each of the seven field margin types, and to evaluate the specificity of each field margin type, we applied the IndVal procedure (Dufrêne and Legendre 1997) which allows determination of species significantly more frequent and more abundant in a cluster than in others (i.e. indicator species). Finally, we calculated the gamma diversity per field margin type and the number of indicator species to reflect the originality of the field margin type.

To identify environmental variables and community characteristics significantly associated with a given field margin type we used the *catdes* function of the FactoMineR package (Husson et al. 2010). For each quantitative variable, this function compared mean values of a variable for each type of field margin with the overall mean of this variable for all field margins (v-test). The v-test can therefore be considered as a test of the hypothesis H_0 "the mean of the variable X for the field margin type q is equal to the overall mean (for all field margin types)", in other words "the variable X does not characterize the field margin type q". For qualitative variables, the *catdes* function assess the differences between field margin types based on Chi-square tests. All analyses were performed using R version 4.1.2 (R Core Team 2021).

3. Results

3.1. Species pool diversity and mean field margin species richness

Among the 532 field margins surveyed in 2013–2017 throughout metropolitan France, 711 distinct taxa were counted (21 only determined at the genus level) spanning 361 genera and 69 families (Table S2). With 16.1 species (standard deviation ± 7.7, min 1, max 61) observed on average per field margin, mean species richness remained very stable (maximum average observed in 2014 = 16.2 species, minimum average observed in 2016 = 16.0 species), with no significant change during the 5 years (Figure 2(a)). There was a difference in richness depending on the type of crop adjacent to the surveyed margin, with a higher species richness at the margins of vineyards (17.6 ± 8.8) and market gardens (17.3 ± 8.0), and a lower species richness at the margins of wheat (15.4 ± 7.3) and maize (15.8 ± 7.3) (Figure 2(b)).

3.2. Diversity partitioning

In the 372 field margins with comprehensive data between 2013 and 2017, a 1 m^2 quadrat contained on average 6.8 species (min 1, max 28). Addition of the four quadrats of the same block added an average of 5.6 species (+81%) leading to a richness of 12.4 species at the scale of the block of 5 m^2 quadrats (min 1, max 50). Addition of the second block of five quadrats of 5 m^2 located at 30 m only added an average of 3.9 supplementary species (+31%) leading to a richness of 16.3 species (min 1, max 61) at the scale of the entire field margin (10 quadrats, 10 m^2). The largest addition was linked to the monitoring of the same field margins over time with an average addition of 21.1 species (+129%) by adding 4 years of monitoring, which led to an average cumulative richness of 37.4 species per margin (min 10, max 106) after 5 years of monitoring (Figure 3).

3.3. Taxonomic affiliations

Based on the entire dataset (532 field margins sampled between 2013 and 2017), Figure 4 shows the 21 most frequent families (representing at least 1% of field margin flora with 7 taxa; all other families had less than 7 taxa). The three most represented families were Asteraceae (112 taxa, 15%), Poaceae (100 taxa, 14%) and Fabaceae (82 taxa, 11%). These were followed by Brassicaceae, Apiaceae, Caryophyllaceae, Lamiaceae, Plantaginaceae and Rosaceae. Most families were represented in field margins at a level expected by the number of taxa present in France, when accounting for all habitat types. However, there was an excess of Poaceae, Fabaceae, Plantaginacae, Polygonaceae, Rubiaceae, Geraniaceae and Malvaceae. By contrast, Rosaceae and Cyperaceae were under-represented in field margins (Figure 4).

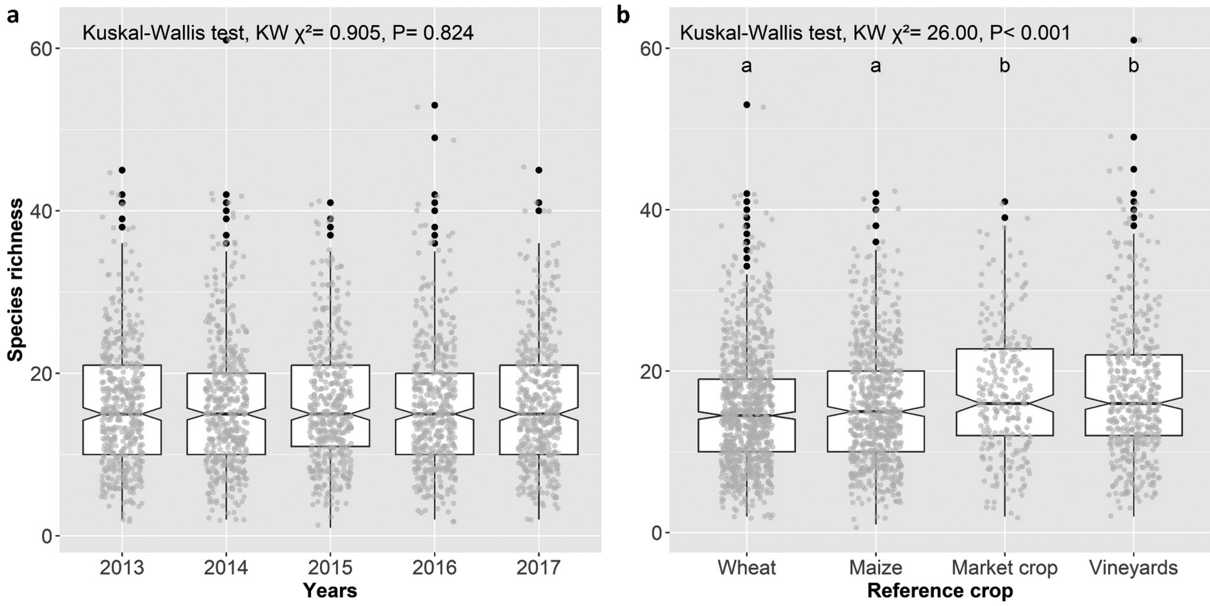

Figure 2. Boxplots representing the distribution of species richness in $n = 532$ field margins (dots in grey) (a) for the first 5 years (2013–2017) of the 500 ENI network and (b) for the four reference crops (different letters indicate significant differences based on a Kruskal-Wallis test followed by a Dunn test). Horizontal lines represent the median, boxes correspond to 50% of the value around the median, and vertical lines represent the 25% lowest and highest values. Black dots represents outlier values.

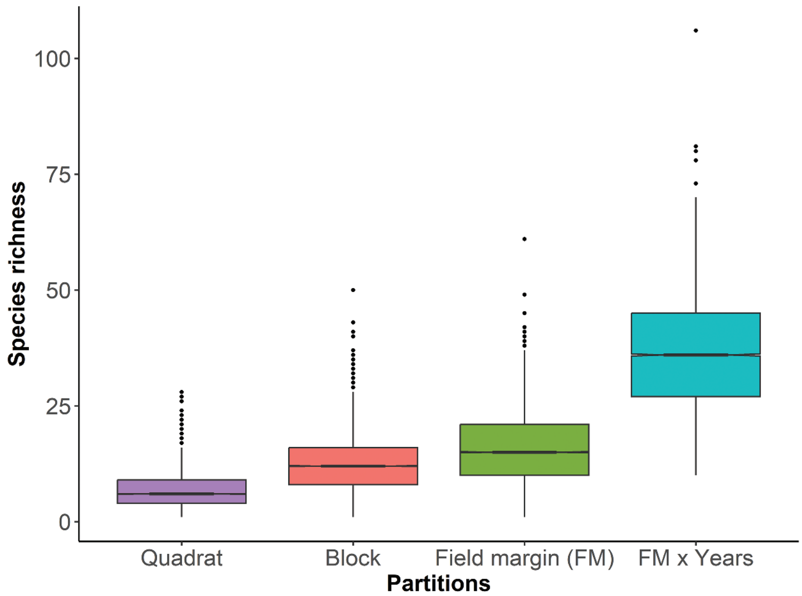

Figure 3. Species richness partition between the four spatiotemporal levels of organisation of field margins. Quadrat = 1 m^2 quadrat; block = block of 5 1 m^2 quadrats (5 m^2); field margin = the entire field margin (10 1 m^2 quadrats = 10 m^2); FM x years = entire field margin surveyed during 5 years.

The 10 most important genera (with the highest number of species) were, by decreasing order of importance, *Trifolium* (18 species), *Lathyrus* (13), *Vicia* (11), *Medicago* (11), *Euphorbia* (10), *Veronica* (10), *Crepis* (9), *Galium* (9) and *Rumex* (8).

3.4. Species chorology, native and conservation status

The 690 taxa (identified at least at the species level) that represented the species pool of field margins in France (based on $n = 532$ field margins) included 87.4% native species and 12.6% non-native species, the latter including 4% archaeophytes (species introduced before 1500) and 8% neophytes (introduced after 1500). This figures could be related to the proportion observed in metropolitan France (for all vegetation type) with 85% native species, 13% neophytes and 2% archaeophytes. Although the 500 ENI network only contained 58 field margins under Mediterranean climate (11% of the network), species with a Mediterranean distribution ($n = 177$) contributed

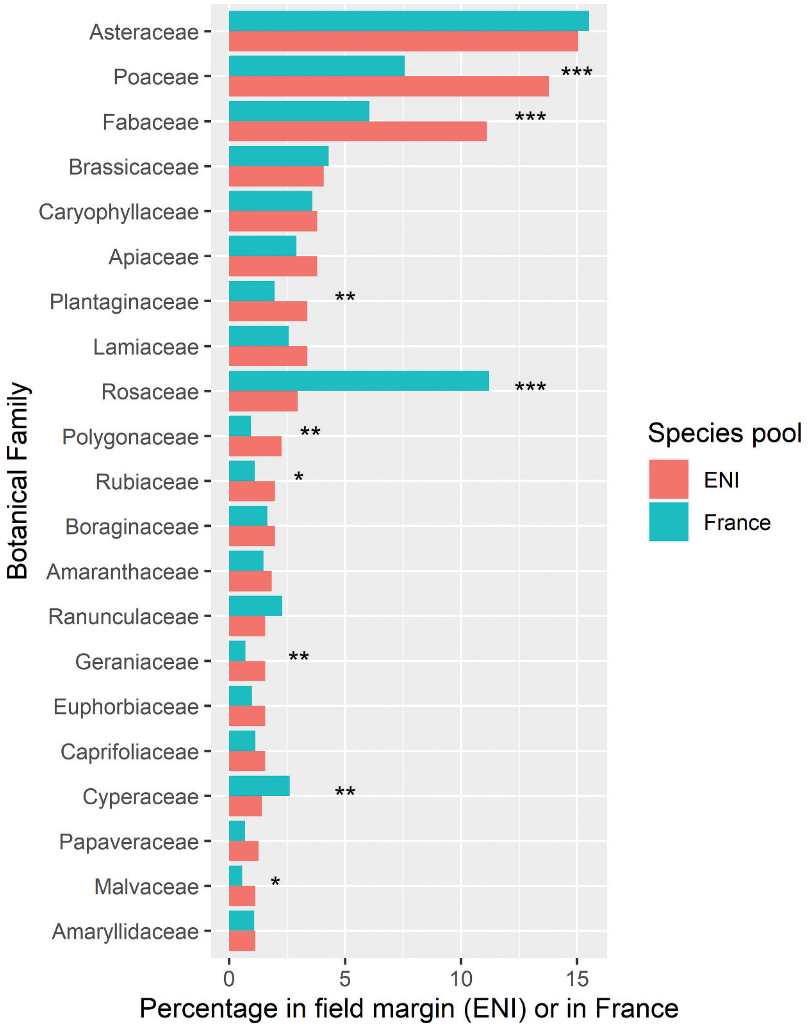

Figure 4. Barplot representing the percentage of species belonging to different botanical families in the species pool of field margins (red) or in the whole France species pool with all habitats included (green). Asterisks indicate significant differences based on Chi-square tests (* < 0.05, ** < 0.01, *** < 0.001).

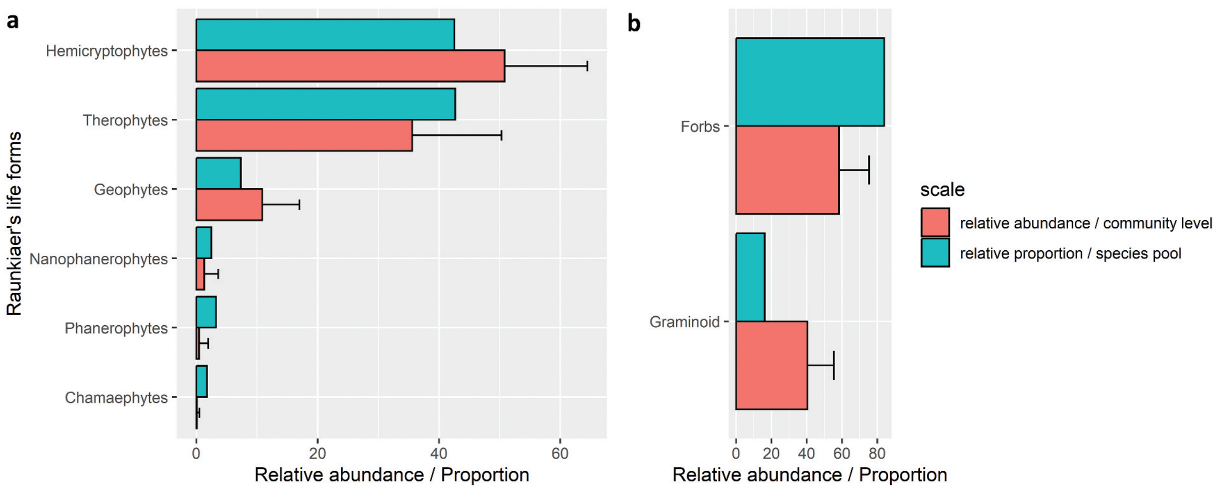

Figure 5. Biological spectrum of field margin flora. (a) mean relative abundance of Raunkiaer's life forms at the community level (red barplots) and the proportion of species of different Raunkiaer's life forms at the species pool level (green barplots). (b) mean relative abundance of forbs and graminoids at the community level (red barplots) and the proportion of species of forbs and graminoids at the species pool level (green barplots).

26% of the species pool (Table 1). Logically, the largest contribution (43%) corresponds to species with a temperate European (19%) and Eurasiatic (24%) distribution. Section 3.7 details the distribution of these chorological types in the different types of field margins.

At the local scale of a field margin, native species represented an average of 93% of the relative abundance, archaeophytes represented 4.7%, and neophytes only represented 2.3%. The most frequent neophytes were *Veronica persica* (46% of the field margin) followed by *Erigeron canadensis* (12%). Among non-native species, only 22 were classified as invasive species and they were relatively rare in field margins. The most common and abundant invasive species included *Ambrosia artemisiifolia* (frequency 5%, mean abundance 3.6), *Erigeron sumatrensis* (4%, mean abundance 3.3), *Xanthium orientale* subsp. *italicum* (2%, mean abundance 4.4), *Senecio inaequidens* (1%, mean abundance 1.6) and *Oxalis pes-caprae* (1%, mean abundance 7.5).

Among the species with conservation value, there was only one protected species at the national scale (*Kickxia commutata*) which occurred in two field margins in Corsica, and one species is considered "near threatened" on the IUCN Red list (*Ornithopus sativus*, occurring in the Landes). All other species assessed on the Red List ($n = 613$) are considered to be in the "Least Concern" category, but among these the trends were divided into species with stable ($n = 393$), decreasing ($n = 72$) and increasing ($n = 11$) population trends (the trend for $n = 137$ species is unknown). Finally, 25 species listed in the national action plan for the conservation of *messicoles* (i.e. that list a total of 102 threatened rare arable weeds) are present in field margins (Table S2). Noteworthy species include *Agrostemma githago* (frequency 1%, mean abundance 4.8), *Anthemis cotula* (5.1%, mean abundance 3), *Bromus secalinus* (2%, mean abundance 3), *Buglossoides arvensis* (1 field margin), *Cyanus segetum* (5%, mean abundance 3.8), *Euphorbia falcata* (1 field margin), *Glebionis segetum* (1 field margin) *Legousia speculum-veneris* (1%, mean abundance 4.7), *Orlaya grandiflora* (2 field margins), *Phalaris paradoxa* (2 field margins), *Ranunculus arvensis* (1%, mean abundance 4.4), *Spergula arvensis* (1%, mean abundance 3.3), *Thlaspi arvense* (1%, mean abundance 2.7) and *Valerianella dentata* (1 field margin).

Table 1. Chorology of the 693 species identified at the species level (or at the genus level when possible to determine the native status) in 532 field margins in France.

Chorology		Number of species	%
	Atlantic	8	1.2
	Circumboreal	23	3.3
	Cosmopolitan	56	8.1
	Thermo-cosmopolitan	7	1.0
	Eurasiatic	165	23.8
	European	134	19.3
	Holarctic	33	4.8
	Mediterranean	177	25.5
	Subtropical	3	0.4
Native		606	**87.4**
	Archaeophyte	29	4.2
	Neophyte	56	8.1
	Unknown	2	0.3
Non-native		87	**12.6**

3.5. Life-form spectra

At the level of the field margin species pool, hemicryptophytes and therophytes dominated, each representing 43% of species. The remaining 14% was shared between geophytes (7%), phanerophytes (3%), nanophanerophytes (2%) and chamaephytes (2%; Figure 5(a)). At the field margin community scale, hemicryptophytes had the highest relative abundance (51%) followed by therophytes (36%) and geophytes (11%). Woody species, including nanophanerophytes (1.4%), phanerophytes (0.5%) and chamephytes (0.1%) accounted for only 2% of relative abundance because, as mentioned above, the selected field margins are all predominantly herbaceous and non-woody (scrub, hedge, etc.). While graminoids represent < 20% of the species pool, at the local scale their abundance reaches 40% (Figure 5(b)).

3.6. Functional traits and indicator species for agricultural disturbances

Forty-seven species were defined as common agrotolerant based on a frequency of occurrence > 10% in agricultural fields in France (Table S2). These common agrotolerant species differed from others (defined as nature-value species) by higher SLA values, earlier flowering onset, a longer period of flowering at the species level, and a higher Ellenberg indicator value for nitrogen (Table 2). Raunkiaer's life forms also distinguished agrotolerant and nature-value species, with agrotolerant mostly annual species (83% versus 40% annuals for nature-value species), while nature-value comprised a wider range of life forms (Table 2) including hemicryptophytes (44%) and geophytes (8%). From a reproduction perspective, agrotolerant species were more autogamous (19% versus 5%) while nature-value species tended to be pollinated by insects (Table 2). Agrotolerant species have no specific means of dispersal (gravity) while nature-value have various means of dispersal including animal dispersal (Table 2).

3.7. Typology of field margins in France

The most balanced classification of sites ($n = 484$ field margins) based on Bray-Curtis dissimilarity index discriminated seven groups (Figure 6). A first division

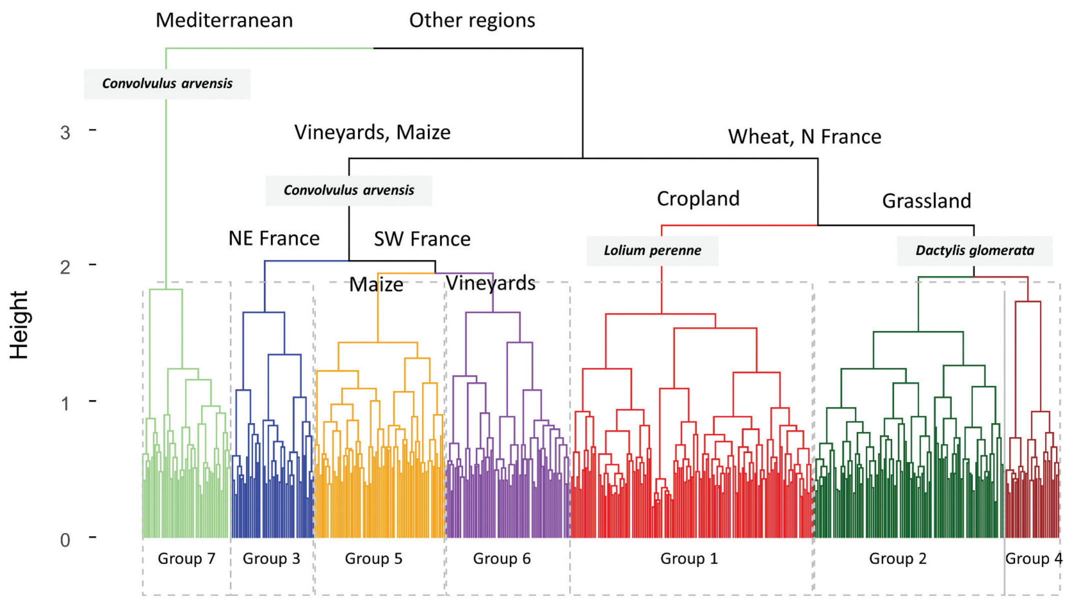

Figure 6. Hierarchical clustering of field margins ($n = 484$) based on dissimilarity (Bray-Curtis index). The main characteristics (region, crop types) of branches are given on the graph. Dominant field margin species are indicated on a grey background.

Table 2. Differences in trait values and Ellenberg indicator values between common agrotolerant species and nature-value species. For quantitative traits, median values are given for each group with minimum and maximum values between brackets; for qualitative traits the proportion is displayed. SLA: specific Leaf area, EIV-L: Ellenberg indicator value for light, EIV-N: Ellenberg indicator value for nitrogen.

Traits	Agrotolerant species ($n = 47$)	Nature-value species ($n = 607$)	
Quantitative traits			**Wilcoxon test**
SLA	26.4 (17.2–48.5)	23.7 (4.7–7.7)	***P* = 0.001**
Maximum plant height (m)	.8 (.2–5)	.8 (.1–30)	*P* = 0.603
Seed mass (mg)	1.19 (.05–28.2)	1.12 (.0007–11.5 × 103)	*P* = 0.709
Flowering onset (month)	4 (1–7)	5 (1–12)	***P* = 0.013**
Flowering duration (month)	5 (2–12)	4 (1–12)	***P* <0.001**
EIV-L	7 (5–8)	7 (3–9)	*P = 0.127*
EIV-N	7 (5–9)	6 (1–9)	***P* <0.001**
Qualitative traits			**Fisher's test**
Life forms			*P <0.001*
Therophytes	83%	40%	
Geophytes	2%	8%	
Hemicryptophytes	15%	44%	
Woody perennials	0%	8%	
Pollination mode			*P* = 0.003
Autogamous, apogamous	19%	5%	
Abiotic (wind, water)	17%	24%	
Facultative entomogamous	34%	27%	
Strictly entomogamous	30%	44%	
Dispersal syndrome			*P* = 0.003
Abiotic (wind, water)	24%	30%	
Gravity	53%	29%	
Animals	23%	41%	

separated field margins of the Mediterranean region (group 7) and all other field margin types (groups 1 to 6). In this latter cluster, a second division differentiated margins of wheat in northern France (groups 1, 2 and 4) and margins of vineyards or maize, mainly in the south-west but also in north-east France (groups 3, 5 and 6). Subsequently, groups were named according to the two most frequent indicator species based on the IndVal procedure.

Field margins of Group 1 ($n = 128$), namely *Lolium perenne-Poa annua*, were associated with intensive agriculture (i.e. highest herbicide TFI and dose of N fertilisation in neighbouring fields), in open-field landscapes (Table 3). Group 1 was concentrated in northeastern France and in the Paris Basin (North and South), an area with a continental climate (low temperature and low rainfall; Figure 7). It is associated with high soil pH and silt percentage, low landscape diversity, a high percentage (74%) of crop in the landscape (with wheat as the main rotation head) and low HNV (Table 3). *Lolium perenne-Poa annua* field margins were characterised by a high share of agrotolerant species (47%) with characteristics of ruderal species including annuals, short stature, high SLA, early flowering, autogamous reproduction and high nutrient requirement (Table 4). This group was also characterised by a higher-than-average abundance of graminoids (45%) and a deficit of both obligate entomogamous species and animal-dispersed species. All 12 indicator species are common arable weed species, namely *Lolium perenne*, *Poa annua*, *Matricaria chamomilla*, *Fallopia convolvulus*, *Alopecurus myosuroides*, *Polygonum aviculare*, *Papaver rhoeas*, *Plantago major*, *Sonchus asper*,

Table 3. Mean values of spatial, climatic, soil, landscape and agricultural variables for the seven field margin types.

		Overall mean	Group1	Group2	Group3	Group4	Group5	Group6	Group7
Group	N	488	128	101	44	29	69	66	47
Spatial	Altitude	155	149	168	186	183	165	153	86***
	Latitude	46.77	48.19***	47.82***	47.06	48.14**	46.29	44.55***	43.42***
	Longitude	2.52	2.60	1.59***	3.69**	2.05	2.66	0.75***	5.65***
Climate	Mean Annual Temp	11.3	10.5***	10.7***	10.9*	10.5**	11.4	12.2***	14.1***
	Min Temperature	0.37	-0.16***	0.34	-0.41**	0.15	0.10	0.84*	2.50***
	Annual precipitation	752	714***	747	750	816**	777*	825***	692***
	Summer precipitation	152	150.2	149.9	152.7	172.8***	159.9*	174.6***	101.9***
Soil	soil pH	6.88	7.08***	6.70***	6.80	6.51***	6.81	6.68***	7.38***
	% sand	30.8	24.1***	30.1	31.5	36.5***	33.8**	34.8***	35.5***
	% silt	44.0	50.0***	46.0**	42.8	41.0*	41.6**	39.6***	37.4***
	% clay	25.2	25.9*	23.9***	25.8	22.5***	25.0	25.6	27.2***
Landscape	High Nature Value	8.39	7.74*	8.56	7.84	11.23***	8.24	8.78	8.17
	Wood (%)	6.40	2.98***	6.81	6.12	4.92	8.85*	7.70	10.19*
	Crop (%)	53.21	74.42***	59.43*	43.59	49.61	53.14	43.95*	8.85***
	Grassland (%)	7.35	4.77*	11.26**	5.38	21.48***	5.91	6.80	1.63**
	Vineyard (%)	12.72	1.98***	1.76***	28.85***	0.00**	12.44	24.80***	40.97***
	SHDI	0.87	0.65***	0.92	0.80	1.07*	0.92	0.94	1.15***
Field margin	Div Adjacent Habitat	1.78	1.88	1.84	2.14*	1.83	2.04*	1.53*	0.96***
	Full light (%)	92	94	92	98	72**	90	91	96
	Semi shaded (%)	8	6	8	2	28**	10	9	4
	Margin width	3.67	4.24	3.92	3.35	2.28	3.10	4.00	3.10
	# Margin management	1.24	1.18	1.27	1.50*	0.84**	1.11	1.35	1.47*
Farming practices	TFI Herbicide	1.37	1.84***	1.43	1.45	1.16	1.22	1.08*	0.62***
	N Fertilisation	208	385**	251	166	95	146	65	33
	Organic (%)	23	17	21	18	28	28	29	28
	Conventionnal (%)	77	83	79	82	72	72	71	72
Reference crop (%)	Wheat (%)	39	58***	50**	25*	72***	26	18***	0***
	Maize(%)	30	28	35	32	21	41*	36	6***
	Market garden (%)	11	12	13	2*	7	12	3*	23**
	Vineyard (%)	20	2***	2***	41**	0	22	42***	70***
Region (%)	Alps	1	0	0	2	0	0	3	0
	North Paris Basin	14	30***	18	0*	41***	3	0***	0***
	South Paris Basin	15	30***	7***	9	0**	23*	8	0***
	B Rhône-Saône-Jura	7	7	9	20**	3	9	2*	0*
	Corsica	2	0*	0	0	0	0	0	23***
	Armorican Massif	11	1***	35***	14	7	3	11	0**
	Central Massif	5	2	8	5	24***	3	3	0
	Mediterranean area	9	0***	0***	2	0	13	0**	74***
	Northeast Zone	16	23*	20	34**	3*	17	0***	2**
	South West Zone	20	7***	4***	14	21	29*	74***	0***

Values followed by an asterisk are significantly different from the overall mean of all field margins (n = 484) according to a v-test for quantitative variables and a Chi2 test for qualitative variables (* < 0.05, ** < 0.01, *** < 0.001).

Chenopodium album, Capsella bursa-pastoris and *Ambrosia artemisiifolia*. This group also had a high number of non-native species (14, including both archaeophytes and neophytes) that amount up to 9.5% of relative abundance in the field margins.

Group 2 ($n = 101$), named *Poa pratensis-Taraxacum officinale*, was found throughout France (except in Mediterranean areas), especially the Armorican Massif (Figure 7). It was associated with mixed landscapes harbouring both cropland (59%) and grassland (11%), in an area with slightly acidic and silty soils (Table 3). This field margin type had an average proportion of agrotolerant and nature-value species, and graminoids (43%) were over-represented in this group. Trait values were somewhat intermediate compared with other groups, with a tendency toward competitive-ruderal strategies (relatively high stature and SLA, and high nutrient requirements), pollinated by wind or insects, and dispersed by animals (Table 4). Species of this group had low temperature requirements and they were hygrophilous, acidiphilous and shade-tolerant. The most frequent

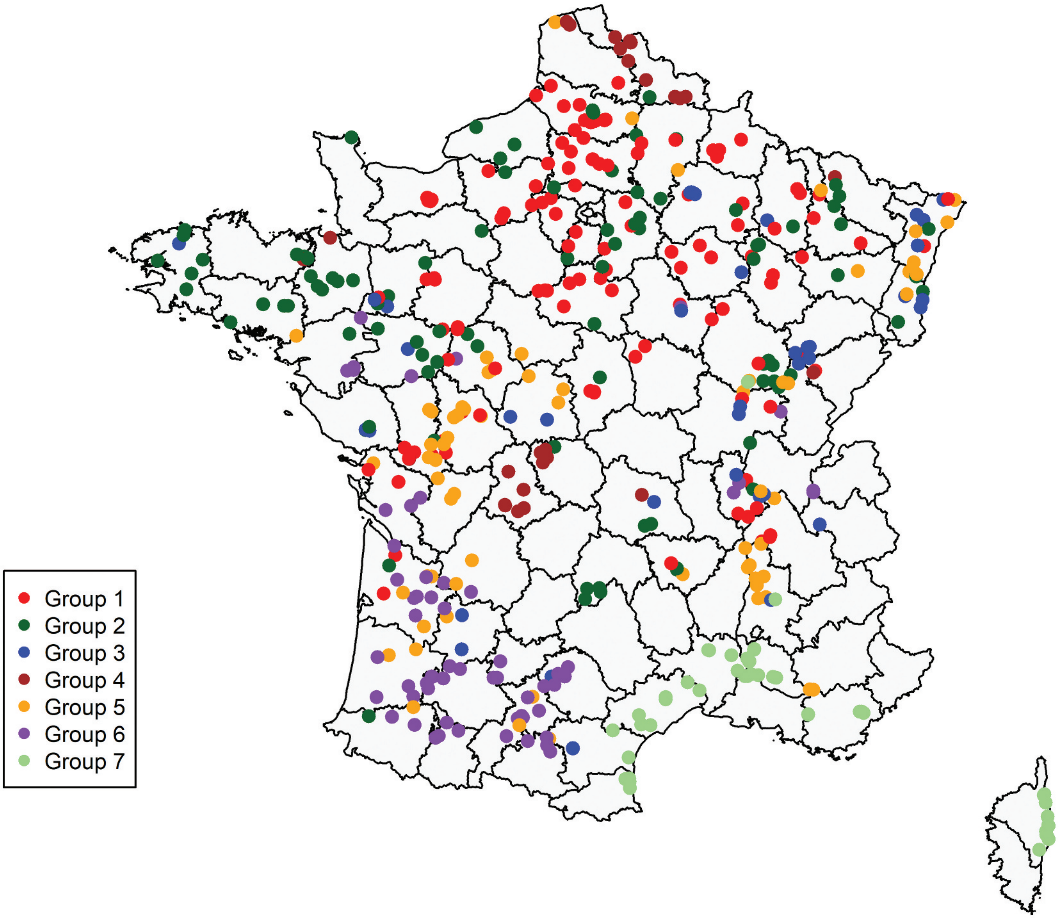

Figure 7. Distribution of the seven field margin types in France.

species of this group were *Dactylis glomerata*, *Lolium perenne* and *Trifolium repens*, and it included five indicator species (*Taraxacum officinale*, *Poa pratensis*, *Rumex crispus*, *Holcus lanatus* and *Schedonorus pratensis*). Species with the highest IndVal values in this group mostly had a European chorology (Table S3).

Group 4 (*Dactylis glomerata-Galium aparine*) was a small group ($n = 29$) typical of the Central Massif (Limousin) and the North Paris Basin in areas with low mean annual temperature, high levels of precipitation, and acidic and sandy soils. This group was associated with diverse landscapes with a high proportion of grassland (21%) and high HNV scores. It was the field margin type with the highest proportion of semi-shaded field margins (28%). This was consistent with a high share of shrubs (hedges) and low Ellenberg-L values. The presence of hedges also implies a lower level of field margin management. There was a high proportion of nature-value species (71%) as well as competitive species with high stature, high SLA and late flowering. Many species were wind-pollinated but rely on animals for dispersal. Species of the group 4 were hygrophilous, acidiphilous, nitrophilous and shade-tolerant. The most frequent species included *Dactylis glomerata*, *Galium aparine* subsp. *aparine*, *Arrhenatherum elatius* subsp. *elatius*, *Anisantha sterilis* and *Poa trivialis*. Common indicator species included *Convolvulus sepium*, *Ranunculus repens*, *Urtica dioica*, *Heracleum sphondylium* and *Lapsana communis*. Regarding chorology, there was a high share of species with a cosmopolitan, Eurasiatic and Holarctic distribution.

The second main cluster is related to field margins of vineyards or maize with *Convolvulus arvensis* as the most frequent species (Figure 6) and typically a higher dominance of forbs (accounting for around two third of relative abundance; Table 4).

Group 3 (*Convolvulus arvensis-Plantago lanceolata*) was found in vineyard margins and landscapes dominated by vineyards (29%) in northeastern France and the Rhône-Saône-Jura basin ($n = 44$; Table 3). In this margin type, the diversity of adjacent habitats was high but the number of management events was also high (Table 3). These margins had the lowest species diversity and low originality with only one indicator species (*Convolvulus arvensis*), and most traits were average in value, but there was a high share of geophytes (14%) and hemicryptophytes (60%). Apart from *C. arvensis*, most frequent species in this group included *Lolium perenne*, *Taraxacum officinale*, *Plantago lanceolata*, *Trifolium repens*, *Potentilla reptans* and *Elytrigia repens*.

Group 5 (*Elytrigia repens-Daucus carota*) represented field margins of maize mainly in southwestern France and in the south of the Paris Basin (and to

Table 4. Mean values of community diversity indices, number of indicator species, community-weighted means of traits and Ellenberg-indicator values for the seven field margin types.

		Overall mean	Group1	Group2	Group3	Group4	Group5	Group6	Group7
	N	488	128	101	44	29	69	66	47
Diversity	Species richness (S)	35.5	33.7	31.2***	22.5***	35.6	41.1***	40.7***	46.0***
	Shannon Diversity (H')	3.14	3.13	3.04***	2.78***	3.12	3.27***	3.26***	3.37***
	Evenness (J)	0.90	0.90	0.90*	0.91*	0.88**	0.89	0.90	0.89
	Abundance	197	189	181**	129***	187	220**	227**	253**
	Gamma diversity	695	256	240	154	180	354	315	361
	# indicator species	-	12	5	1	40	30	53	127
CWM	Agrotolerant	37.4	46.9***	37.1	36.7	29.2*	33.9***	26.2***	38.5
	Nature-value	61.7	53.1***	62.9	63.3	70.8***	66.1***	73.8***	61.5
	Graminoid	40.1	45.1***	43.0*	39.6	36.1	35.9**	38.6	31.6***
	Forbs	58.9	55.8**	55.5**	57.0	57.4	64.4**	61.4	65.7***
Life forms	Therophytes	35.6	42.3***	28.8***	23.0**	32.1	34.0	28.6***	57.8***
	Hemicryptophytes	50.8	45.9***	56.8***	59.8***	49.1	45.9	60.9***	32.1***
	Geophytes	10.8	10.8	11.6	13.9	15.5***	11.0	8.0***	7.2***
	Chamephytes	0.08	0.01*	0.02	0.00	0.11	0.20**	0.07	0.31***
	Nanophanerophytes	1.30	0.36***	0.97	2.18**	2.71***	2.85***	1.13	0.84
	Phanerophytes	0.44	0.22	0.42	0.12	0.45	1.18***	0.24	0.63
Traits	SLA	26.2	26.5***	26.4	26.0	27.0***	25.5***	25.8**	25.9
	Max Plant Height	1.14	1.07*	1.14	0.99*	1.46***	1.39***	1.03*	1.06
	Seed mass	5.76	4.29	3.83	3.83	5.36	11.28**	7.12	5.94
	Flowering onset	4.70	4.63**	4.66	4.68	4.88***	4.90***	4.72	4.56***
	Flowering duration	5.20	5.51***	5.31*	5.43**	4.65***	4.92***	5.02**	4.94***
	Anemogamous	43.0	46.0**	47.3***	42.6	49.7**	38.1***	41.2	31.1***
	Auto- & apogamous	6.7	8.4***	6.6	7.9	4.8*	5.1**	5.1	7.4
	Facult entomogamous	26.7	28.4**	22.4**	24.6	22.6**	29.6**	26.0	32.5***
	Oblig entomogamous	22.7	16.8***	22.3	24.0	22.8	25.9**	26.7***	27.9***
	Wind	16.2	15.6	17.3	12.8***	15.0	17.6	13.8	22.4***
	Gravity	46.2	50.9***	43.4**	55.2***	35.3***	42.6**	47.7	40.5***
	Endozoochore	1.9	0.7***	1.5	2.2	4.5***	4.0***	1.3	1.4
	Epizoochore	34.7	32.4**	36.4*	28.7***	45.1***	34.4	36.2	34.6
Ellenberg indicator values	EIV-L	7.04	7.01	6.96***	7.04	6.73***	7.03	7.10*	7.42***
	EIV-F	5.01	5.02	5.15***	5.06	5.20**	4.92**	5.14***	4.51***
	EIV-K	4.79	4.90***	4.86***	4.85*	4.77	4.76	4.73**	4.40***
	EIV-R	5.72	5.62***	5.53***	5.60*	5.55**	5.80*	5.77	6.37***
	EIV-T	5.30	5.17***	5.15***	5.20*	5.20	5.32	5.36	6.05***
	EIV-N	6.36	6.56***	6.45**	6.33	6.63***	6.22***	6.00***	6.20**

Values followed by an asterisk are significantly different from the overall mean of all field margins ($n = 484$) according to a v-test for quantitative variables and a Chi2 test for qualitative variables (* < 0.05, ** < 0.01, *** < 0.001).

a lesser extent the Mediterranean area and northeastern France; $n = 69$; Figure 7). It was characterised by sufficiently high rainfall over the year and in summer (160 mm), sandy soils and an average proportion of crop, grasslands and vineyards, but a higher-than-average proportion of wood and a high number of habitats next to margins (Table 3). Vegetation was species-rich (second richest after Mediterranean margins) and dominated by forbs (66%) and nature-value species (64%), mostly hemicryptophytes but with a high proportion of woody species (4% shrubs and trees). Species had low water and nutrient requirements, low SLA values, and were pollinated by insects and dispersed by animals (endozoochory). The most frequent indicator species included *Elytrigia repens*, *Daucus carota*, *Rubus* spp., *Picris hieracioides*, *Avena fatua/sterilis*, *Silene latifolia* and *Hypericum perforatum*. Species chorology was mostly European and Eurasiatic with some Mediterranean species (Table S3).

Group 6 (*Potentilla reptans-Trifolium repens*) was strongly associated with South-West France combining high annual rainfall (Atlantic influences) and high mean annual temperature on sandy acidic soil ($n = 66$). It encompasses mostly vineyard margins (42%) and to a lesser extent maize margins (36%), with few herbicide treatments in adjacent fields and located in vineyard (25%) and cropland dominated (44%) landscapes. Margins were species-rich (40.7 species on average) with a high number of indicator species (53). Most were hemicryptophytes and nature-value species with low stature, low SLA, late flowering onset and a high proportion of insect-pollinated species (Table 4). Many were heliophilous and water-demanding but had low nutrient requirements. The most frequent species included *Convolvulus arvensis*, *Potentilla reptans*, *Lolium perenne*, *Trifolium repens*, *Plantago lanceolata* and *Dactylis glomerata*. The most frequent indicator species were *Geranium dissectum*, *Vicia sativa*, *Schedonorus arundinaceus*, *Trifolium pratense*, *Agrostis stolonifera* and *Lotus corniculatus*. Species chorology was similar to that of group 5 (European and Eurasiatic with some Mediterranean influences).

Group 7 (*Avena barbata-Hordeum murinum*, *n* = 47) represented Mediterranean field margins characterised by high temperature, low rainfall (especially in summer) and low altitude (Figure 7, Table 3). Margins of group 7 were located next to vineyards and market garden crops using few herbicide and N fertilisation (Table 3), in diverse landscapes with mostly vineyards (41%) and woods (10%). Group 7 was the most species-rich (average of 46 species per margin) and the most original, based on a high number of indicator species (127). It was characterised by the predominance of annuals (58%) and also a significantly higher relative abundance of chamaephytes than other margins. Many species were insect-pollinated and wind-dispersed. Vegetation of this field margin type included heliophilous, xerophilous, thermophilous, basiphilous and others typical of nutrient-poor soils (Table 4). The most frequent species were *Convolvulus arvensis*, *Avena barbata*, *Hordeum murinum*, *Plantago lanceolata* and *Cynodon dactylon*. Species with the highest indicator scores included *Crepis sancta*, *Malva sylvestris*, *Anisantha madritensis*, *Lolium rigidum*, *Medicago minima* and *Medicago polymorpha*. The majority of species in this group had a Mediterranean chorology (Table S3).

Discussion

This work constitutes the first synthesis of field margin vegetation, an overlooked habitat from a botanical perspective, although it is widely studied as an ecological model to understand the interplay of farming practices and landscape on biodiversity. The flora of field margins is highly diverse; compared with monitoring carried out at the same spatial extent (France) in cultivated fields, the species pool in field margins is more than twice as important (*n* = 711 taxa) as the pool of arable weed species found within fields, with *n* = 332 taxa (Munoz et al. 2020). This represents ~ 12% of the flora of France. As in arable fields, the Mediterranean region appears to be the most species-rich area, and also has the highest share of species with conservation value. This is probably also linked to the richer pool of Mediterranean species, in a region that is considered one of the world's biodiversity hotspots (Blondel and Aronson 1999).

Based on the flora of cultivated fields reported by Jauzein (1995) which lists 1402 taxa, 383 species observed in the field margins of the 500 ENI network (55%) can also be observed in cultivated fields. This shows that almost half (45%) are species that occur only in field margins (and other open herbaceous habitats such as grasslands), making this area a very valuable habitat that brings originality to agricultural landscapes, especially when dominated by cropland. This ratio of 45% field margin-specific species is in agreement with previous studies (Aavik and Liira 2009; Fried, Le Corre et al. 2022). Although there are few species with conservation value (on a national scale), field margins nevertheless host many species whose populations are considered to be in decline at the national level. Field margins thus appear as a very valuable habitat that brings originality to agricultural landscapes, especially when dominated by cropland. This is particularly the case for field margin groups 5, 6 (*Lathyrus hirsutus*, *Lathyrus nissolia*) and 7 (*Aira cupaniana*, *Astragalus hamosus*, *Gastridium ventricosum*, *Linum strictum*, *Tolpis umbellata*). Besides the ecosystem services they provide, the intrinsic botanical value of field margins may thus contribute to the conservation of biodiversity.

Diversity partitioning shows that the greatest spatial variation in composition is found at the local scale of the five quadrats (+82% species than the local scale of the quadrat). The most important gain is achieved between the different years of monitoring (+129%). This result is in line with previous work showing strong temporal beta diversity in field margins (e.g. Alignier and Baudry 2016; Boinot and Alignier 2023). This high temporal variability can be related to the presence of annual species (43% of the pool, 30% of the relative abundance) whose inter-annual variations may depend on the particular meteorological conditions of the year (level of precipitation at the time of germination; see also Wietzke et al. 2020), crop rotations, with each crop able to favour a different set of species as well as past management of the field margin itself (Alignier 2018; Boinot and Alignier 2023). Inter-annual differences may also be linked to ease of identification (which depends on the development stage of the plant at the time of survey) as well as changes in the identity of observers over time, since the field margins monitored had an average of 1.85 different observers over the 5 years analysed here (Poinas, Meynard et al. 2023). Lastly, we cannot exclude unmeasured deterministic or stochastic processes as driving forces of the observed plant patterns (Chase 2010).

We found that field margins also included 47 species (7% of the species pool) that are arable weeds with a frequency > 10% in French cultivated fields and are considered here as common agrotolerant species according to Aavik and Liira (2009). This mix of weed species and species of natural open herbaceous environments is reflected in the biological spectrum of the flora of field margins. In cultivated fields, the biological spectrum is clearly dominated by therophyte species, accounting for > 60% (Bourgeois et al. 2019) and in some cases up to 90% of species (Fried et al. 2009). By contrast, undisturbed open herbaceous environments (lawns, meadows) are dominated by hemicryptophytes that can account for 66% (Bourgeois et al. 2019). Here, the biological spectrum of the flora of field margins is exactly intermediate; hemicryptophytes dominate (~50%, reflecting an environment with a grassland appearance) but therophytes are numerous (~30%) due to disturbance and the proximity of the cultivated habitat. This result confirms that field margins are one of the few habitats that can be devoted to the conservation of a mix of plant species, either arable either more disturbance-sensitive species.

By comparison with nature-value species, we showed that agrotolerant species exhibit a ruderal strategy combining high SLA, rapid life cycle (annual species, early flowering) and high nutrient requirements. The result is highly consistent with a previous study comparing the trait values of weeds and non-weeds from open herbaceous habitats (Bourgeois et al. 2019). Agrotolerant plants were also found to be characteristic of the Group 1 field margin vegetation typology associated with the most intensive agricultural system (high herbicide use, high fertilisation, landscape dominated by cropland) in the Paris Basin and northeastern France. Interestingly, field margins in the most intensive landscapes (Group 1 of the typology) can also be characterised by particular indicator species. In this sense, our results are similar to those of Cirujeda et al. (2019) and Fried et al. (2022) showing that field margins dominated by weeds or ruderal species such as *Fallopia convolvulus*, *Lolium perenne*, *Plantago major*, *Poa annua* and *Polygonum aviculare* are associated with the most unfavourable set of conditions for biodiversity (high herbicide pressure, high fertilisation level, low landscape diversity). This is also in accordance with the idea behind the Ecobordure indicator (Alignier et al. 2018) that uses the relative presence of a list of weeds (with forest and grassland species) as indicative of highly disturbed field margins. Beyond the percentage of annual species sometimes used as an indicator of the level of disturbance (Fanfarillo et al. 2018; Boinot and Alignier 2023), some relevant traits of the plant species (e.g. SLA, Ellengerg-N) must also be considered as they are better correlated with intensive management practices and simplified landscape context. In our network, the percentage of annuals is also linked to Mediterranean field margins, which can be explained by the fact that in this context many annual plants are stress-tolerant species (adapted to summer drought) (Poinas, Meynard et al. 2023).

The typology of field margins has a strong spatial structure and depends on soil and climatic conditions, agricultural context (landscape, main type of crop), and the level of intensification. Analysis of field margin types according to their traits (community weighted-means) and their agro-ecological conditions provides interesting information beyond simple classification. Previous research on the ecology of field margins has mainly focused on the context of field crops in Northern Europe or temperate systems (Mkenda et al. 2019), with little attention paid to the Mediterranean region (Bassa et al. 2011, 2012; Cirujeda et al. 2019), or the margins of perennial crops such as vineyards (Fried, Plantureux et al. 2022). The unprecedented coverage of the 500 ENI network made it possible to reveal a very different composition in vineyard margins on the one hand and in the Mediterranean region on the other. These two types of margins are more open, dominated by *Convolvulus arvensis*, and have a high proportion of forbs. The Mediterranean region stands out very clearly, notably by field margins harbouring a high proportion of annual species (due to drought), forbs, and insect-pollinated species while the margins of vineyards were mainly dominated by heliophilous, basiphilous and thermophilous species. These ecological preferences probably reflect the fact that vineyards are more often positioned on highly-exposed slopes and on clay-limestone soils. The margins of vine plots are also more often managed and disturbed by the passage of the tractor. Both perennial crops and the Mediterranean region require specific studies to uncover particular patterns and processes underpinning the flora of field margins.

In northern France, our results showed very different field margins depending on the type of landscape and the level of intensification, with margins dominated by *Dactylis glomerata* and other grassland species in livestock regions with grasslands in the landscape, and margins dominated by *Lolium perenne* and agrotolerant plants in the large cereal plains. The significant influence of landscape composition on field margin flora is consistent with the findings of Berquer et al. (2021), who observed that field margin richness was positively correlated with the proportion of grassland in the surrounding landscape. Additionally, previous studies have also highlighted the significant impact of neighboring habitats on field margin composition (Aavik et al. 2008; Blaix et al. 2020; Boinot and Alignier 2022).

Although there are no specialist species of field margins, the vegetation of this habitat forms original assemblages mixing species of different ecological origin (arable and grassland, and to a lesser extent scrub and woodland). In addition, the presence of declining species especially in intensive cereal plains makes them of particular interest for biodiversity conservation. The attainment of this conservation objective could be made possible through the new Common Agricultural Policy (CAP) for the period 2023–2027 in the European Union. Under this policy framework, farmers will be eligible for green direct payments only if they adhere to specific mandatory practices, including the allocation of 5% of arable land for Ecological Focus Areas (EFA). Considering field margins as an EFA, this policy might favour establishment and maintenance of field margins. Indeed, as pointed out by Mkenda et al. (2019), social learning (to counteract insufficient knowledge on the ecological benefits of field margins and poor knowledge related to the design of appropriate field margins) and economic incentives are one of the main levers that guarantee wide adoption of field margin establishment.

To conclude, the typology developed here can serve as a reference; it may be useful to study the impacts of new management practices for instance, by taking into account the seven types of field margins, and through them a more homogeneous agro-ecological context and species pool. Indeed, one cannot directly compare the floristic richness between the Mediterranean region and the north of France. The different nature of the species can also make them sensitive to different practices, as reported by Poinas, Fried et al. (2023) who showed that the negative impact of fertilisation is stronger in the Mediterranean region, probably because there are more oligotrophic species in this region. Another perspective to this work would be to analyse the link between the type of field margins and their interest for wild fauna, especially birds and beetles, which are also monitored by the 500 ENI network.

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Author contributions

GF conceived the study and analysed data; LH participated in data analysis by producing some of the explanatory variables used; GF wrote the first draft with significant contributions from IP, LH and AA. All authors contributed to the final version of the manuscript.

Data availability statement

The raw data are the property of the Ministry of Agriculture and are open to French public research on request. The consolidated data used for this article were produced by the GT STEP and the GTP. They are available on request from the authors and under conditions, by signing a charter of use.

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