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Beetle communities in agricultural landscapes: relative influences of climate, landscape, plant communities and agricultural practices

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ABSTRACT

Agricultural field margins are semi-natural habitats that play a key role in conservation and restoration, supporting threatened biodiversity of agroecosystems. However, most research on field margin biodiversity has focused on plant communities, while insect populations remain largely understudied. To address this gap, we leveraged a national monitoring network across France to provide a comprehensive taxonomic and functional characterisation of beetles, a highly diverse insect group of significant agricultural interest. We examined how climate, landscape, vegetation and agricultural practices influence the structure of field margin beetle communities. Using a combination of molecular and morphological approaches and multivariate analyses, we investigated beetle communities within the herbaceous field margins of 374 agricultural sites across continental France sampled between 2020 and 2023. Our surveys revealed a high diversity of beetles, with 797 species recorded, including hundreds of flower visitors and auxiliary species. Estimates based on accumulation curves suggest a richness of up to 1200 species, corresponding to approximately 10 % of the French beetle fauna. We also identified five community types, each having specific taxonomic and functional characteristics and associated with specific climatic, soil, landscape and agricultural environments. While large-scale climatic gradients were the main drivers shaping these community types, local vegetation played a key role in determining species richness. By contrast, agricultural practices appear to be an important structuring factor for both community types and richness. Finally, this study provides the first in-depth characterisation of beetle communities in French field margins, offering a solid baseline for future research and improving our understanding of the complex interactions among climatic, landscape, vegetation, and agricultural drivers.

1. Introduction

Insects provide key ecosystem services (Schowalter et al., 2018; Yang and Gratton, 2014), that greatly benefit agricultural systems. Among them, pollination is the most widely recognized, with about 75 % of crops dependent on pollinators (Klein et al., 2007). But insects also

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support other essential functions, such as plant growth by enhancing soil fertility through decomposition (Anderson et al., 2024), and regulation of agricultural pests, a service valued at 4.5 billion dollars annually in the United States alone (Losey and Vaughan, 2006). However, we are currently witnessing an unprecedented global decline in insect populations (Outhwaite et al., 2022; Wagner, 2020), which in some cases far exceeds those observed in other taxa (Thomas et al., 2004). In slightly less than 30 years, 75 % of the insect biomass in protected natural habitats has already disappeared (Hallmann et al., 2017). This observation is even more staggering in some agricultural landscapes, where biomass decrease can reach 95 % (Ziesche et al., 2024).

Agricultural practices have been identified as one of the main drivers of insect decline, particularly the most intensive ones (Outhwaite et al., 2022; Raven and Wagner, 2021; Sánchez-Bayo and Wyckhuys, 2019; Wagner et al., 2021). Indeed, modern agriculture has been developed through the use of synthetic chemicals to control pests and improve soil fertility (Matson et al., 1997; Tilman et al., 2011; Zabel et al., 2019). Present individually or in combination in the environment, these synthetic chemicals are toxic compounds that can also affect habitat quality and therefore have lethal or sublethal effects on surrounding biodiversity (Nessel et al., 2023; Tosi et al., 2022). Fertilisers for example, particularly nitrogen when combined with phosphorus, have been associated with declines in insect abundance of up to 56 % (Nessel et al., 2023). Herbicides and fungicides (Abraham et al., 2018; Bernauer et al., 2015; Geiger et al., 2010), similarly to insecticides (Main et al., 2018, on neonicotinoids), have been associated with lower diversity, survival, and reproduction rates in insects. The intensive use of several chemical treatments in agricultural landscapes has therefore an important role in insect declines in agroecosystems.

In parallel, modern agriculture has also been associated with landscape simplification, where semi-natural habitat cover has decreased while field size has increased (Benton et al., 2003; White and Roy, 2015). The consequence has been a homogenisation of insect communities (Gámez-Virués et al., 2015), with a collapse in the richness, diversity, and abundance of both pollinators (Le Féon et al., 2010) and pest-regulating auxiliaries (Carbonne et al., 2022). Yet, semi-natural habitats support communities of insects that can provide ecosystem services (Holland et al., 2017) and enhance landscape heterogeneity (*i.e.* diversity of cover and structural configuration) which is a key feature that influences insect communities' composition and promotes their diversity (Benton et al., 2003; Priyadarshana et al., 2024; Tscharntke et al., 2005). The positive influence of landscape heterogeneity on biodiversity has even been described as surpassing those of local management practices (Purtauf et al., 2005; Trichard et al., 2013).

In Europe, agri-environment schemes (AES) have been established to enhance diversity, mitigate the loss of ecosystem services and reduce the impacts of agriculture (EU Agri-Environment regulation 90/20788/EEC). Among them, the development and conservation of agricultural field margins, *i.e.* uncropped semi-natural vegetation cover immediately adjacent to a cultivated plot (Greaves and Marshall, 1987), has become a key management tool for enhancing landscape heterogeneity and biodiversity (Haaland et al., 2011; Marshall and Moonen, 2002). Field margins also support insect diversity and associated ecosystem services (Mkenda et al., 2019) by serving as refuge habitats, dispersal corridors, nesting sites, and complementary foraging areas (Bennewicz and Barczak, 2020; Marshall and Moonen, 2002; Nicholls and Altieri, 2013). However, the effectiveness of field margins for insect conservation is still under debate. Plant communities associated with these environments are generally well-known as field margin diversity studies have focused on vegetation. This has resulted, for example, on a classification of different types of plant communities in field margins along gradients of climate and agricultural practices (Fried et al., 2024), highlighting their diversity, conservation interest (*e.g.* Fried et al., 2009, 2024) and potential to provide ecosystem services (Marshall and Moonen, 2002; Mkenda et al., 2019). However, when it comes to insects, knowledge is more limited. Studies focusing on field margins have shown that these are more diverse than the adjacent agricultural fields (Haaland et al., 2011; Rischen et al., 2021), and that their plant composition drives insect communities (Woodcock et al., 2008). In some instances, field margins are also similar to road verges, for which complementary studies exist and have notably shown that these habitats act as pollinator hotspots despite the negative effects of traffic and road pollution on insect populations (Phillips et al., 2019, 2020). However, the species composition of field margin and road verges can differ markedly (Hovd and Skogen, 2005) and contrasting results have also been reported within field margin. For example, Rischen et al. (2021), (2022) found both enhancement and null effects of field margins on the diversity of ground beetles (Carabidae) within the same agricultural region. Moreover, field margin diversity studies tend to focus on low-resolution structural proxies such as type of field margin (*e.g.* grass margins versus sown wildflower margins — Haaland et al., 2011), or broad indicators of landscape composition (*e.g.* percent of agricultural land covered by field margins) rather than on on-the-ground data regarding agricultural practices. Some neglect environmental context (*e.g.* climatic conditions or landscape characteristics), despite being one of the most important drivers of insect distributions in agroecosystems (Muneret et al., 2023). Total insect biomass is also regularly used as an indicator of insect responses as a whole (*e.g.* González del Portillo et al., 2021; Reddersen, 1997; Woodcock et al., 2010), ignoring the differential responses to disturbances that different groups may have (van Klink et al., 2020).

Most studies also tend to focus on a few insect families or even species, which often belong to the same functional group (see Phillips et al., 2020). This bias is particularly evident for bees (Anthophila) (*e.g.* Carvell et al., 2007; Haaland et al., 2011; Main et al., 2020; Nicholls and Altieri, 2013) and ground beetles (*e.g.* Alignier and Aviron, 2017; Bennewicz and Barczak, 2020; Petit et al., 2023; Rischen et al., 2021), which are much more studied than other insect groups. Studies focusing on beetles (Coleoptera) other than ground beetles are rare (but see Rischen et al., 2022; Woodcock et al., 2007). Yet, with more than 400,000 known species (McKenna et al., 2019), this insect order is by far the most diverse (Foottit and Adler, 2009). About half of all described insects in the Palearctic region are beetles (Konstantinov et al., 2009), of which only about 10 % are ground beetles, which are either predaceous and/or granivorous. Collectively, other beetle groups provide far more diverse ecosystem services of great interest for agriculture. For instance, true ladybirds (Coccinellidae: Coccinellini) play a key role in pest control (Obrycki et al., 2009), scarab beetles (Scarabaeidae) and earth-boring dung beetles (Geotrupidae) are involved in decomposition supporting plant growth (Anderson et al., 2024) and soft-winged flower beetles (Melyridae) in pollination (Mawdsley, 2003), among many others. Conversely, in some families including the most important agricultural pests such as Curculionidae, Chrysomelidae and Nitidulidae (Williams, 2010), many studies focus only on deleterious species. These families are very diverse and also include neutral or beneficial species which can support biocontrol of weeds, pollination, or decomposition and are less studied.

Recognizing and including this diversity is essential to address the urgent need for a deeper understanding of field margin biodiversity, the ecological services it provides, and the complex interactions between climate, landscape, vegetation, and agricultural practices that shape beetle community structure. In this study, we rely on a standardized national biodiversity monitoring network set up throughout continental France and focusing on field margin beetle communities. We anticipated that field margin would be an area of great interest in terms of species diversity (Marshall and Moonen, 2002; Nicholls and Altieri, 2013; Reddersen, 1997) and functional diversity (Hatt et al., 2015; Holland et al., 2017; Nicholls and Altieri, 2013), but would not fully reflect national diversity because the species present there must be adapted to open, highly disturbed habitats with a high pressure of agricultural practices. As insect species assemblages are predominantly linked to the vegetation component (Konstantinov et al., 2009; Rischen et al., 2022;

Woodcock et al., 2008), we also expected turnover of beetle communities depending on the types of vegetation present in those margins (Fried et al., 2024 - Appendix S1). Overall, an influence of biogeographical conditions is expected on beetle diversity as well, in line with the large-scale nature of this study (Baselga, 2008; Hortal et al., 2011; Konstantinov et al., 2009; Willig et al., 2003). Finally, we also expected an influence of landscape variables such as landscape habitat diversity and crop diversity, as has been widely documented in other systems (Priyadarshana et al., 2024), and, to a lesser extent, effects of local agricultural management (Purtauf et al., 2005; Trichard et al., 2013). Ultimately, our main goals were: i) characterizing beetle community diversity in agricultural landscapes at the national scale, ii) classifying beetle communities into different types according to their composition along biogeographical, landscape, agricultural and vegetation gradients, and iii) characterizing the main factors influencing the richness and abundance of beetles within field margins at the national scale.

2. Materials and methods

2.1. Study sites and types of crops monitored

This study was conducted within the 500ENI network (Andrade et al., 2021), a national biodiversity monitoring effort launched in 2012 by the French Ministry of Agriculture to follow the non-intended effects of agricultural practices in field margins. The network consists of 500 sites surveyed annually following a standard protocol designed to represent the diversity of pedoclimatic conditions and agricultural practices across the country. The sites include field margins adjacent to the four main cropping systems in France — wheat, maize, vineyards, and market gardening — and their contrasting production methods (e.g., organic vs. conventional). However, as our analysis includes species identifications that complement the standard 500ENI protocol (see below) and therefore requires additional resources, our study was conducted on a subset of the network comprising 374 sites and spanning the period from 2020 to 2023. Wheat and maize, both annual cereal crops, were the most represented in these samples, with 163 and 102 monitored sites, respectively. Wheat was found predominantly in northern France, while maize was widely distributed. Vineyards, a perennial crop, ranked third, with 71 sites, primarily located in the Mediterranean region, southwest France (Bordeaux vineyards), and eastern France (Alsace, Burgundy, and Champagne wine-growing regions). Finally, market gardening, characterized by multi-cropping per season, and thereafter referred to as “lettuce” was represented by 38 sites and distributed across the country.

2.2. Beetle sampling and functional trait features

Beetles were sampled directly in the vegetation of field margins, which had an average height between 10 and 40 cm, between 2020 and 2023. Sampling was carried out thrice a year during spring using sweeping nets along two ten-meter transects positioned 30 m apart (see Andrade et al., 2021 for the detailed protocol). Specimens were then collected using insect aspirators, preserved in vials filled with 96 % ethanol, and further sent to our laboratory. These field samples ($n = 1779$), underwent species-level identification through a human-assisted molecular identification protocol (HAMI protocol - Penel et al., 2025), which combines molecular metabarcoding and morphology. At first, each sample underwent a rapid sorting of individuals into morphogroups, which were photographed and then subjected to molecular identification based on a fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene. This process included DNA extraction and sequencing, with raw data processed through a standardized and reproducible bioinformatic pipeline (Penel et al., 2025) following current best-practice recommendations for metabarcoding. Cross-validation of molecular identification with photographic records was then produced to ensure the highest-quality taxonomic identification, along with recording of abundance data.

In parallel, a comprehensive literature review was conducted for every species identified in more than 1 % of the monitored sites (375 species). Key functional traits were compiled, including feeding habits for both adults and larvae, but also habitat type, body size, wing morphology, pilosity, and potential roles in pollination, regulation processes (*i.e.* ecological processes that prevent the outbreak of populations of crop pests or weeds), and pest status. These traits were selected because they are ecologically relevant and widely used in insect functional ecology (Fountain-Jones et al., 2015; Moretti et al., 2017). They are also relatively simple to document across taxa. The list of references and the generated database are provided as supplemental information (Appendix S2).

2.3. Environmental and agricultural data

To characterize the environment and agricultural practices of the monitored field margins, climatic, soil, landscape, agronomic, and vegetation data were gathered. Climatic conditions were summarized using six bioclimatic variables: mean annual temperature, minimum and maximum temperature, total annual precipitation, and the total amount of precipitation in the driest and wettest months. These variables are known to capture the major climatic gradients that structure insect species distributions (Hortal et al., 2011; Wagner et al., 2021), and the vegetation community at the study sites (Fried et al., 2024). These data were extracted from the CHELSA climate database for the period 1979–2013 at a 1 × 1 km resolution (Karger et al., 2017). For soil data, six top-soil characteristics (< 5 cm deep) were directly measured from soil samples taken from all the sites in the 500ENI network. They included soil pH in water, soil content of silt, sand, and clay, as well as organic carbon and nitrogen levels - factors known to influence both beetle abundance and diversity (Bernardes et al., 2020). Additional data were extracted from the SoilGrids database (resolution 250 m — Hengl et al., 2017) for missing values ($n = 23$; corresponding to the sites that did not have soil samples associated with them). For landscape data, 22 land-use categories were extracted from Henckel et al. (2025), who provided annual landscape descriptions of monitored sites within a 1-km radius, from 2013 to 2018. They included two urban covers (buildings and roads); six natural or semi-natural covers (forest, field margin, grassland, hedges, mineral surface and water point) and fourteen agricultural cover types (aromatic and pharmaceutical crops, beetroot fields, cereal crops, fallow land, fibre plant crops, flax field, maize field, market gardening crops, rape field, oilseeds field, sunflower field, tree plantations, vineyard crop and other). The annual data were subsequently averaged at the site level and used to calculate two supplementary landscape indices based on Shannon diversity (Turner and Gardner, 2015). Landscape heterogeneity was estimated based on urban, natural and semi-natural cover. Crop diversity was estimated based on the agricultural cover.

Agricultural practices were collected through yearly interviews with the farmers who owned the monitored fields (Andrade et al., 2021). These interviews provided the full record of field operations, including fertilizer and pesticide applications (*i.e.* number of applications and quantities), crop types, rotation systems, and tillage depth and frequency. Field margin management included the type of vegetation cover, a categorical estimate of the height of the vegetation ranging from 1 to 5 (with 1 corresponding to very low (<10 cm), 5 to tall (>40 cm) vegetation, and intermediate values corresponding to vegetation roughly 10–40 cm high) and the frequency and nature of mowing (Appendix S3). Additionally, landscape plant protection treatment frequency index (TFI), which integrates all active substances used and provides a global measure of pesticide intensity per hectare, was extracted from the Solagro database based on practices in 2021 at the municipality level (Solagro, 2024a, 2024b).

Annual vegetation surveys were carried out alongside beetle sampling at the peak of the flowering season (Andrade et al., 2021). The presence/absence of plant species was assessed in ten 1 m^2 quadrats, producing semi-quantitative data on species abundance at field margins once the data were pooled. Plant species richness and Shannon diversity were further calculated for each site. Key functional traits of plant species, including dispersal strategy, flowering duration, life form (perennial *vs* annual), plant type (forbs *vs* graminoids), pollination and dispersal strategy, were collected and/or synthesized from the Baseflor database (Julve, 1998). In complement, Specific Leaf Area (SLA) was obtained using the TRY database (Kattge et al., 2020). The community weighted means, for quantitative traits, and the proportion of each specific type for qualitative traits, were further calculated for each site based on the pooled data. Additionally, vegetation types of field margins within the 500ENI network were directly extracted from Fried et al. (2024), who identified seven vegetation types in France based on plant species composition and abundance, ranging from species-rich Mediterranean margins dominated by forbs to northern margins dominated by grasses.

2.4. Data analysis

Beetle abundance data were averaged at the site level ($n = 374$) for the analyses (Appendix S4), with exception of species accumulation curves and species richness extrapolation that have been produced within raw data and site level data (Appendix S5). This reduces the impact of stochastic effects and compensates for the methodological limitations of the sweeping-net approach, such as the presence of vegetation of an unexpected height within one sampling event. When considering functional diversity, only sites monitored for at least two years, with at least five species recorded, and where 80 % of specimens had trait data, were considered ($n = 187$ sites).

1. Characterising beetle field margin communities

The number and proportion of identified beetle families, genera, and species within the 500ENI network were directly compared with their counterparts for mainland France, obtained through the list of species in the French national biodiversity inventory database (INPN, 2024). Species accumulation curves were also generated to assess whether the sampling effort was sufficient at both the site and national scales (Appendix S5).

Several taxonomic and functional diversity indices were calculated to characterize beetle diversity. Taxonomic diversity indices included species richness (S), Shannon diversity (H'), which was exponentially transformed to mitigate saturation effects (Jost, 2006), and Evenness (J) using Pielou's index (Pielou, 1966). We recorded functional diversity through the richness of flower visitors, of pest species, and of predators and their respective average abundances. Using 'dbFD' function of the 'FD' package in R (Laliberté and Legendre, 2010), we measured three independent functional diversity indices: functional richness (FRic), functional divergence (FDiv), and functional evenness (FEve) (Villéger et al., 2008). These indices were calculated based on Bray-Curtis distance matrices of beetle traits.

2. Types of beetle communities

The classification of beetle field margin communities into homogeneous groups was carried out using data from sites that had been monitored for at least two years ($n = 228$ sites). This conservative approach was applied to limit interannual variability while maintaining strong statistical power. We performed a hierarchical clustering using the Ward algorithm, using the average abundance across years, per site, standardized by the maximum abundance recorded for each species, and Bray Curtis dissimilarity (Legendre and Legendre, 2012). This procedure were carried out using the hclust(method = "ward.D2") from R and vegdist functions from vegan R packages (Oksanen et al., 2025). The standardisation allows to reduce the influence of dominant species and give more weight to rare and minor species in the dissimilarity calculation. Optimal classification was defined by the sharpest drop in inertia and the best balance in group sizes. Finally, a Pearson Chi-squared test was conducted to explore the link between beetle clusters and field margin vegetation types (as defined by Fried et al., 2024).

We then explored the characteristics of each cluster and the agroecological environments they occur in using the 'catdes' function of the 'FactoMineR' R package (Husson et al., 2008, 2010). This function applies a descriptive multivariate analysis, allowing the characterization of groups using both categorical and continuous variables. For each quantitative variable, it compares the mean values of the variable for each cluster with the overall mean of this variable (v-test). In other words, it is determining whether *X* variables specifically characterize a given cluster *c*. For qualitative variables, differences between clusters were assessed using Chi-square tests. Climate, soil, landscape and vegetation data were used directly without transformation, except for plant richness, which was accumulated, and vegetation type, which was extracted from Fried et al. (2024). Agricultural practices varied slightly over time. When possible (*i.e.* quantitative variables) we averaged at the site level across the years 2020–2023. For categorical variables, we selected the dominant type. For example, for crop type, we considered the main crop of the rotation, and for the production system, we used the dominant system across years, regardless of any changes during the study period. A similar approach was applied to the community characteristics of the clusters by using functional traits (*e.g.* body size, wing morphology and feeding habits), alongside the previously estimated taxonomic and functional diversity metrics. Quantitative variables were used without transformation while qualitative ones were transformed into proportions (*e.g.* proportion of phytophagous specimens at site level).

Finally, an indicator species analysis was performed using the IndVal procedure (Dufrêne and Legendre, 1997) to identify families and species that were significantly associated with a given cluster — referred to as indicator families (IF) and indicator species (IS).

3. Environmental factors structuring beetle diversity

We used Boosted Regression Trees (BRT) to identify the main biogeographical, landscape, agricultural, and vegetation drivers of beetle diversity. BRT is a machine learning method that can accommodate both quantitative and qualitative variables, without a priori assumptions about variable distributions, and can handle nonlinear complex relationships (Elith et al., 2006). Since most biodiversity indices were strongly correlated (Appendix S6 — Fig. S6.1), we focused our subsequent analysis on beetle richness and abundance as response variables. BRTs were implemented alongside Gaussian Process Regression (GPR), using 'gbm.step' from the 'dismo' package (Hijmans et al., 2013). Parameter tuning was made by testing multiple parameter combinations: shrinkage [0.05, 0.01, 0.005, 0.001, 0.0005], bag fraction [0.5, 0.6, 0.7], and tree complexity [2, 3, 4, 5, 7]. Optimal parameters were selected based on the Akaike Information Criterion (AIC). Given the large number of predictors, only those with a relative influence greater than 3 % were retained for discussion. This threshold, based on Müller et al. (2013) formula, corresponds to twice the expected value under random selection and identifies top structuring predictors. Finally, residual autocorrelation was evaluated using Moran's I test (Thioulouse et al., 2018), based on a spatial weight matrix including all neighbouring sampling points within a 60-km radius, following Meynard and Quinn (2008). Because there is some variability in BRT results between runs, each model was run 100 times and the adjusted pseudo-R^2 was estimated as the average across iterations, accounting for the number of predictors in the model.

All analyses were conducted in R version 4.1.2 (R R Core Team, 2023).

3. Results

3.1. General characteristics of field margin beetle communities

A total of 1,779 field samples (sites x years) from the 500ENI network were collected and analysed for this study. 39,711 beetle specimens were identified, representing a total of 797 species belonging to 376 distinct genera and 45 families, including species associated with a wide range of habitat types (*e.g.* agricultural habitats, grasslands, forests and wetlands). Species accumulation curves indicated that a plateau has not yet been reached (Appendix S5 - Fig. S5.1). Based on these projections, the total number of beetle species within the field margins of the 500ENI network at the national scale was estimated to range between 900 and 1,250. At the site level, we observed an average species richness of 30 ± 11 (considering only sites monitored for more than two years), an abundance of 113 ± 92 individuals, a Shannon index of 15.3 ± 6.6, an evenness of 0.8 ± 0.1, a FRic of 0.011 ± 0.006, a FDiv of 0.78 ± 0.09, and a FEve of 0.66 ± 0.08.

Twelve families were particularly frequent in our sampling, each representing more than 2 % of the field margin beetle fauna (Fig. 1A). Chrysomelidae and Curculionidae were the most dominant families, accounting for 21 % (170 taxa) and 18 % (143 taxa) of the recorded species, respectively. Most of these 12 families were better represented in field margins compared to their expected proportions at the national scale, based on the French beetle species pool inferred from INPN (2024) records across all habitat types. This pattern was particularly pronounced for Chrysomelidae, Brentidae, and Coccinellidae, for which representation in the field margins was twice as high as at the national level (Fig. 1A). Conversely, the Staphylinidae and Carabidae families appeared to be less represented in our field margin samples compared to the national representation (Fig. 1A). Despite being frequently observed in the 500ENI network, these dominant families (Brentidae, Carabidae, Cerambycidae, Chrysomelidae, Coccinellidae, Curculionidae, Elateridae, Latridiidae, Melyridae, Mordellidae, Nitidulidae and Staphylinidae) exhibited lower species diversity relative to their national scale diversity (Fig. 1B), meaning they were represented by proportionally fewer species each.

Twenty-one beetle species were identified as each representing more than 1 % of the total abundance, occurring on average in 26 % of all field samples (Appendix S7). The majority of these species belonged to the families Chrysomelidae (five species), Coccinellidae (three species), Curculionidae (three species), Melyridae (two species), and Oedemeridae (two species). Among these species, one stood out due to its particularly high abundance: *Brassicogethes aeneus* (Nitidulidae), present in 50 % of field samples, and accounting for 12.2 % of the total abundance. In comparison, the second (*Tytthaspis sedecimpunctata* – Coccinellidae) and third (*Psilothrix viridicoeruleus* – Melyridae) most abundant species were found in 46.6 % and 35.5 % of samples, contributing 6.2 % and 4.7 % to the total abundance, respectively.

Functionally, ten of these 21 species were identified as potential pollinators, including the abundant *P. viridicoeruleus*, one of the 115 flower-visiting species recorded. Three species were classified as zoophagous, potentially contributing to biological control, alongside 74 other, less abundant predatory species. Conversely, seven species,

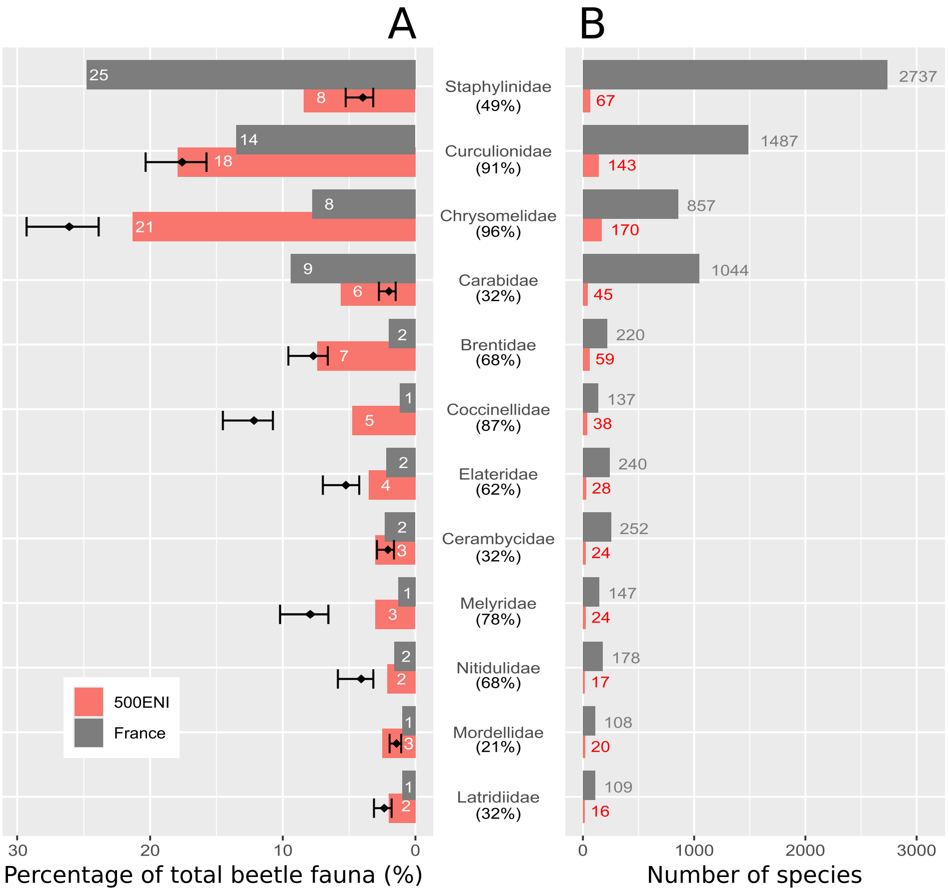

Fig. 1. Overview of the beetle fauna in the 500ENI network (red) compared to the national species pool of France (grey) with, in (A), the percentage of total beetle species belonging to each family and, in (B), the raw number of species in each beetle family. In panel (A), points indicate the mean proportion of a family per site and error bars represent 95 % confidence intervals estimated using a bootstrap procedure at the site level. Percentages shown in parentheses below each family name indicate the average probability of occurrence of that family across sites.The numbers in or next to the bars indicate the exact percentage (A) or number of species (B). Only families accumulating more than 2 % of the fauna observed in the network are represented in the graph.

including *B. aeneus*, were recognized as crop pests, in addition to 60 others less abundant species. In terms of abundance, 40.6 % of all specimens encountered within field margins were typical flower visitors, 36.5 % were tagged as pests and 18.8 % were zoophagous at least at some point in their lifecycle.

3.2. Typology of beetle communities

The most informative and balanced classification of beetle communities ($n = 228$ field margins), yielded five distinct clusters (Fig. 2 A). Cluster 4 and 2 were the biggest clusters, aggregating 96 and 69 sites, respectively. All clusters were spatially distributed across France first on a north-south axis, and, secondarily, on a west-east axis (Fig. 2B). Clusters 1–3 are mainly distributed in the north, and more precisely north-east for cluster 3, while cluster 1 partly overlaps with clusters 2 and 3. Clusters 4 and 5 are mainly in the south, with the former mainly along the Atlantic coast on the western side and the latter along the Mediterranean coast towards the east (Fig. 2B and Table 1).

In addition to spatial zonation, these clusters were also associated with distinct agro-environments (Table 1). Temperature (mean, max, min) and the amount of precipitation during the driest months, emerged as the strongest determinants of beetle community types (Table 1, Appendix S8 — Table S8.1). Clusters 1–3 were mainly associated with cold, wet climates, while cluster 4 occupied Atlantic regions with the highest rainfall regimes, and cluster 5 occupied hot, dry climates with highly seasonal rainfalls. At the landscape level, cluster 2 was typically found in areas that are dominated by arable land (covering around 68 % of the landscape on average), marked by a strong cereal specialization (mainly wheat) and intensive agricultural practices, including very large fields, high nitrogen inputs, and a low proportion of organic farming (only 7 % of fields on average). Cluster 4 occupies heterogeneous landscapes, with high crop diversity (although maize was prevailing), and low input. Cluster 5 was associated with highly specialised viticultural landscapes (with vineyard covering around 73 % of the landscape on average), marked by high landscape-level input intensity (municipality TFI), yet also by high proportion of organic farming (21 % of fields within the viticultural landscape on average). Cluster 1, occurred in viticulture-dominated landscapes too. In terms of vegetation, cluster 4 was associated with rich field margins, where the proportion of perennial and hemerophilous species were high. Cluster 5 was found in field margins

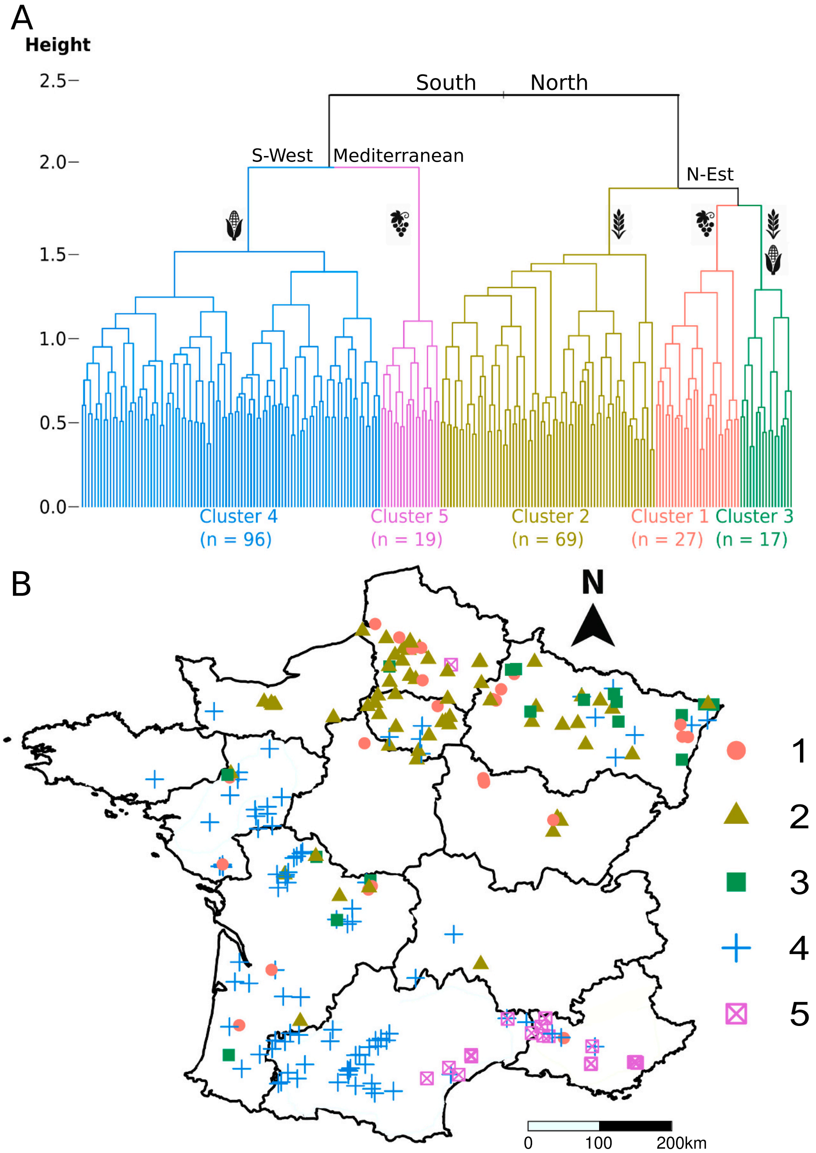

Fig. 2. (A) Hierarchical clustering of the field margins according to beetle community composition ($n = 228$) based on dissimilarity matrix (Bray-Curtis index) and (B) the distribution of these sites across metropolitan France. The crop icons indicate the main crops to which the beetle clusters are associated. The lines on the map correspond to the administrative boundaries of the French regions.

Table 1

Mean values of spatial, climatic, soil, landscape, agricultural, and vegetation variables for the five beetle community types. The colour indicates a significant association between a variable and a cluster. The darker the colour, the greater the significance. Blue indicates a negative relationship, while red indicates a positive association. Additional details are provided in the supplementary file (Appendix S10 — Tab. S10.1).

			Overall mean	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
		N =	228	27	69	17	96	19
Spatial								
	Latitude		46.84	48.07 **	48.73 ***	48.16 *	45.47 ***	44.03 ***
	Longitude		2.38	3.15	2.64	4.23 **	1.19 ***	4.74 ***
	Region (%)							
		North Paris Basin	18.86	22.23	49.28 ***	5.88	1.04 ***	5.26
		South Paris Basin	9.65	3.7	8.7	5.88	14.58 *	0 *
		Northeast Zone	21.93	44.44**	28.99	64.71 ***	7.29 ***	0 **
		Mediterranean area	10.96	3.7	0 ***	0	6.25	94.74 ***
		South West Zone	26.32	11.12	2.9 ***	5.88 *	56.25 ***	0 **
Climate								
	Mean annual temperature (°C)		11.99	11.29 *	10.84 ***	11.01 **	12.66 ***	14.63 ***
	Min temperature (°C)		1.6	0.95 *	0.87 ***	0.42 ***	2.09 ***	3.78 ***
	Max temperature (°C)		24.82	24.07 *	23.17 ***	24.15	25.71 ***	27.93 ***
	Annual precipitation (mm)		765.19	748.9	727.94 **	816.8	793.84 **	732.7
	Precipitation at driest month (mm)		45.59	47.04	47.48	52.64 **	46.93	23.63 ***
	Precipitation at wettest month (mm)		83.5	78.74	75.23 ***	84.71	87.29 **	100 ***
Landscape								
	Shannon landscape		3.5	3.67	3.35	3.29	3.64 *	3.57
	Shannon crop		4.1	3.48	4.26	3.8	4.44 **	2.85 ***
	Crop (%)		59.78	58.66	68.47 ***	56.13	55.37 **	55.29
	Grassland (%)		12.23	8.92	9.07 *	19.1 *	15.34 **	7.02
Agricultural practices								
	- Landscape							
	Total TFI		4.25	5.67 **	4.38	2.74 *	3.57 ***	6.64 ***
	Organic (%)		10.49	7.3	6.94 **	7.24	12.43 *	21 ***
	- Field							
	Size		7.94	4.33 *	11.33 ***	7.77	7.56	3 *
	Quantity of nitrogen		88.95	112	122.89 ***	97	55.15 ***	50.75
	Number of input of PPP		8	11.31 **	5.95 **	5	9.13 *	9.88
	Number of rotation		1.41	1.67 *	1.43	1.38	1.48	1.2
	Maximum deepth of tillage (cm)		14.23	11.65	16.431 **	13.62	11.26 ***	21.20 **
	- Crop type (%) :							
		Wheat	41.67	29.63	75.36 ***	41.18	28.13 ***	5.26 ***
		Maize	28.95	14.81	21.74	47.06	37.5 *	15.79
		Lettuce	9.21	18.52	2.9 *	5.88	12.5	5.26
		Vineyard	20.18	37.04 *	0 ***	5.88	21.88	73.68 ***
	- Field Margin							
	Vegetation height		3.14	2.79 *	3.21	3.14	3.26	2.82
	Mean number of mowing		1.15	1.89 ***	1.06	1.07	1.14	0.64 *
Field margin vegetation								
	Richness		34.69	31.19	33.22	32.82	36.79 *	35.89
	Weed (%)		31.06	37.41 *	37.37 ***	27.82	23.74***	39.46 *
	Forbs (%)		60.67	64.35 *	59.39	57.29	61.32	62.09
	Entomogamous (%)		49.91	49.02	45.74 **	43.86	53.15	55.7
	Non entomogamous (%)		50.01	50.98	54.17 **	56.14	46.75	44.15
	Nectar plant (%)		44.53	41.52	42.77	40.24	45.28	55.70 ***
	Non nectar plant (%)		51.34	52.14	54.51 **	54.7	49.66	43.72 **
	- Vegetation type (%) :							
		T1	26.75	37.03	55.07 ***	23.53	8.33 ***	5.26 *
		T2	19.3	11.12	27.54 *	23.53	18.75	0 *
		T3	9.21	22.23 *	4.34	17.65	9.38	0 *
		T4	5.7	7.41	4.35	11.76	6.25	0
		T5	8.77	7.41	4.35	11.76	12.5 *	5.26
		T6	15.79	7.41	0 ***	5.88	34.38 ***	0 *
		T7	10.09	3.7	0 ***	0	5.21 *	89.47 ***
		NA	4.39	3.7	4.34	5.88	5.21	0

with the high proportion of nectariferous species (with 56 % of species being nectariferous on average) and entomogamous species, as well as a high floristic richness. Clusters 1–3, occurred within impoverished plant communities, dominated by weed species in clusters 1 and 2, also depleted of entomogamous and nectariferous species in cluster 2. Although vegetation field margin types *sensu* Fried et al. (2024) were significantly associated with beetle clusters (Pearson's chi-squared test, $x^2 = 222.81$, df=24, $p < 0.001$), Cramér's V indicated only a moderate relationship ($V = 0.51$), with cluster 5 being the only beetle cluster to be fully associated to one specific vegetation type (type 7 — Mediterranean — Fried et al., 2024; standardized residual = 11).

Beetle clusters were characterised by distinct taxonomic and functional properties (Table 2). Cluster 4 was associated with a high taxonomic and functional diversity. Cluster 5 was characterized by a high number of indicator families and indicator species that are endemic of the Mediterranean region and highly specific to this cluster, although generally rare (Table 2 and Appendix S9 - Tab. S9.1). Pest species were also scarcely represented in cluster 5 (13 % of individuals, compared with a national average of 33 %). Clusters 1 and 2 were taxonomically and functionally poor, with cluster 2 being notably dominated by species with pest status (42 % of the sampled specimens). Cluster 3 displays taxonomic and functional compositions that closely reflect patterns typically observed at the national scale.

3.3. Estimation of richness and abundance with BRT models

Based on AIC, we selected a bag fraction of 0.8, a shrinkage rate of 0.01, and a tree complexity of 5 as the set of parameters for both the richness and abundance BRT models. Models based on abundance data showed evidence of spatial autocorrelation (Moran's I; p-values < 0.0001). Spatial coordinates were thus included in the final abundance models. The inclusion of spatial coordinates slightly reduced the

Table 2

Mean values of community diversity indices, number of indicator species, morphological features, feeding behaviours, and habitat specificity for the five beetle community types. The colour indicates a significant association between a variable and a cluster. The darker the colour, the greater the significance. Blue indicates a negative relationship, while red indicates a positive association.

	Overall mean	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
N =	228	27	69	17	96	19
Taxonomic Diversity						
Richness	16.85	11.78 ***	14.13 ***	15	20.61 ***	16.58
Abundance	78.82	44.48 ***	74.41	55.38 *	96.41 ***	75.84
Shannon	9.90	7.74 **	7.98 ***	9.17	12.01 ***	9.87
Evenness	0.8	0.86 **	0.78 **	0.82	0.81	0.82
Indicator species (IS)	-	2	10	17	16	49
- IS Specificity (A)	-	0.73	0.6	0.76	0.7	0.84
- IS Fréquence (B)	-	0.24	0.5	0.32	0.33	0.29
Functional Diversity						
Richness of flower visitors	11.75	8.70 ***	10.88	9.12 *	13.78 ***	11.26
Abundance of flower visitors	35.61	20.30 **	31	24.12	42.26 **	31.16
Percentage of flower visitors	57.68	59.29	62.40 **	51.07	56.76	52.61
Richness of pest	7.88	6.48 *	8.42	8.18	8.61 **	3.95 ***
Abundance of pest	24.17	15.34 *	31.45 **	24.82	24.38	8.68 **
Percentage of pest	33.16	37.51	41.87 ***	43.77 **	27.87 ***	12.59 ***
FRic	0.0016	0.0011 **	0.0012 ***	0.0013	0.0021 ***	0.0018
FEve	0.71	0.77 ***	0.69 *	0.74	0.71	0.68 *
FDiv	0.85	0.86	0.83 **	0.85	0.86 **	0.81 **
Morphological features						
Size (mm)	4.14	4.05	3.54 ***	3.92	4.35 **	5.15 ***
Macropter (%)	98.74	100	99.93	99.69	97.86	96.82
Brachypter (%)	0.31	0	0	0	0.71 **	0
Apter (%)	0.91	0	0	0.31	1.41	2.93
Hairy (%)	64.62	57.08 *	65.73	66.7	65.82	65.25
Glabrous (%)	35.38	42.92 *	34.27	33.3	34.18	34.75
Feeding behaviours (%)						
- Imago stage						
Phytophagous	74.16	73.97	82.19 ***	77.85	67.20 ***	80.82
Zoophagous	12.85	18.81 **	10.86	10.83	11.74	16.45
Omnivore	4.73	3.66	2.21 **	3.66	7.64 ***	0.85 *
- Larvae stage						
Phytophagous	61.05	63.1	69.08 ***	67.96	54.54 ***	59.42
Zoophagous	20.67	23.17	16.78 **	18.45	22.07	23.27
Omnivore	4.79	3.56	4.05	2.54	4.98	9.81 **
Habitat specificity (%)						
Wood	1.81	1.87	1.04	1.04	2.2	2.73
Grassland	49.83	47.45	38.84 ***	37.72 *	58.68 ***	54.03
Wet area	1.4	1.16	2.99 ***	0.31	0.96	0.41
Shrubland	0.14	0	0 *	0	0.03 *	1.34 ***
Mix	32.12	33.73	42.86 ***	43.50 **	24.99 ***	22.52 *

magnitude of Moran's I values (from 0.1556 to 01465), although residual spatial autocorrelation remained significant.

Nine variables were identified by richness BRT models as structuring (R^2 of 0.08). They included four variables related to vegetation, three to biogeographic conditions, and two to agricultural practices (Fig. 3A-J). Richness peaked at intermediate values of field margin vegetation height (Fig. 3B) and plant functional evenness (Fig. 3F), and was highest in Fried et al.'s (2024) vegetation type 5 (Fig. 3C). In contrast, richness declined steadily with increasing treatment frequency index (TFI; Fig. 3D, G), and showed a sharp decline at low nitrogen input levels, followed by stabilization (Fig. 3I). Climatic variables such as seasonality of precipitation (Fig. 3E) and mean annual temperature (Fig. 3H) had a positive effect on richness, before reaching a plateau at intermediate values. The relationship with plant diversity (Shannon index) was less clear, suggesting a bimodal response with peaks at low and intermediate diversity levels (Fig. 3J). By contrast, the BRT models exploring beetle abundance was inconclusive ($R^2 \leq 0$).

4. Discussion

This study represents an unprecedented effort to characterise the taxonomic and functional structure of beetle communities in agricultural landscapes at a national scale. As a result, we revealed a species-rich group within mainland France field margins through a nationally standardised, multi-year monitoring program. While some families may have been underrepresented for methodological reasons — notably leaf-litter and ground-dwelling beetles such as Staphylinidae and Carabidae which are not well captured in sweeping nets — our findings show that beetle communities in agricultural field margins are still quite distinct. Furthermore, if vegetation structure and composition significantly influence beetle richness, insect communities did not align with vegetation types. Lastly, we found that local agricultural practices strongly influenced both species richness and community composition, while large-scale biogeographic gradients had more variable effects. On the contrary, beetle abundance remains unexplained. These results are discussed point by point below.

4.1. *Taxonomic and functional diversity of field margin beetles*

In total, 797 beetle species were identified within the French field margins, while cumulation curves estimated a species richness between 950 and 1250 species. Similarly to previous observations on field margin flora (Fried et al., 2024; Marshall and Moonen, 2002) and Carabidae (Alignier and Aviron, 2017), we observed that field margins host some insect species that are common in agricultural environments, but also some species from the surrounding ecosystems such as forests, grasslands, and wetlands (Duelli et al., 1999). As a result, field margins harbour a high beetle species richness, representing approximately 10 % of France's beetle fauna. This is a remarkable figure, especially given the relatively homogeneous habitat type sampled (open grasslands),the restriction to mainland France, and the use of a sampling method that captures only a fraction of beetle diversity. This proportion could be even higher if complementary sampling techniques were employed, such as pitfall (Barber) traps, which target ground-dwelling fauna (Barber, 1931; Greenslade, 1964). Overall, this reinforces the idea that field margins host particularly diverse insect communities (Haaland et al., 2011; Rischen et al., 2021) and can represent an important habitat for conservation of non-agrotolerant species, whether it be as a temporal dispersal habitat, or as a refuge from adjacent disturbances.

At a national scale, the field margins also appear to be highly

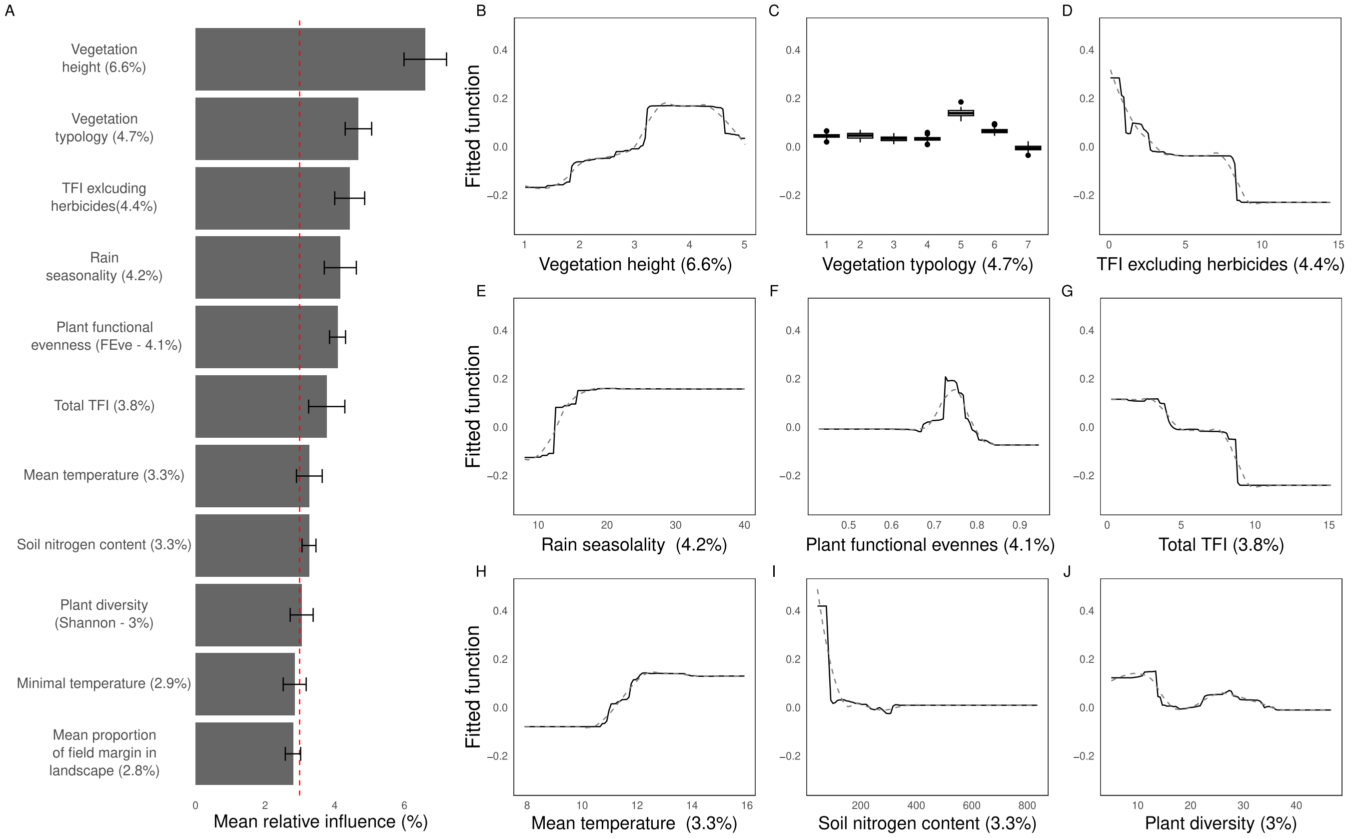

Fig. 3. Relative influence of main structural predictor variables in boosted regression tree models (A) and their incidence on the mean richness of beetles per site (B:J). In (A), red dotted lines indicate the relative influence threshold below which an influence is random and therefore not discussed (see Müller et al., 2013), while the light grey dotted line in (B:J) is the distribution of the predictors. TFI = Treatment Frequency Index.

dominated by one species: *Brassicogethes aeneus* (synonym: *Meligethes aeneus*). Also known as the common pollen beetle or rape pollen beetle, *B. aeneus* is an important pest of oilseed rape crops that can cause serious yield losses of up to 80 % (Hansen, 2004). Although oilseed rape was included in the crop rotation on about 8 % of our study sites, our surveys did not specifically target this crop, and *B. aeneus*, being specific to Brassicaceae (Hokkanen, 2003), does not cause damage to the other crops we monitored. This observation suggests that field margins can provide favourable environments for certain pest species, by acting as dispersal corridors or offering habitat and alternative food sources during the off-season.

Our data also show that these habitats harbour diverse beetle communities that are not limited to pest species, and therefore underscores their importance for conservation at the landscape scale**.** In particular, we recorded about a hundred of flower-visiting beetle species, some of which were dominant in the community and recognised for their importance as pollinators (Muinde and Katumo, 2024; Ollerton, 2017). This also aligns with the general findings that semi-natural habitats, including field margins, support pollination services (*e.g.* Shi et al., 2021), a service which is increasingly threatened by intensive agriculture (Potts et al., 2010). Field margins also contribute to pest regulation, ***i.e.*** the potential control of pest outbreaks through predation or other biological interactions, another ecosystem service provided by several beetle groups (Kromp, 1999; Holland et al., 2017). However, in our samples, auxiliary predaceous beetles — notably Carabidae and Staphylinidae — were not particularly diverse or even abundant. The latter can be explained by our reliance on a sweeping-net sampling strategy, which is better adapted to capture insects that dwell on plants rather than on the ground. Conversely, this sampling bias also means that families comprising a few or no ground dwelling species are better represented here than what they usually are in pitfall trap studies (Duelli et al., 1999). Together, these results demonstrate that agroecosystems harbour diverse coleopteran communities.

4.2. Importance of plant components on insect diversity

We have identified different types of beetle communities across France. These communities were generally associated with field margin vegetation types defined by Fried et al. (2024). The overlap was, however, less than anticipated, based on the existence of strong trophic links between insect and plant communities (Konstantinov et al., 2009; Rischen et al., 2022; Woodcock et al., 2008). Cluster 5, restricted to the Mediterranean coast, was the only beetle cluster fully associated with a specific field margin vegetation type (Table 2: ‘Mediterranean type’). This is all the more surprising given the sweeping-net sampling method which is biased toward phytophagous species (Hwang et al., 2022), as discussed above. The Mediterranean cluster still stood out for its originality, with numerous endemic and specialised species, and the lowest level of pests for all indicators combined, probably due to the fact that this region is dominated by vineyards, a crop which is not attacked by beetle species in mainland France (Esmenjaud et al., 2008).

Despite the lack of strict associations between vegetation and beetle types, our results suggest that local vegetation structure and diversity are the most structuring factors of insect richness. Different hump-shaped responses of beetle species richness were observed along vegetation gradients, with the highest richness occurring at intermediate values. This was notably observed with the field margins vegetation height and plant functional Evenness (FEve), which display the highest beetle richness at intermediate values. Such responses for vegetation height were already observed for ground beetles and can be explained by the unfavourable conditions of low vegetation for most insects (Carabidae - Muneret et al., 2023). The absence of vegetation limits trophic resources, increases exposure to extreme abiotic conditions (temperature, desiccation, etc.) and reduces access to shelter (Danne et al., 2010; Landis et al., 2000). Conversely, overgrown vegetation closes off the environment and is not beneficial to predators either (Brose, 2003). These hump-shaped responses in relation to the taxonomic and functional diversity of plants were, however, unexpected, and contradict studies that instead show a gain in insect richness with an increase in plant diversity (*e.g.* Scherber et al., 2010; Siemann et al., 1998). Indeed, at higher levels of plant diversity, it is generally assumed that a greater availability and variety of resources is available, as well as host plants and microhabitats, thus providing a wider range of niches for insects (Lewinsohn et al., 2005). However, an explanation could be that, when plant diversity is higher, potential host plants are present in insufficient numbers, which limits the ability of specialist phytophagous insects to establish themselves, favouring generalist species (Root, 1973; Stephens and Myers, 2012). That said, our data also suggest that certain beetle species, possibly disturbance-tolerant or pest taxa (Baliddawa, 1985; Ratnadass et al., 2012), may actually benefit from uniform margins dominated by a handful of plant species as suggested by the peak in beetle richness when plant diversity is very low.

4.3. Interplay between biogeography, landscape, and agriculture on beetle communities

As expected, and in line with general biogeographical patterns observed for insects within the Palearctic region (Baselga, 2008; Hortal et al., 2011; Konstantinov et al., 2009; Willig et al., 2003), latitudinal gradient and climate conditions were identified as the strongest structuring factors of beetle community types, with Mediterranean communities in the south having more distinct faunas than in other regions in mainland France. Understanding these compositional differences is fundamental to propose coherent conservation strategies. However, climate and latitude did not emerge as key structuring factors of beetle species richness. These results are in line with those previously observed for the vegetation of our field margins, with biogeographic factors (mostly climate) being important for plant community composition but secondary for species richness (Poinas et al., 2023). This may be a specificity of agricultural field margins where plant resources may not be related to a latitudinal gradient because the adjacent fields are fertilized artificially, creating environments that may not limit species richness *per se* but rather the identity of the species that can thrive in these highly disturbed environments and those particular climatic conditions.

Agricultural practices appear to be an important structuring factor for both beetle community composition and richness, a result that echoes what has been reported for multiple insect groups (*e.g.* Carbonne et al., 2022; Gámez-Virués et al., 2015; Habel et al., 2019; Sirami et al., 2019). Regional insect communities, initially structured by climatic conditions, are subsequently reshaped by local agricultural practices; therefore supporting the long-established pattern that different crop types are associated with distinct insect species (*e.g.* pest species - Hansen, 2004; Hokkanen, 2003; Williams, 2010) and communities of varying diversity (Boetzl et al., 2024). We could notably observe this for vineyards and cereal crops that are spatially clustered in the north-eastern part of France but display distinct insect communities (clusters 1 and 3). These systems differ not only in crop duration but also in management intensity. For instance, phytosanitary practices vary considerably, with French vineyards reaching a TFI of 12.4, due to high fungicide applications (Simonovici and Caray, 2023), whereas cereal crops such as maize show a TFI of 4.9, dominated by herbicides and insecticides (Agreste, 2019). These divergent practices therefore shape distinct local environments that filter and structure beetle communities. Pesticide use, in particular, showed a significant and expected negative impact on insect communities, in line with previous findings (*e.g.* Abraham et al., 2018; Geiger et al., 2010; Main et al., 2020). Similar conclusions can be drawn across other components of taxonomic and functional diversity, which were all correlated in our study (Appendix S6 — Fig. S6.1) and consistently reported in the literature (Carbonne et al., 2022; Habel et al., 2019; Outhwaite et al., 2022; Raven and Wagner, 2021). Other studies have also documented a decrease in the number of indicator species when agricultural intensity is higher (Tonelli et al., 2017). A recent analysis of the potential ecosystem services provided by field margin plant communities also highlight the negative impact of pesticide use, for example on the availability of floral resources and on the diversity of nature-value plant diversity (Genty et al., 2026), which could then have cascading effects on beetle communities. Overall, these results highlight the potential structural negative effects of intensive agricultural practices on biodiversity, which go beyond the limits of the field. Conversely, direct management of the field margin was not associated with any unintended effects on beetle diversity, although the literature generally reports measurable impacts of interventions such as mowing (Berger et al., 2024). This likely reflects the fact that in-field agricultural practices are not only more intensive but also more persistent over time than those applied to field margins. This is notably what could suggest some studies by highlighting that interventions aimed at improving field margins may be undermined by in-field practices (Carvell et al., 2007) and that the richness and composition of current field-margin carabid communities are better explained by past practices (Alignier et al., 2017).

Regarding abundance, our results were not conclusive. This can be due to several factors, including, of course, shortcomings of our analyses such as having missed other important environmental variables that are at play. Biotic interactions, which were not considered in this study, could play a crucial role in shaping insect communities, as processes like predation, facilitation, and competition can significantly influence local population dynamics (Kaplan and Denno, 2007). Additionally, given that field margins are likely to receive fertilizers and other resources through drift, overall abundance may not be limited by resources. In this case, other environmental filters determining species composition rather than their abundance may be more important.

5. Conclusions

This study represents an unprecedented effort to characterise agricultural field margin beetle communities at a national scale using a standardized protocol. Our results show that beetle communities represent an important diversity that can have interesting conservation value and potentially valuable ecosystem services. As expected, climate, vegetation and adjacent crop type had important effects on beetle communities, particularly on composition. This suggests that agricultural environments exert a strong environmental filtering to select species that are pre-adapted to their characteristic high disturbance regimes accompanied by constant fertilization and chemical applications. Climatic factors notably appeared to be the main drivers of community composition, whereas richness seemed more dependent on local vegetation characteristics, including vegetation height and plant species composition. Overall, both community composition and richness are subsequently reshaped by the intensity of agricultural practices. Regarding the beetle community typology, although it is not strictly linked to the plant community types of Fried et al. (2024), similar spatial patterns emerge, including a Mediterranean type, a northern intensive type, and South-Western extensive type. This raises the question of whether beetles could be used as indicators of field margin quality or management intensity at a local scale, similar to how plant communities are employed regionally (Ecobordure indicator - Alignier et al., 2018). Otherwise, typologies provide homogeneous species pools occurring in homogeneous agro-ecological contexts, which can serve as reference to better interpret the interplay of structural factors and investigate the non-intentional effects of agricultural practices. This also establishes a baseline for future monitoring and for assessing changes over time. Finally, abundance was not conclusive. This can be due to several factors, including, of course, shortcomings of our analyses. However, processes that are inherent to agricultural systems may also play an important role. Most notably, the artificial addition of resources for plant growth in the adjacent fields may cascade up the food chain to lift important resource limitations for phytophagous species, translating on beetle communities that are not necessarily limited in terms of abundance, but rather on their composition, by the intensive agricultural practices, a hypothesis that would need further exploration in future studies.

Ethics statement

Our study was carried out by scientists based in the same country as the study itself, respecting national data collection and sharing rules. Our working group strives to have a gender balance and be inclusive in all dimensions. We also lead a working group with relevant stakeholders within the 500ENI network to encourage exchange and share results from our research.

CRediT authorship contribution statement

Penel B.: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Genty L.:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Marty C.:** Writing – review & editing, Resources. **Bourdonné A.:** Writing – review & editing, Resources. **Clamens A.-L.:** Writing – review & editing, Resources. **Benoit L.:** Writing – review & editing, Resources. **Soldati L.:** Writing – review & editing, Resources. **Migeon A.:** Writing – review & editing, Resources. **Kergoat G.J.:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Haran J.:** Writing – review & editing, Supervision, Methodology, Funding acquisition. **Fried G.:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Meynard C.N.:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used DeepL and ChatGPT in order to improve the readability and language of the manuscript. After using this tool/service, the authors reviewed and edited the content as needed and took full responsibility for the content of the publication.

Declaration of Competing Interest

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110252.

Data availability

All the R scripts and database are availale in a Zenodo repository (url provided in the manuscript).

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