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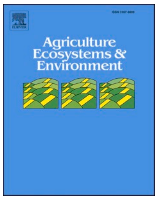

Impacts of agricultural intensification on weed floral and competitive traits: A spatiotemporal study in French vineyards and annual crops

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ABSTRACT

Weeds play a dual role in agroecosystems, offering both ecosystem services and disservices. Agricultural intensification, particularly herbicide use, has reshaped weed communities, with distinct effects in annual and perennial cropping systems. However, how intensification influences weed multifunctionality—especially in terms of competition and pollination—remains limited. This study explores how weed communities respond to agricultural intensification along spatial and temporal gradients, focusing on traits related to competition and pollination. Specifically, (1) the variation in floral and competitive traits across cropping systems, (2) their responses to management practices, especially herbicides, using national weed surveys from annual crops and vineyards, and (3) long-term changes in floral functional diversity, using two diachronic weed survey datasets, are examined. The results show that vineyards support weed communities more favourable to pollinators than annual crops. While herbicides reduce floral resources in annual systems, practices such as tillage and mowing in vineyards can help maintain floral diversity. In contrast, competitive traits showed no consistent response to herbicide use, highlighting context-dependent effects. Over time, diverging trends in weed floral diversity were observed: a decline in annual crops from the 1970s to 2020 s, and an improvement in vineyards from the 1980s onward. These results underscore the importance of considering both functional roles of weeds and their management context. To fully grasp the contribution of weeds to agroecosystem multifunctionality, long-term monitoring of weed–pollinator interactions and farming practices is essential.

1. Introduction

Biodiversity within agroecosystems plays a fundamental role in supporting essential agricultural functions (Moonen and Bàrberi, 2008). This biodiversity includes both planned biodiversity, such as cultivated crops, and spontaneous biodiversity, including weeds. Weeds are a double-edged sword, providing both ecosystem services and disservices, with their perception varying across different cropping systems. On the one hand, in annual cropping systems, weeds are predominantly considered as competitors, significantly contributing to yield loss (Oerke, 2006). Consequently, research has largely focused on their competitiveness, often neglecting their important ecological functions, such as enhancing soil stability (Gould et al., 2016), supplying habitat for wildlife, and supporting trophic networks (Holland et al., 2006). On the other hand, in perennial cropping systems, weeds are generally more tolerated because they often have less impact on the crop while providing services (Garcia et al., 2018). Moreover, the effect of weeds—whether beneficial or detrimental—varies significantly depending on regional conditions and management practices (Bopp et al., 2022b).

Differences between annual and perennial cropping systems are closely linked to variations in weed management practices and their disturbance intensities. Annual cropping systems undergo greater disturbances than perennial crops and create a constantly changing environment for weeds due to crop rotation. Despite these differences, both cropping systems encountered an intensification after the Second World War, marked by increased mechanisation and reliance on chemical inputs, such as mineral fertilisation and pesticides. This intensification has led to a widespread decline across numerous taxa, related to the arable habitat, including plants (Storkey et al., 2012), insects (Raven and Wagner, 2021) and birds (Rigal et al., 2023). Weed communities, in particular, have been profoundly transformed over the past 50 years,

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with changes in management practices differing between annual and perennial cropping systems (Jauzein, 2001; Maillet, 1992). In annual crops, the widespread use of herbicides in the 1960s revolutionised weed control by increasing crop productivity but also reshaping weed communities. In vineyard, shift from tillage to chemical weeding occurred in the 1970s and early 1980s, leading also to significant changes in weed flora (Maillet, 1992). By the late 20th century, this reliance on chemical weeding raised concerns about herbicide resistance and environmental impacts (Heap, 1997; Powles and Yu, 2010). In vineyards, these concerns were further intensified by issues such as soil erosion and a decline of soil fertility, resulted from the prolonged bare soil caused by weed management practices (Rodrigo-Comino et al., 2018). In response to the challenges, since the 1990s, diversification of weeding practices has emerged (Swanton and Weise, 1991). This diversification has helped slow down the decline of arable flora in terms of species richness (Richner et al., 2015). In vineyards, the shift toward more sustainable weed management has been even more pronounced with the adoption of inter-row spontaneous vegetation, primarily managed by mowing (Fernández-Mena et al., 2021). The transition has been further accelerated by regulatory measures, including the ban on the use of glyphosate in inter-rows in 2021 (ANSES, 2020). As a result, vineyard weed communities have been reshaped, promoting greater taxonomic and functional diversity (Bopp et al., 2025).

To date, studies examining the impact of intensification on weed communities have mainly focused on taxonomic indicators (Fried et al., 2009, 2008). More broadly, weed community responses to agricultural practices have predominantly focused on annual cropping systems, with an emphasis on competition (Delpuech and Metay, 2018; Oerke, 2006; Romillac et al., 2023). However, studies addressing the multifunctionality of weed communities—particularly across different spatio-temporal scales and within diverse cropping systems—remain scarce (Bretagnolle and Gaba, 2015). More recently, a shift has been adopted toward trait-based approaches to investigate the mechanisms driving weed community responses to environmental gradients and agricultural practices (Bopp et al., 2022a; Carmona et al., 2020; Fried et al., 2012). Functional approaches offer valuable insights for assessing both services and disservices associated with weed communities (Yvoz et al., 2021). Among the various ecological functions involving weeds, pollination plays a crucial role, yet its relationship with agricultural practices remains insufficiently explored (Kreitzman et al., 2022). Especially, the understanding of the floral functional structure of weed communities, and how it is affected by agricultural practices and crop types, remains limited. The lack of data on key weed floral traits, such as nectar and pollen quantity and quality, further restricts the assessment of their role in pollination networks and services.

In this study, these gaps are addressed by conducting a multifunctionality analysis of weed communities, focusing on their dual roles as both competitors and providers of floral resources for pollinators. Using datasets integrating weed traits related to both their competitive ability and their pollination potential, the response of weed to a gradient of agricultural intensification is investigated. Datasets used include a spatial intensification gradient between cropping systems and agricultural practices of different intensity, and a temporal intensification gradient between the 1970s-1980s and 2000s-2020s. Specifically, the following questions are tackled: 1. How does the weed community's functional structure—encompassing both floral and competitive traits—respond to different cropping systems? 2. How does the floral and competitive functional structure of weed communities respond to weed management practices, particularly herbicides, which remains the predominant weeding method in annual cropping systems? 3. How have the trajectories of the weed floral and competitive functional structure evolved over time in annual crops and vineyards?

It is hypothesised that:

1. Weed communities in vineyards likely exhibit greater taxonomic and floral functional diversity than those in annual crops, due to lower disturbance, which also favours competitive traits. In contrast, higher disturbance in annual systems promotes ruderal traits (Kreitzman et al., 2022).
2. Herbicide use in both systems likely reduces floral diversity and pollinator resources (Gabriel and Tscharntke, 2007). In vineyards, while tillage promotes ruderal species; herbicides and mowing favour mixed strategies—competitive-ruderal and competitive-stress-tolerant, respectively (Fried et al., 2022). In annual crops, herbicide and tillage mainly promote ruderal species.
3. Finally, agricultural intensification likely decreased weed floral diversity in annual crops until the 2000s, while recent changes in vineyard management may have increased it, enhancing pollinator resources.

2. Materials and methods

2.1. Dataset of weed surveys

This study combined four datasets from weed monitoring conducted across extensive spatial and temporal scales. Two derived from weed surveys conducted in annual crops and the other two from surveys in vineyards. For each system—annual crops and vineyards—the data encompass (1) a large-scale spatial component, covering either all of France or a broad north-to-south gradient, and (2) a large-scale temporal component, tracking the same plots within specific regions (Côte-d′Or in northeastern France and Hérault in southern France) with diachronic monitoring at intervals of 30–40 years. Weed surveys were conducted uniformly across all four datasets. Surveys were performed by trained personnel who walked through the sampling area, recording each species encountered. The density of each species was estimated using the density classes developed by Barralis (1976), which categorise the number of individuals per m^2 into specific scores: '1' for fewer than 1 individual/m^2, '2' for 1–2 individuals/m^2, '3' for 3–20 individuals/m^2, '4' for 21–50 individuals/m^2, and '5' for more than 50 individuals/m^2. These scores were then transformed into quantitative estimates by using the median of the range for each density class, as follows: '1' corresponds to 0.5 individuals/m^2, '2' to 1.5 individuals/m^2, '3' to 11.5 individuals/m^2, '4' to 35.5 individuals/m^2, and '5' to 75 individuals/m^2. For all datasets, a 2000 m^2 area was surveyed in each field, except for the regional diachronic monitoring of vineyard flora dataset, where the sampled area was 400 m^2. For each dataset, trained surveyors conducted interviews with farmers to collect information on their agricultural practices at the end of each cropping season.

1) The French annual crops weed monitoring program involved 5595 weed surveys conducted across French arable fields of annual crops from 2002 to 2010 (see Fried et al. (2008) for details). As previously mentioned, each field was surveyed over an area of 2000 m^2, located at least 20 m from the edge of the field. In addition to the main survey area, a corresponding control plot was established in an adjacent area not sprayed with herbicides. The four following crops were studied: winter cereals, rapeseed, maize, and sunflower which represent 83 % of the whole dataset. For winter crops (e.g., winter cereals and rapeseed), surveys were conducted one month after sowing and again in spring (from March to early April) following the last herbicide treatments. For spring-sown crops (sunflower and maize), surveys were also carried out one month after sowing and in summer (July), after the last herbicide treatment. In a first analysis, only the second survey from the main area (*i.e.,* after the last treatment) was used to assess the effect of herbicide use gradient on weed communities across different fields. In a second analysis, the second survey from the control plot was added to precisely evaluate the impact of herbicide by comparing weed communities between the treated and control plots within the same field, ensuring that any differences observed are due to the herbicide treatment rather than other factors such as soil or climate.

2) The French vineyards weed monitoring program encompasses 270 weed surveys conducted in three main French vineyard regions: i)

Languedoc, ii) Vallée du Rhône, and iii) Champagne, from 2006 to 2012 (see Bopp et al. (2022b) for details). A total of 46 vineyards were surveyed during this period, with each vineyard being surveyed three times per year, in spring, summer, and autumn. Each field was surveyed over an area of 2000 m^2, including vine rows and inter-rows. In the first analysis, a subset of surveys from late spring and summer was selected, which approximately correspond to the period following the last weeding event, allowing for comparison with the French annual crops monitoring program. In a second analysis where the response of weed to agricultural practices was analysed the whole data set was used.

3) The Regional diachronic monitoring of annual crop flora dataset comprises 575 weed surveys from two studies conducted 40 years apart in Côte-d′Or, eastern France. The first study surveyed 245 annual crop fields between 1968 and 1976, with multiple surveys conducted in each field over the years. The second study, carried out in 2005 and 2006, revisited 158 of the original fields, with only one survey per field per year (Fried et al., 2009). Surveys for winter-sown crops (winter cereals and rapeseed) were conducted in April, while surveys for spring-sown crops (sunflower and maize) took place in June. Each field was surveyed over an area of 2000 m^2. For this study, the 158 plots surveyed during both periods were retained. To account for the imbalance in the number of surveys between periods, a bootstrap resampling approach was used to randomly select two surveys per plot for the 1970s period. This procedure was repeated 1000 times to assess the robustness of the results.

4) Regional diachronic monitoring of vineyard flora dataset includes 40 vineyard plots in the Hérault region of southern France, which were also the subject of a diachronic study. The initial sampling took place in the late 1970s (1978–1979), followed by a second sampling in the early 2020 s (2020–2021) (Bopp et al., 2025). The surveys were conducted across three different seasons: spring, summer, and autumn. Each field was surveyed over an area of 400 m^2, including both vine rows and inter-rows. Data from all three seasons were included in the analysis.

2.2. *Functional traits data*

2.2.1. *Floral traits*

At the flower level, visitation by flower-visiting insects is influenced by three main plant-level criteria: (i) visual attractiveness, (ii) flower accessibility, and (iii) floral reward. Visual attractiveness was evaluated using two traits: flower colour (classified as black, blue, brown, green, pink, white, or yellow) (Backhaus, 1993) and flower symmetry (categorised as actinomorphic or zygomorphic) (Møller et al., 1995). Both traits were sourced from the baseflor database (Julve, 2016). Flower accessibility was assessed through inflorescence type, which influences pollinator access to floral resources (Lehrer and Campan, 2005). Classifications were obtained from the BiolFlor database (Kühn, 2004) and are detailed in Appendix Table A1. Floral rewards were evaluated based on nectar presence (binary: yes/no) and nectar quantity (categorised as none, present, little or plenty), with data sourced from BiolFlor (Kühn, 2004). Additionally, flowering onset from baseflor (Julve, 2016) was included to assess the temporal availability of floral resources. Finally, pollination type was included to examine the extent to which weeds rely on insect pollinators for reproduction, using data from the baseflor database (Julve, 2016).

2.2.2. *Community-level floral structure*

To have floral structure at the community level, Floral Rao index, community-weighted variance (CWV) of flowering onset, density of entomogamous plants within the weed community, density of nectar-offering plants within the weed community, inflorescence diversity, and flower colour diversity within the weed community were calculated (Table A2).

The floral functional diversity index was calculated using the Rao index, a metric well-suited to the study as it accounts for both functional richness and the abundance of traits within the community (Botta-Dukát, 2005). The calculation incorporated the following traits: flower colour, inflorescence type, flower symmetry, flowering onset, presence of nectar, and nectar amount (Table A2). The CWV flowering onset represents the time period during which weeds will bloom (Table A2). The density of entomogamous plants within weed communities reflects the number of weeds that rely on insects for reproduction, while the density of nectar-offering plants within weed communities indicates the potential nectar resources available to pollinators (Table A2). To account for the accessibility of weed communities to a diverse range of pollinators, the inflorescence diversity within these communities, defined as the number of different inflorescence types, was calculated. Additionally, to assess the breadth of weed attractiveness, the diversity of flower colours, measured as the number of distinct flower colours present within these communities was analysed. To handle missing trait data for certain species, the mice package was used for data imputation (Van Buuren and Groothuis-Oudshoorn, 2006), ensuring a complete trait dataset prior to calculating all the floral community-level traits (Figure A2).

2.2.3. *Community-level competitive traits*

Weeds pose the greatest competitive threat to crops when they occupy the same space at the same time and exhibit superior efficiency in absorbing limited resources such as light, nitrogen, and water. To assess the competitiveness of weeds relative to crops, four key traits were selected. Specific leaf area (SLA) is associated with rapid resource acquisition (Westoby, 1998), while plant height is positively correlated with a weed's ability to outcompete crops for light (Cavero et al., 1999). Seed dry mass is a valuable indicator of the ecological strategies adopted by plants and is closely linked to seedling establishment and the persistence of weeds in the field (Moles and Westoby, 2006). Additionally, Ellenberg's indicator for nutrients (Ellenberg N) has proven to be a reliable proxy for evaluating a plant's capacity to compete for nitrogen (Moreau et al., 2013).

For each plant community, the community weighted mean (CWM) for these four traits was calculated using species that represented at least 80 % of the total abundance (Grime, 1998) (Table A4). Additionally, the Competition Potential (CP) was calculated as a composite index reflecting the potential of each weed species to compete with the crop, incorporating both trait similarity and flowering synchrony (Table A4). The trait similarity was assessed using a weighted ratio of weed and crop values for specific leaf area (SLA), Ellenberg N, and plant height, applied for annual crops. For annual crops, the coefficient of synchrony was computed based on the temporal overlap between weed and crop flowering periods, following criteria adapted from Yvoz et al. (2021); detailed scoring rules are provided in Table A3. In vineyards, CP was calculated without considering plant height, based on the assumption that light competition between vines and weeds is negligible (Table A4). Additionally, the synchrony coefficient was defined as the ratio between the flowering onset of the weed species and that of the vine, given that the period between flowering and bunch closure is the most sensitive stage for vines in terms of weed competition (Hirschfelt, 1998) (Table A4).

To ensure comparability of values between cropping systems, the competition potential (CP) was normalised using the following formula:

$$Normalised\ CP = \frac{CP - \min(CP)}{\max(CP) \quad - \min(CP)} \quad . \tag{1}$$

Normalised competition potential ranges from 0 (no competition) to 1 (similar or higher trait performance, indicating strong competitiveness).

All the SLA, seed dry mass, plant height values were collected on TRY database (Kattge et al., 2020) and Ellenberg N values were collected from data from (Tichý et al., 2023). To address missing trait data for certain species, the mice package was used for data imputation prior to the calculation of the community-level competitive traits (Figure A1).

2.3. Data analysis

2.3.1. Analysis of national monitoring data on annual crop and vineyard flora (spatial gradients)

First, to evaluate the effect of the cropping system, floral and competitive traits between annual crops and vineyards were compared using the two national datasets and Wilcoxon tests. To enhance comparability, a subset of surveys conducted in spring and summer from the French vineyard weed monitoring program dataset was selected. This period roughly corresponds to the post-weeding phase, allowing for a meaningful comparison with the French annual crops monitoring program dataset.

Secondly, a more detailed investigation into the effect of agricultural practices on the weed floral and competitive structure within each cropping system was conducted, without restricting the vineyard surveys to spring and summer data (Figure A2). To do so, generalised linear mixed models (GLMMs) were fitted using the *lme4* (Bates et al., 2015) and *glmmTMB* (Brooks et al., 2017) packages, and linear mixed models (LMMs) were implemented with the *nlme* package (Pinheiro et al., 1999). A Poisson distribution was applied for modelling inflorescence and flower colour diversity within weed communities. For the species richness, the density of entomogamous plants and nectar-offering plants within weed communities, a negative binomial distribution was used to account for overdispersion.

LMMs were used to analyse community-level competitive traits. Only the results from models that met the assumptions of homoscedasticity and residual normality are presented. The Floral Rao Index, flower colour diversity within weed communities, CWM SLA, and competition potential could not be modelled for neither annual crops nor vineyard dataset due to violations of model assumptions. Additionally, CWM plant height could not be analysed for the vineyard dataset for the same reason.

For annual crops, the following explanatory variables were included in the modelling:

- Position of the plot: represented by latitude and longitude (in degrees), to capture geographical variations (Rohde, 1992).

Position of the plot: represented by latitude and longitude (in degrees), to capture geographical variations (Rohde, 1992).

- Frequency of tillage
- Frequency of herbicide use
- Current crop: the crop present at the time of the survey. Four crop types were considered—maize, rapeseed, sunflower, and winter cereals. Crop type, defined by the crop species and its associated agricultural practices, is a key determinant of the taxonomic and functional structure of weed communities (Perronne et al., 2015).
- Diversity in crop sowing dates within the crop sequence: A binary variable (yes/no) indicating whether the current crop was sown at the same time as the previous crop. Diversity in crop sowing dates within the crop sequence is a component of the crop sequence. It has been shown that the main effect of crop sequence on weed communities rely on the differences of crop sowing dates (Mahaut et al., 2019).
- Crop type diversity: A binary variable (yes/no) indicating whether the current crop is of the same type (monocotyledon or dicotyledon) as the previous crop.
- For vineyards, models included:
- Position of the plot: Latitude and longitude to account for geographical variations.
- Frequency of herbicide in the inter-row (IR)
- Frequency of herbicide use in the row (R)
- Frequency of tillage in the IR
- Frequency of tillage in the row R
- Frequency of mowing in the IR

For both annual crops and vineyards, month and year of the survey were included as random variables to account for temporal variability. Model selection followed a backward stepwise procedure.

2.3.2. Paired Wilcoxon tests for herbicides sprayed/unsprayed area comparison

To precisely assess the effects of herbicide use, its impacts on floral and competitive traits were evaluated in the following annual crops: winter cereals, rapeseed, sunflower, and maize. Using the data of the French annual crops weed monitoring program, paired Wilcoxon tests were performed to compare weed traits between herbicide-sprayed and unsprayed areas within the same field (Figure A2).

2.3.3. Analysis of regional diachronic monitoring data on annual crop and vineyard flora

Finally, to assess the impact of agricultural intensification over time, the community-level floral and competitive traits were compared between two periods: 1970–1980s and 2000–2020s. For the regional diachronic monitoring of the annual crop flora dataset, the mean value of each trait was calculated using the two selected surveys per period and per plot, giving a single representative value per plot for each period. For regional diachronic monitoring of vineyard flora dataset, the mean of each trait was calculated per period, per plot and per season, resulting in a single value for each season within each period for every plot. These means were then compared using the paired Wilcoxon test to identify significant changes over time (Figure A2).

All the data were handled, computed and analysed via R version 4.4.1 (R Core Team, 2024) within the RStudio environment (Posit Team, 2025).

3. Results

3.1. Annual and perennial cropping systems drive weed floral functional structure

In annual crops, weed communities exhibit significantly lower species richness, averaging 6 species, with approximately 60 % of them being entomogamous (Fig. 1, Table 1). In contrast, weed communities in vineyards were more diverse, averaging 18 species, of which 71 % were entomogamous (Fig. 1, Table 1). In vineyards, weed communities exhibited not only greater taxonomic diversity but also a significantly higher floral Rao index compared to annual crops (Fig. 1). Additionally, vineyard weed communities supported higher densities of entomogamous and nectar-offering plants, as well as greater flower colour and inflorescence diversity (Fig. 1). Moreover, the community-weighted variance (CWV) for flowering onset was also higher in vineyards.

In addition to differences in floral functional structure, significant variations were observed in competitive traits between the two cropping systems (Fig. 2). Weed communities in annual crops exhibited higher specific leaf area (SLA), greater plant height and higher Ellenberg N values compared to those in vineyards (Fig. 2). However, competition potential was higher in vineyards, with an average of 0.4, compared to approximately 0.1 in annual crops.

3.2. Factors affecting weed communities in annual crops and vineyards

3.2.1. Latitude

In annual crops, latitude was negatively correlated with weed species richness (Table 2). In contrast, in vineyards, latitude was positively correlated with species richness (Table 2). Additionally, latitude was negatively correlated with the density of entomogamous plants in vineyard weed communities (Table 2) and with nectar-producing plant density in annual crop weed communities (Table 2). Regarding competitive traits, latitude was negatively correlated to CWM SLA in annual crops (Table 3). While, in vineyards, CWM Ellenberg N was positively correlated to latitude (Table 3).

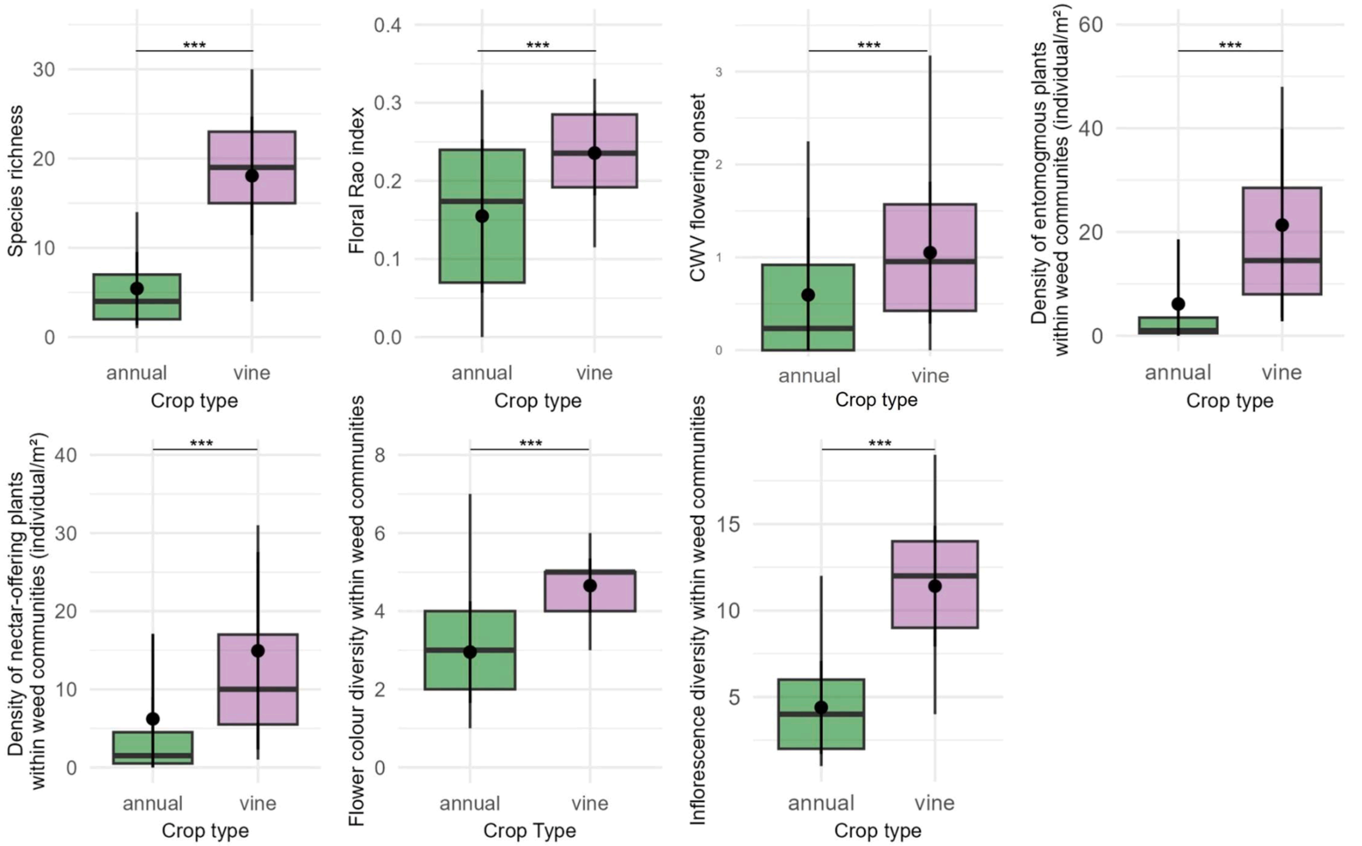

Fig. 1. Boxplots of floral traits of weed communities between annual cropping systems and vineyards. Each box represents the interquartile range, with the median shown as a bold horizontal line. The mean is indicated by the black dot. Error bars are the standard deviations. Stars above the boxplots indicate significant differences based on Paired Wilcoxon tests. Significance levels are indicated as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Note that the scale on the y-axis varies between sub-figures. CWV: community-weighted variance.

Table 1
Mean species richness (± Standard deviation (Sd)) within weed communities measured over 2000 m^2 area and mean proportion of entomogamous species (± Standard deviation (Sd)) within weed communities in annual crops and vineyards.

Cropping system	Mean species richness ± Sd	Mean entomogamous proportion ± Sd
Annual	5.96 ± 4.08	59.72 ± 22.68
Vine	17.97 ± 7.42	70.64 ± 10.65

3.2.2. *Longitude*

Longitude also influenced weed community traits. In annual crops, density of entomogamous plants and nectar-offering plants within weed communities was negatively correlated with longitude indicating a decline in floral resources at increasing longitudes (i.e., eastern France) (Table 2). CWM seed dry mass and CWM plant height were positively correlated with longitude suggesting an increase in those competitive traits in eastern regions (Table 3).

3.3. *Crop type*

In annual crops, the current crop significantly influenced the composition and the functional structure of weed communities. Weed species richness varied significantly with crop type, with sunflower fields exhibiting 1.2 more species than maize fields, while winter cereal fields had significantly lower richness, showing a decrease of one species compared to maize fields (Table 2). Weed communities in rapeseed, sunflower, and winter cereals had a higher density of entomogamous plants compared to weed communities in maize (Table 2). Only the communities in rapeseed and sunflower crops showed a significantly higher density of nectar-producing weeds, with 1.8 and 1.3 times more individuals, respectively, compared to maize. Inflorescence diversity within weed communities was higher in sunflower fields and lower in winter cereals compared to maize (Table 2). For competitive traits, CWM SLA was higher in winter cereals compared to maize. Seed dry mass was greater in rapeseed, sunflower, and winter cereal fields than in maize fields (Table 3). CWM Ellenberg N was lower in rapeseed and winter cereals compared to maize (Table 3).

Variations in crop sowing dates within the crop sequence significantly impacted species richness, the density of nectar-offering plants, and inflorescence diversity. When the current crop was sown within the same sowing window as the previous crop, it reduced the number of species, the density of nectar-offering plants and the diversity of inflorescences within weed communities (Table 2).

3.4. *Management practices*

Among weed management practices in annual crops, each unit increase in herbicide frequency reduced species richness by a factor of exp (-0.08412) ≈ 0.92, representing an average decline of 8 % (Table 2). Herbicide frequency was also negatively correlated with the density of entomogamous and nectar-producing plants, and inflorescence diversity within weed communities. In vineyards, tillage frequency in the row had a positive effect on the density of entomogamous and nectar-offering plants within weed communities. Furthermore, tillage frequency and mowing in the inter-row were positively correlated to weed inflorescence diversity (Table 2).

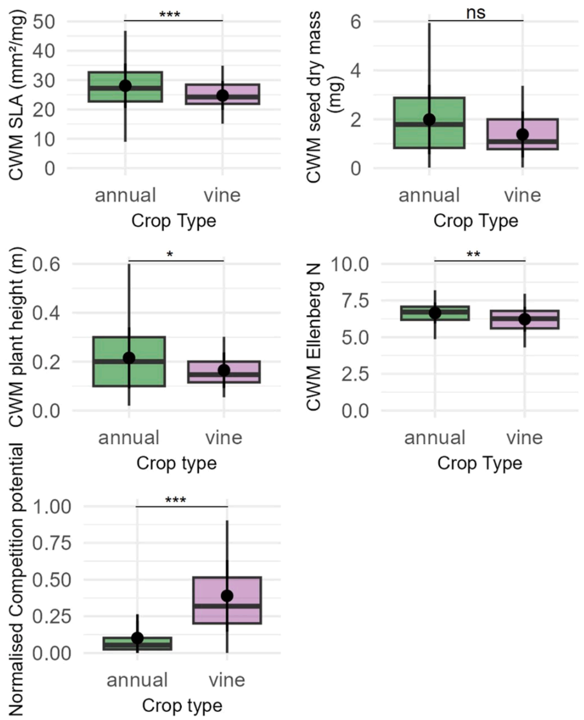

Fig. 2. Boxplots of competitive traits of weed communities between annual cropping systems and vineyards. Each box represents the interquartile range, with the median shown as a bold horizontal line. The mean is indicated by the black dot. Error bars are the standard deviations. Stars above the boxplots indicate significant differences based on Paired Wilcoxon tests. Significance levels are indicated as follows: *p < 0.05, **p < 0.01, ***p < 0.001. Note that the scale on the y-axis varies between sub-figures. CWM: community weighted means; Ellenberg N: Ellenberg's indicator for nutrients, SLA: specific leaf area.

In annual crops, herbicide frequency was positively correlated to plant height and CWM of seed dry mass (Table 3). In vineyards, herbicide frequency in the inter-row was negatively correlated to CWM seed dry mass (Table 3).

For both annual crops and vineyards, model results indicated that inter-annual and inter-seasonal variations were minimal, with most variance explained by the fixed effects included in the models.

3.5. Weed communities' responses to herbicide uses in annual cropping systems in France

Across all crop types, weed communities in unsprayed areas (T) exhibited significantly higher species richness and greater densities of entomogamous and nectar-offering weeds compared to sprayed areas (P) (Fig. 3). In terms of trends, entomogamous weed density in unsprayed areas was approximately 3–6 times higher than in sprayed areas, depending on the crop (with the highest difference observed in maize and the lowest in rapeseed). Similarly, nectar-offering weed density was about 2–9 times higher in unsprayed areas (T) compared to sprayed areas (P) (with the highest difference observed in maize and the lowest in rapeseed).

Additionally, unsprayed areas supported a significantly higher diversity of inflorescence and flower colour across all crop types (Fig. 3). Floral Rao index was also greater in maize, rapeseed, and winter cereals in unsprayed areas (T), though this effect was not observed in sunflower crops. In terms of trends, the floral Rao index in unsprayed areas (T) was approximately 1.2–1.3 times higher than in sprayed areas (P), with the lowest difference observed in maize and the highest in winter cereals.

No significant difference in the variance of flowering onset was observed between herbicide-sprayed areas (P) and unsprayed areas (T) across crop types, except in winter cereals, where variance was higher in unsprayed areas (T) (Fig. 3).

In maize, weed communities in sprayed areas (P) exhibited a higher specific leaf area (SLA) compared to unsprayed areas (T) (Fig. 4). In both maize, sunflower and winter cereals fields, seed dry mass as well as plant height was greater in sprayed areas (P) (Fig. 4). Additionally, in both maize and sunflower fields, weed communities in sprayed areas (P) showed a lower affinity for nitrogen-rich conditions (Fig. 4), whereas, in winter cereal fields, sprayed areas (P) were associated with a higher affinity for nitrogen-rich conditions (Fig. 4).

3.6. Comparison of floral weed traits between the 70s-80s and the 2000s-2020s

3.6.1. Diachronic comparison of floral traits

A comparison of weed communities between the 1970s and the 2000s revealed a significant decline in species richness in annual cropping systems, with an average of 16 species in the 1970s and 10 in the 2000s (Fig. 5). Floral Rao index, densities of entomogamous and nectar-offering weeds were significantly lower in the 2000s than in the 1970s (Fig. 5). A significant decline was also observed in the diversity of inflorescence and flower colour. However, no difference was observed in the variance of flowering onset (Fig. 5).

In contrast to annual crops, vineyard weed communities exhibited opposing trends when comparing floral traits between the 1980s and the 2020 s (Fig. 6). By the 2020 s, weed communities in vineyards exhibited significantly higher species richness than in the 1980s, with an average of 21 species in the 1980s and 30 in the 2000s. The 2020 s communities also showed significantly higher CWV flowering onset and higher densities of entomogamous and nectar-offering weeds (Fig. 6). Additionally, the diversity of inflorescence and flower colour was significantly higher in the 2020 s than in the 1980s. Despite these changes, weed communities in the 2020 s displayed lower overall floral functional diversity (Floral Rao index) compared to those in the 1980s (Fig. 6).

3.6.2. Diachronic comparison in competitive traits

In annual crops, significant differences were observed for three competitive traits. Weed communities from the 2000s exhibited a significantly lower seed dry mass and plant height compared to those from the 1970s (Fig. 7). Additionally, CWM Ellenberg N was higher in the 2000s compared to the 1970s, suggesting a shift towards species associated with more nutrient-rich conditions.

In contrast, weed communities in vineyards during the 2020 s exhibited a significantly higher SLA, a higher Ellenberg' s index for nutrients and greater competition potential compared to those in the 1980s. Whereas, the CWM plant height was significantly lower in the 2020 s than in the 1980s (Fig. 8).

4. Discussion

4.1. Weed communities in vineyards support greater pollinator potential than in annual crops

The differences between weed communities in vineyards and annual crops appear driven by distinct agricultural practices in perennial versus annual systems, shaping contrasting ecological dynamics.

Vineyard weed communities exhibit higher taxonomic diversity than those in annual crops. This pattern is consistent with findings by (Kreitzman et al., 2022), who reported higher plant, invertebrate and bird diversities in woody perennial systems compared to annual cropping systems. In vineyards, this increased diversity can be attributed to their perennial nature, lower planting density (more space for weeds), and reduced disturbance intensity compared to annual crops, such as shallower tillage and more diverse weeding strategies, including mowing (Gaviglio, 2013). Additionally, vineyards often occupy a wider range of abiotic conditions (*e.g.*, rocky limestone hillsides, sandy soils),

Table 2
Results of generalised linear mixed models (GLMM) analysing the effect of agricultural practices and environment variables on species richness and floral traits for annual crops and vineyards.

Cropping system	Explained variable	Variable	Estimate	Std. Error	z-value	Pr(>|z|)	Pseudo R^2 (Nagelkerke)
Annual crops	**Species richness**	**(Intercept)**	3.61820	0.49628	7.291	**3.09e−13** ***	0.072
		Crop rapeseed	0.06592	0.07230	0.912	0.361890	
		Crop sunflower	0.19090	0.06491	2.941	**0.003270** **	
		Crop winter cereals	−0.10074	0.04604	−2.188	**0.028653** *	
		Same sowing yes	−0.08187	0.04058	−2.017	**0.043649** *	
		Frequency herbicide	−0.08412	0.02861	−2.940	**0.003283** **	
		latitude	−0.03868	0.01083	−3.573	**0.000353** ***	
	Density of entomogamous plants within weed communities (individuals/m²)	**(Intercept)**	1.91498	0.11677	16.400	**< 2e−16** ***	0.042
		Crop rapeseed	0.66058	0.12116	5.452	**4.97e−08** ***	
		Crop sunflower	0.44097	0.11355	3.883	**0.000103** ***	
		Crop winter cereals	0.22733	0.08189	2.776	**0.005502** **	
		Frequency herbicide	−0.10303	0.05205	−1.979	**0.047761** *	
		longitude	−0.04200	0.01503	−2.795	**0.005195** **	
	Density of nectar-offering plant within weed communities (individuals/m²)	**(Intercept)**	4.08812	0.90792	4.503	**6.71e−06** ***	0.061
		Crop rapeseed	0.60774	0.14796	4.107	**4.00e−05** ***	
		Crop sunflower	0.25067	0.11861	2.113	**0.034568** *	
		Crop winter cereals	0.16457	0.10811	1.522	0.127943	
		Same sowing yes	−0.14813	0.07272	−2.037	**0.041662** *	
		Frequency herbicide	−0.12139	0.05193	−2.338	**0.019409** *	
		latitude	−0.03941	0.01997	−1.973	**0.048510** *	
		longitude	−0.05704	0.01577	−3.618	**0.000297** ***	
	Inflorescence diversity within weed communities	**(Intercept)**	1.64062	0.06238	26.299	< 2e−16 ***	0.053
		croprapeseed	−0.04191	0.05973	−0.702	0.482896	
		Crop sunflower	0.19916	0.04694	4.243	**2.21e−05** ***	
		Crop winter cereals	−0.13505	0.04104	−3.291	**0.000999** ***	
		Same sowing yes	−0.06339	0.02972	−2.133	**0.032950** *	
		Freqency herbicide	−0.09511	0.02087	−4.558	**5.17e−06** ***	
Vineyards	**Species richness**	(Intercept)	−1.07356	1.09228	−0.983	0.325676	0.128
		latitude	0.08537	0.02377	3.592	**0.000328** ***	
	Density of entomogamous plants within weed communities (individuals/m²)	**(Intercept)**	9.84442	2.91486	3.377	**0.000732** ***	0.150
		Frequency tillage R	3.93869	1.29604	3.039	**0.002374** **	
		Latitude	−0.14898	0.06409	−2.325	**0.020092** *	
	Density of nectar-offering plant within weed communities (individuals/m²)	**(Intercept)**	2.700	0.117	23.08	**< 2e−16** ***	0.087
		Frequency tillage R	4.573	1.185	3.86	**0.000114** ***	
	Inflorescence diversity within weed communities	**(Intercept)**	2.18147	0.05387	40.494	**< 2e−16** ***	0.190
		Frequency tillage IR	0.63093	0.31200	2.022	**0.0432** *	
		Frequency mowing IR	1.21782	0.25972	4.689	**2.75e−06** ***	

The table presents the estimated coefficients (Estimate), standard errors (Std. Error), z-value, and associated p-values (Pr(>|z|)). Significance levels are indicated as follows:
*$p < 0.05$
**$p < 0.01$
***$p < 0.001$.
The Pseudo R^2 (Nagelkerke) value indicates the model's explanatory power.

Table 3
Results of the linear mixed model (LMM) analysing the effect of cropping systems and environmental variables on log-transformed community weighted mean (CWM) seed dry mass (mg), log-transformed community-weighted mean (CWM) plant height (m).

Cropping systems	Explained variable	Variable	Value	Std. Error	t-value	p-value	Pseudo R^2 (Nagelkerke)
Annual crops	**log(CWM SLA) (mm^2/mg)**	**(Intercept)**	3.823890	0.24855633	15.384400	**0.0000*****	0.049
		Crop rapeseed	−0.013436	0.04414869	−0.304340	0.7609	
		Crop sunflower	−0.059090	0.03395312	−1.740340	0.0821	
		Crop wintercereals	0.110320	0.03208690	3.438151	**0.0006*****	
		latitude	−0.011267	0.00535804	−2.102786	**0.0357***	
	log(CWM seed dry mass) (mg)	(Intercept)	0.0024217	0.10951454	0.022113	0.9824	0.080
		Crop rapeseed	0.9122953	0.13707040	6.655669	**0.0000*****	
		Crop sunflower	0.4263656	0.13194384	3.231417	**0.0013****	
		Crop winter cereals	0.2008626	0.08430443	2.382586	**0.0174***	
		Frequency herbicide	0.1083487	0.05438493	1.992256	**0.0466***	
		longitude	0.0967516	0.01535245	6.302025	**0.0000*****	
	log(CWM plant height) (m)	**(Intercept)**	−2.0248854	0.08462593	−23.927481	**0.0000*****	0.050
		Frequency herbicide	0.0991209	0.03388502	2.925214	**0.0035****	
		longitude	0.0682879	0.01024894	6.662924	**0.0000*****	
	CWM Ellenberg N	**(Intercept)**	6.788241	0.06384908	106.31696	**0.0000*****	0.033
		Crop rapeseed	−0.555988	0.09822157	−5.66055	**0.0000*****	
		Crop sunflower	0.013604	0.07374021	0.18449	0.8537	
		Crop winter cereals	−0.161971	0.07301430	−2.21834	**0.0267***	
Vineyards	**log(CWM seed dry mass) (mg)**	**(Intercept)**	0.7810586	0.1870785	4.175031	**0.0001**	0.082
		Frequency herbicide IR	−2.8172219	0.9811347	−2.871392	**0.0054****	
	CWM Ellenberg N	(Intercept)	0.5186213	2.2106188	0.2346046	0.8152	0.053
		latitude	0.1234770	0.0481795	2.5628547	**0.0126***	

The table presents the estimated coefficients (Estimate), standard errors (Std. Error), t-values, and associated p-values (Pr(>|t|)). Significance levels are indicated as follows:
*$p < 0.05$
**$p < 0.01$
***$p < 0.001$.
The Pseudo R^2 value represents the explanatory power of the model.

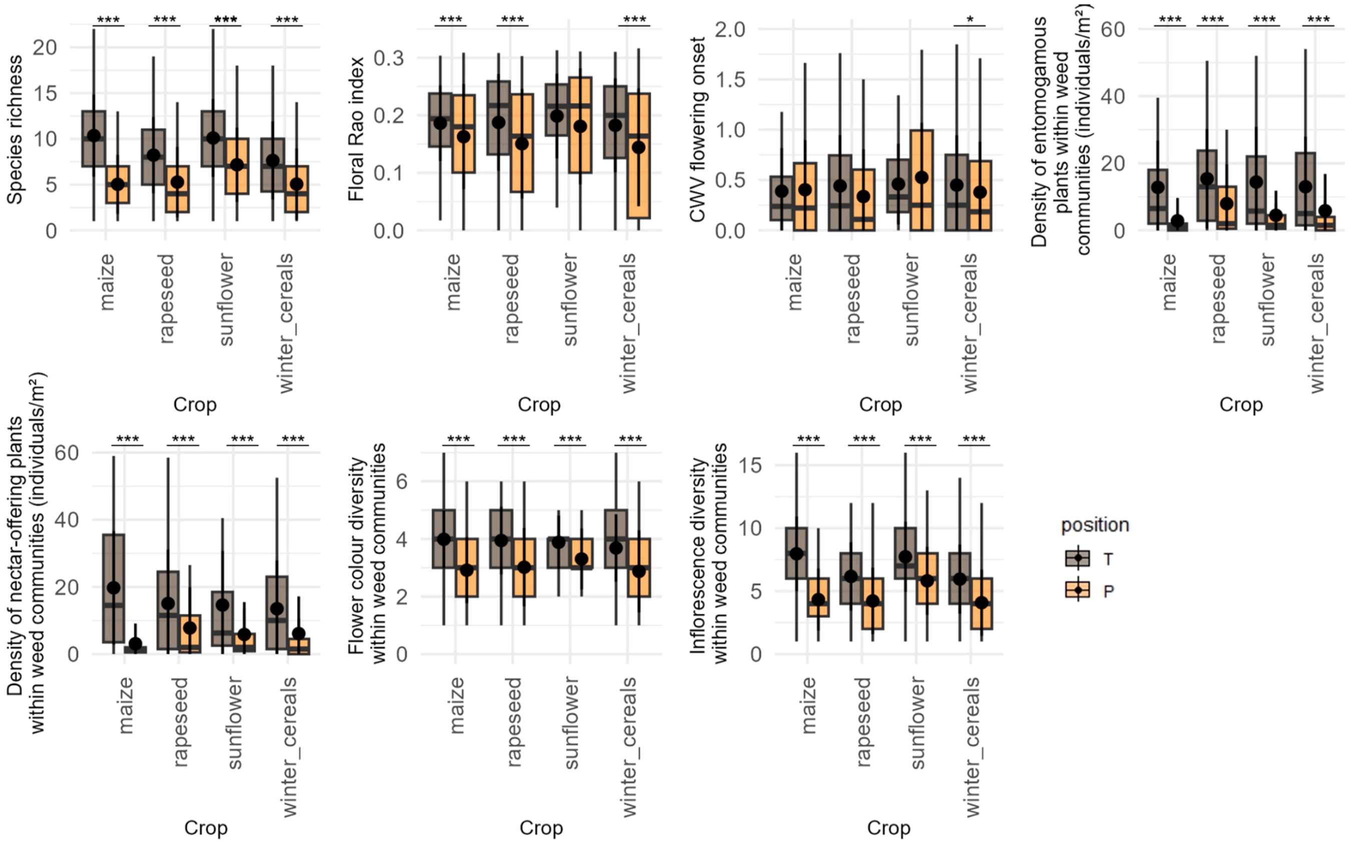

Fig. 3. Boxplots of floral traits of weed communities between herbicide-sprayed area (P) and unsprayed area (T) in 4 annual crops. Each box represents the interquartile range, with the median shown as a bold horizontal line. The mean is indicated by the black dot. Error bars are the standard deviations. Stars above the boxplots indicate significant differences based on Paired Wilcoxon tests. Significance levels are indicated as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Note that the scale on the y-axis varies between sub-figures. CWV: community-weighted variance.

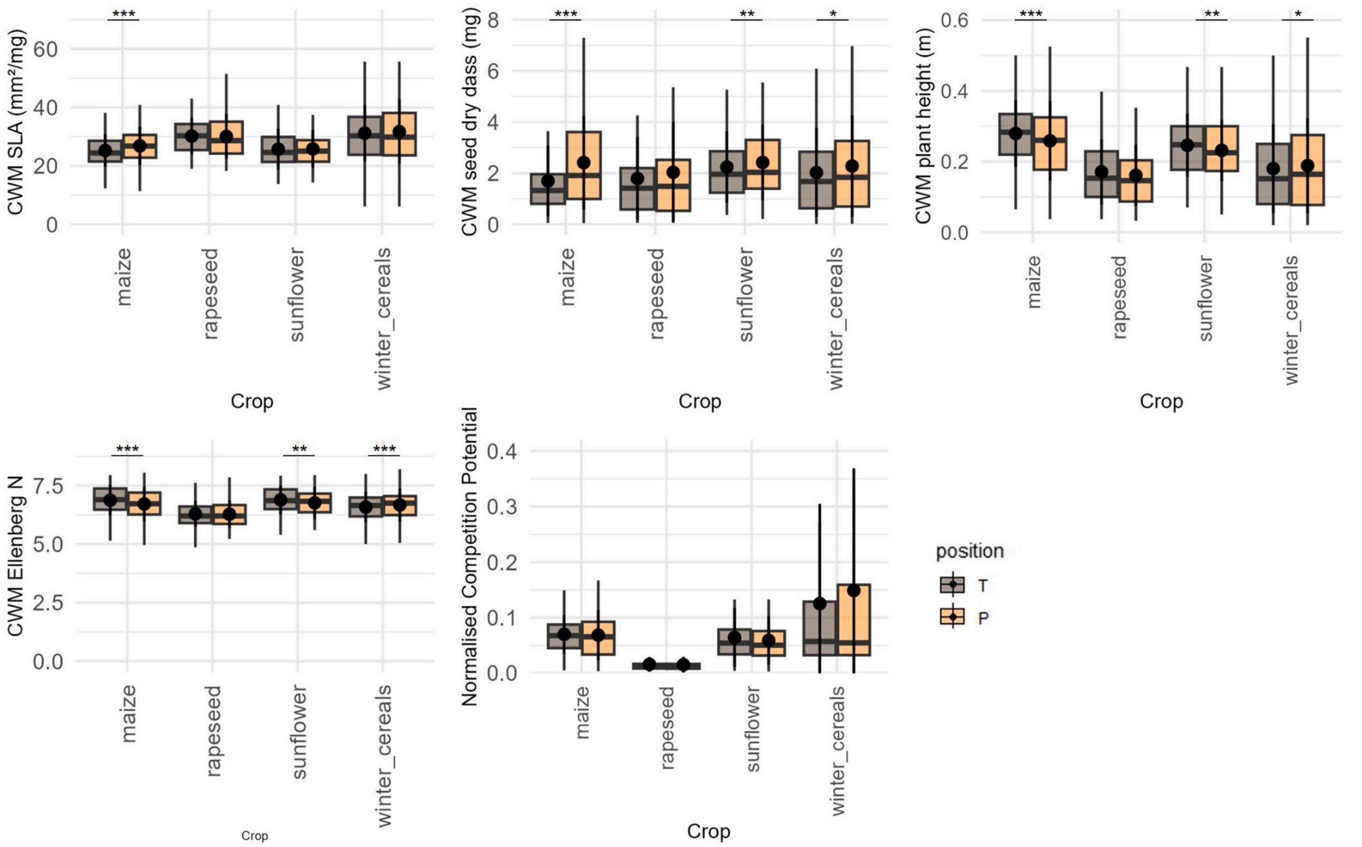

Fig. 4. Boxplots of competitive traits of weed communities between herbicide-sprayed area (P) and unsprayed area (T) in 4 annual crops. Each box represents the interquartile range, with the median shown as a bold horizontal line. The mean is indicated by the black dot. Error bars are the standard deviations. Stars above the boxplots indicate significant differences based on Paired Wilcoxon tests. Significance levels are indicated as follows: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Note that the scale on the y-axis varies between sub-figures. CWM: community weighted means; Ellenberg N: Ellenberg index for nutrients, SLA: specific leaf area.

allowing the establishment of a larger pool of species, including more stress-tolerant species adapted to nutrient-poor soil conditions (Metay et al., 2022). These conditions not only increase taxonomic diversity but also enhances functional floral diversity within weed communities, including a wider variety of flower colours, a greater inflorescence diversity, and an increased density of entomophilous and nectar-producing species. However, it's important to note that while our study focuses on the potential of weed communities to support pollination, it does not directly measure pollination services. Importantly, the surrounding landscape plays a crucial role in shaping pollinator communities, particularly the presence of semi-natural habitats and overall habitat heterogeneity (Carrié et al., 2017; Hopfenmüller et al., 2014; Rivers-Moore et al., 2020; Williams et al., 2010).

Differences in agricultural practices between perennial and annual systems also influence weed competitive traits. In annual crops, weed communities are predominantly composed of fast-growing, resource-acquisitive species with high SLA and Ellenberg N values. This is a result of ecological filtering in arable fields driven by high fertilisation, especially nitrogen (average 140 kg/ha) and intense disturbance (Bourgeois et al., 2019). In contrast, vineyard weed communities display lower SLA and Ellenberg N values, reflecting lower fertilisation levels (around 20–90 kg/ha) and the typical establishment of vineyards on hillside slopes with shallower, nutrient-poor soils (Metay et al., 2015).

4.2. *Chemical vs. mechanical weed control: divergent impacts on floral traits in annual and perennial system*

In this study, increasing herbicide frequency in annual cropping systems~~,~~ is negatively correlated with the abundance and diversity of floral resources. While the effects of mechanical disturbance such as grazing on floral traits has been well-documented—*e.g.*, reduced flower colour diversity with increased grazing in grasslands (Binkenstein et al., 2013; Goulnik et al., 2021)—the influence of herbicides on weed community floral traits remains largely unexplored. However, indirect evidence points to significant herbicide impacts. For example, Milberg et al. (2025) found a higher abundance of pollinator-friendly weeds in organic fields compared to conventional ones, while Rivers-Moore et al. (2023) demonstrated that increased herbicide application frequency reduced pollination success. Additionally, the comparison between unsprayed areas (T) and sprayed areas (P) across the four studied annual crops further supports these findings. Although floral trait diversity (Rao index) was only 1.1–1.3 times higher in unsprayed (T) than in sprayed (P) areas, the density of entomogamous and nectar-offering species was reduced in spayed areas (P) by factors of 6–9. In addition, flowering time ranges were less affected, suggesting that species with different floral traits and flowering periods persist, but in much lower numbers. These results indicate that herbicide use does not entirely homogenise weed communities but rather limits their abundance thereby limiting the quantity of nectar and pollen resources. Such scarcity is concerning, as it may create ecological traps (Battin, 2004; Ganser et al., 2019), especially if remaining flowers are contaminated by pesticide mixtures (Zioga et al., 2023).

In contrast, in vineyards, the effects of weed management practices on floral traits appear less direct than in annual systems. Increased inter-row tillage and mowing frequency were found to be positively correlated with inflorescence diversity. This may be due to the frequent combination of multiple weed control methods in vineyards, which increases habitat heterogeneity and creates diverse ecological niches, thereby

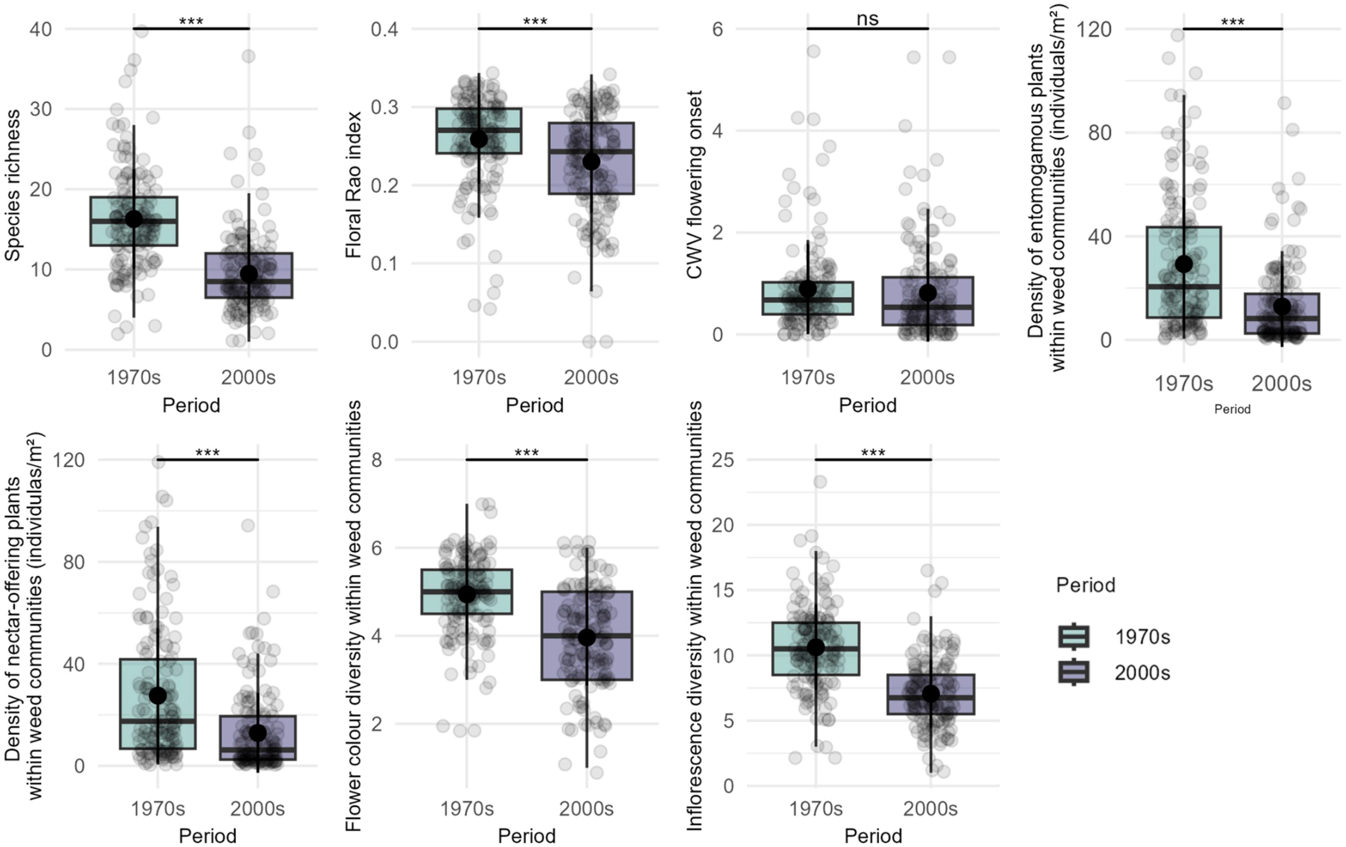

Fig. 5. Boxplots of floral traits of weed communities between the 1970s and the 2000s. Each box represents the interquartile range, with the median shown as a bold horizontal line. The mean is indicated by the black dot. Error bars are the standard deviations. Stars above the boxplots indicate significant differences based on Paired Wilcoxon tests, "ns" indicates that Paired Wilcoxon tests do not indicate significant differences. Significance levels are indicated as follows: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Note that the scale on the y-axis varies between sub-figures. CWV: community weighted variance.

promoting functional floral diversity (Fried et al., 2022). These findings suggest that the diversity of management strategies, rather than the intensity of any single practice, may be key to enhancing floral trait diversity in perennial systems. Overall, while herbicides tend to suppress floral resources in annual crops, alternative strategies such as tillage or mowing may, under certain conditions, support floral diversity in perennial cropping systems.

Regarding, competitive traits, in annual cropping systems, herbicide frequency was positively correlated with seed mass, supporting previous findings that larger-seeded species benefit from herbicide use through enhanced germination and colonisation (Kazakou et al., 2021). Through comparing unsprayed (T) and sprayed (P) areas, the effects of herbicides on competitive traits appear more variable than on floral traits. These effects seem to be context-dependent, likely shaped by crop-specific management practices and local species composition.

In contrast, in vineyards, herbicide frequency is negatively correlated with seed mass, suggesting a different environmental filtering effect. This may reflect differing interactions between herbicides and tillage practices between annual crops and vineyards. Indeed, herbicides in annual crops often accompany deep tillage, favouring large seeds (Armengot et al., 2016), while in vineyards, herbicides replace tillage, which tends to favour smaller seeds (Cordeau et al., 2020). Species composition may also play a role. *Erigeron sumatrensis*, common in vineyards and resistant to herbicides, produces numerous small seeds (Florentine et al., 2021), potentially contributing to the observed pattern.

Beside herbicides, other management practices and environmental factors were identified as key divers of the functional structure of weed communities. First, dicotyledonous crops (such as oilseed rape and sunflower) host a higher number of entomogamous weed species. This pattern may be explained by the unintentional selection of dicotyledonous weed species in dicotyledonous crops through herbicide use, in line with the principle of Vavilovian mimicry (Fried et al., 2019; McElroy, 2014).

Secondly, diverse crop rotation is a key practice for maintaining agroecosystem diversity. Varying disturbance timing promotes niche differentiation, enhancing both taxonomic and floral diversity, and potentially supporting a more diverse pollinator community (Fründ et al., 2010; Mahaut et al., 2019).

Finally, weed diversity and functional traits vary across spatial gradients, reflecting the indirect effects of climate, soil conditions, local agricultural practices, and landscapes. In annual crops, species richness, SLA, and the density of nectar-offering plants decline with increasing latitude, following biogeographical patterns where environmental factors such as temperature and climatic variability constrain plant diversity and productivity (Hulshof et al., 2013; Lyons and Willig, 2002; Swenson et al., 2012). In contrast, in vineyards, species richness increases with latitude, likely reflecting the influence of local management practices, particularly soil maintenance strategies in response to water stress in southern regions (Romero et al., 2022). Additionally, Ellenberg N scores increase with latitude in vineyards, indicating underlying gradients in soil fertility (Romero et al., 2022). Finally, longitudinal gradients reflect the east–west shift in agricultural specialisation in France (Rey, 1987). Landscape structure and dominant crop types, shaped by regional farming practices, influence weed community composition at the landscape scale (Petit et al., 2016).

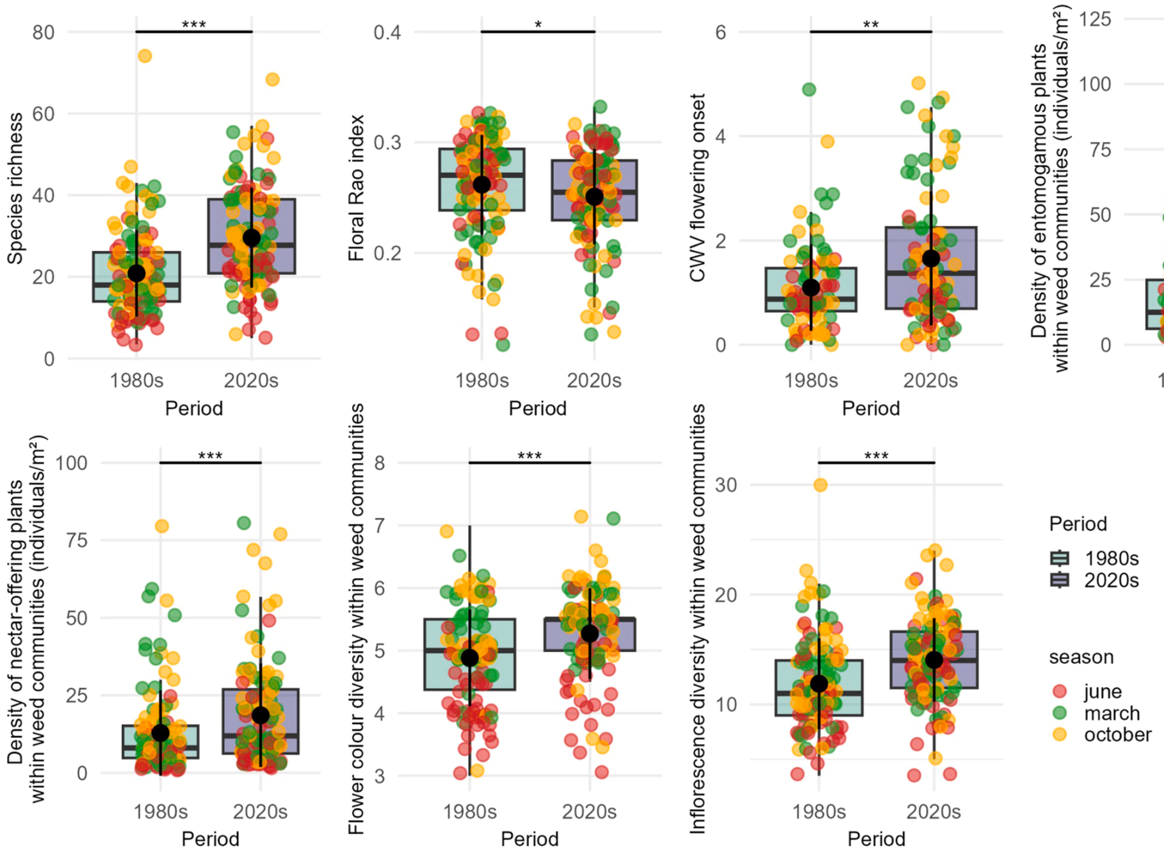

Fig. 6. Boxplots of floral traits of weed communities between the 1980s and the 2020 s. Each box represents the interquartile range, with the median shown as a bold horizontal line. The mean is indicated by the black dot. Error bars are the standard deviations. Points are colour-coded by the season of the botanical survey. Stars above the boxplots indicate significant differences based on Paired Wilcoxon tests, "ns" indicates that Paired Wilcoxon tests do not indicate significant differences. Significance levels are indicated as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Note that the scale on the y-axis varies between sub-figures. CWV: community weighted variance.

4.3. *Contrasting temporal shifts in floral and competitive traits between annual crops and vineyards*

Contrasting trajectories in weed floral responses between annual crops and vineyards over time were observed. In annual crops, from the 1970s to the 2000s, there was a significant decline in weed species richness, floral functional diversity (including the Floral Rao index, flower colour and inflorescence diversity). Specifically, weed species richness decreased from 16 species in the 1970s to 10 species in the 2000s. Nectar offering weed density was twice as high in the 1970s compared to the 2000s, indicating a substantial loss of resources for pollinators. These trends are consistent with national-scale findings in the UK, where Baude et al. (2016) reported a decline in nectar source diversity—both in floral morphology and nectar provision—between 1978 and 1990. This loss of weed diversity and floral functional traits mirrors the broader decline in pollinator populations, exacerbated by the increasing use of pesticides (Nicholson et al., 2023). Goulson et al. (2015) underscore the importance of incorporating diverse floral resources into agricultural landscapes to sustain bee populations, highlighting their role in mitigating pollinator declines.

In contrast, vineyards in Languedoc showed a significant improvement in weed floral traits from the 1980s to the 2020 s. Weed species richness increased from 20 species in the 1980s to 30 species in the 2020 s, reflecting a greater plant diversity. Additionally, the density of nectar-offering weeds increased by 45 % compared to the 1970s, indicating a rise in available floral resources for pollinators. This positive trajectory likely reflects a shift toward greater tolerance of weeds in inter-rows since the early 2000s. The improvements in floral resource provisioning, as well as in flower colour and inflorescence diversity, suggest potential benefits for pollinators within regional vineyard landscapes. However, despite this rise in flower colour and inflorescence diversity, the decline in the Floral Rao index suggests a loss of ecological specialisation, which could have negatively impacted more specialised plant-pollinator networks.

No consistent trends were observed across competitive traits in neither annual crops nor vineyards. In annual crops, Ellenberg N increased between the 1970s and the 2000s, likely reflecting the intensification of fertiliser use in French arable systems over the past decades (Agreste, 2007). Fried et al. (2009) also reported this increase in Ellenberg N and suggested that nitrogen availability exerts a strong long-term selective pressure in arable fields. Additionally, the significantly lower CWM of seed dry mass in the 2000s may also be linked to increased fertilisation, as nutrient-rich environments reduce resource limitations, allowing both large-seeded species that rely on their internal reserves and smaller-seeded species to establish and grow.

These shifts suggest increasing weed competitiveness under intensified fertilisation, consistent with findings of Storkey et al. (2021), who demonstrated that yield loss increased with higher nitrogen addition over time, reflecting a shift towards greater weed competitiveness. However, weed competition potential doesn't show significant changes between the two periods, likely due to the use of average trait values per species for the computation, which can mask significant intraspecific variability, especially for traits such as plant height (Siefert et al., 2015). Including more in situ-measured traits to assess weed competitiveness could enhance the accuracy of this indicator in reflecting yield loss due to weed competition.

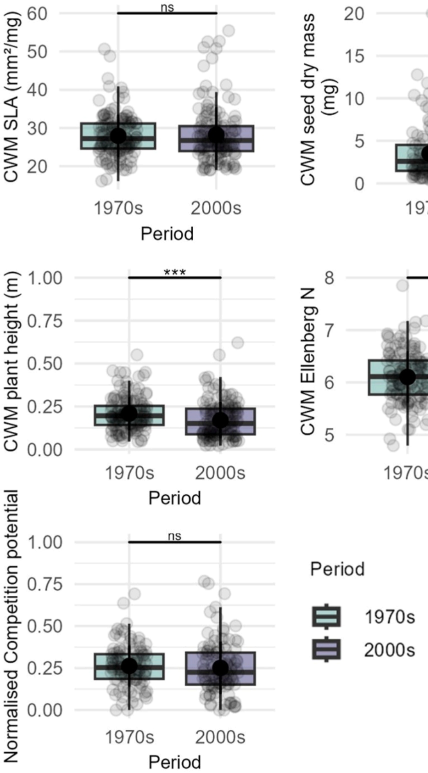

Fig. 7. Boxplots of competitive traits of weed communities between the 1970s and the 2000s. Each box represents the interquartile range, with the median shown as a bold horizontal line. The mean is indicated by the black dot. Error bars are the standard deviations. Stars above the boxplots indicate significant differences based on Paired Wilcoxon tests, “ns” indicates that Paired Wilcoxon tests do not indicate significant differences. Significance levels are indicated as follows: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. Note that the scale on the y-axis varies between sub-figures. CWM: community weighted means; Ellenberg N: Ellenberg index for nutrients, SLA: specific leaf area.

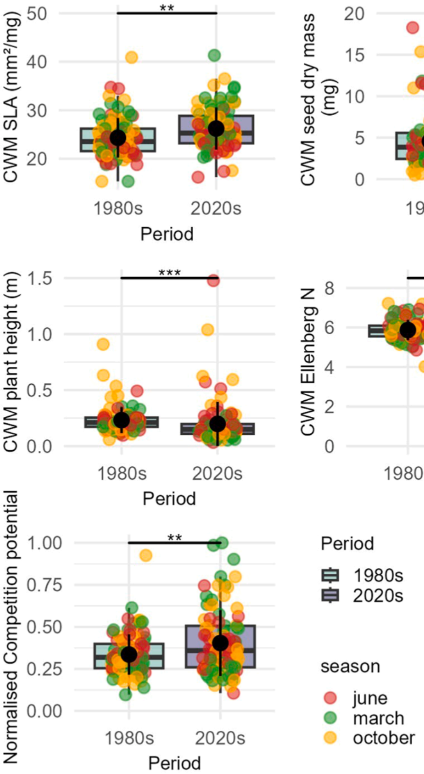

Fig. 8. Boxplots of competitive traits of weed communities between the 1980s and the 2020 s in vineyards. Each box represents the interquartile range, with the median shown as a bold horizontal line. The mean is indicated by the black dot. Error bars are the standard deviations. Points are colour-coded by the season of the botanical survey. Stars above the boxplots indicate significant differences based on Paired Wilcoxon tests, “ns” indicates that Paired Wilcoxon tests do not indicate significant differences. Significance levels are indicated as follows: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. Note that the scale on the y-axis varies between sub-figures. CWM: community weighted means; Ellenberg N: Ellenberg index for nutrients, SLA: specific leaf area.

In contrast, in vineyards, an increase in competition potential and SLA was recorded, a pattern also observed by Bopp et al. (2025), likely due to shade effects in the denser weed communities of the 2020 s (Vendramini et al., 2002). The increase in Ellenberg N between the 1980s and 2020 s was unexpected, as Mediterranean vineyards typically receive minimal fertilisation (Metay et al., 2015), with level decreasing in recent decades (Verdenal et al., 2021).

Besides, in vineyards, an increase in both pollinator-friendly traits and competition potential within weed communities between the 1980s and the 2020 s was observed. While this may imply a trade-off between pollination services and competition, interpretation requires caution. The assessment of weed competition in vineyards stems from an annual crop perspective, which may be less relevant in vineyards. Indeed, unlike in annual crops, in vineyards, controlled competition by weeds, is used to manage vine vigour and improve grape quality (Van Leeuwen et al., 2009). Thus, higher weed competition potential may represent a desirable agronomic outcome in vineyards. It highlights the need for system-specific interpretations in evaluating weed competition, considering both its ecological and agronomic implications.

5. Conclusions and perspectives

To conclude, this study only assesses the potential of weeds to support pollination services. The lack of quantitative weed floral trait data and the absence of direct weed-pollinator interaction data remain limitations. Moreover, understanding the role of landscape-scale weed management is crucial for fully capturing its impact on pollination services (Petit et al., 2011). Beyond pollination, these findings call for the need to consider weeds through their multifunctionality, encompassing competition, soil quality, pollination, and natural regulation (Beaumelle et al., 2023). The balance between these functions is essential for sustainable agroecosystem management. Importantly, our results suggest that while weeds can indeed act as valuable floral resources for pollinators, their disservices—such as competition with crops for light, water, and nutrients—must be assessed in context. For instance, in vineyards, controlled weed management (e.g., mowing or reduced tillage) can preserve floral diversity without severely impacting yield. In contrast, in annual cropping systems, intensive herbicide use may reduce disservices but also eliminates key floral resources.

Therefore, the trade-off between services and disservices is not binary, but depends on crop type, management intensity, and landscape context. Strategic integration of weeds into agricultural planning can support the design of more resilient and sustainable agroecosystems, capable of sustaining both biodiversity and production.

Declaration of Competing Interest

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

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Appendix

Table A1
Inflorescence type from BiolFlor database (Kühn, 2004)

Inflorescence type
spike of spikelets
spike of capitula
spike of three-flowered cymes
simple spikeépi simple
cone
compound capitula
simple capitula
corymb
corymb of capitulacorymbe de capitules
cyathe
dichasial cyme
biscorpioid cyme
capitulum-like cyme
cyme of spikes
cyme of capitula
cyme of glomerules
cyme of umbels
polychasial cyme
helicoid monochasial cyme
scorpioid monochasial cyme
solitary lateral flower
solitary terminal flower
glomerules
spike-like glomerules
compound umbel
simple umbel
simple umbel of spikes
panicle of spikelets
spike-like panicle
capitulum-like raceme
raceme of spikes
raceme of capitula
raceme of dichasial cyme
raceme of helicoid monochasial cyme
raceme of scorpioid monochasial cyme
compound raceme
raceme of umbels
simple raceme
spadix

Table A2
Functional floral indicators calculated for weed communities with their corresponding formulas and units

Floral Traits	Formula	Units
Density of Entomophilous plants within weed communities (DE)	$DE_i = \sum_{j=0}^{n} d_{ij} \times d_j$: density of the species *j* (individuals/m^2) *i*: community index *j*: entomogamous plant index *n*: total number of entomogamous in the community	Individuals/ m^2
Density of nectar-offering plants within weed communities (DN)	$DN_i = \sum_{j=0}^{n} \mathrm{d}_{ij} \times d_j$: density of the species *j* (individuals/m^2) *i*: community index *j*: nectar-offering plant index *n*: total number of nectar-offering plant in the community	Individuals/ m^2
CWV Flowering Onset	$CWV_j = \sum_{j=0}^{n} (trait_i - CWM_j)^2 \times a_{ij} \times a_i$: relative abundance of the species *i* of the community *j* $trait_i$: trait value of the specie *i* CWM_j: community weighted mean of the flowering onset for the community *j* *n*: total number of entomogamous in the community	/

(*continued on next page*)

Table A2 (*continued*)

Floral Traits	Formula	Units
Floral Rao Index	$\mathit{Floral\ Rao\ Index}_i = \sum_{i=1}^{S}\sum_{i=1}^{S} d_i \times d_j \times fd_{ij} \times d_j$: density of the species i (individuals/m^2) d_j: density of the species j (individuals/m^2) fd_{ij}: functional distance for the following traits: Flower colour, Inflorescence type, Flowering Onset, Nectar presence, Nectar Amount, Symmetry S: total number of species in the community	/

Table A3
Coefficient of synchrony (CO) as described in Yvoz et al., (2021)

Case	Value of the coefficient of synchrony
The weed flowering period starts the same month or one month earlier than the crop flowering onset	1
The weed flowering starts two months earlier than the crop flowering onset	0.7
The weed ends flowering one month later than the crop flowering onset	0.7
The weed flowering starts three months (or more) earlier than the crop flowering onset	0.3
The weed ends flowering two months later than the crop flowering onset	0.3
The weed ends flowering three months (or more) later than the crop flowering onset	0.1

Table A4

Functional competitive traits calculated for weed communities with their corresponding formulas and units

Competitive Traits		**Formula**	**Units**
CWM	SLA Seed dry mass plant height Ellenberg N	$CWM_j = \sum_{j=0}^{n} trait_i * a_{ij}$	mm^2/mg mg m /
		a_i: relative abundance of the species i of the community j $trait_i$: trait value of the specie i n: total number of entomogamous in the community	
Competition potential for annual crop		$CPa_j = \sum_{i=1}^{n} \frac{SLA_i}{SLA_{crop}} \times \frac{PH_i}{PH_{crop}} \times \frac{EN_i}{EN_{crop}} \times CO_i \times a_{ij}$	/
		SLA: SLA value (mm^2/mg) PH: Plant Height value (m) EN: Ellenberg N value CO: Coefficient of synchrony value a_{ij}: relative abundance of the specie i in the community j j: community index i: species index n: total number of species in the community $crop$: crop in which the community is surveyed	
Competition potential for perennial crop		$CPp_j = \sum_{i=1}^{n} \frac{SLA_i}{SLA_{vine}} \times \frac{EN_i}{EN_{vine}} \times FO_i \times a_{ij}$	/
		SLA: SLA value (mm^2/mg) EN: Ellenberg N value FO: Flowering onset value a_{ij}: relative abundance of the specie i in the community j j j: community index i: species index n: total number of species in the community	

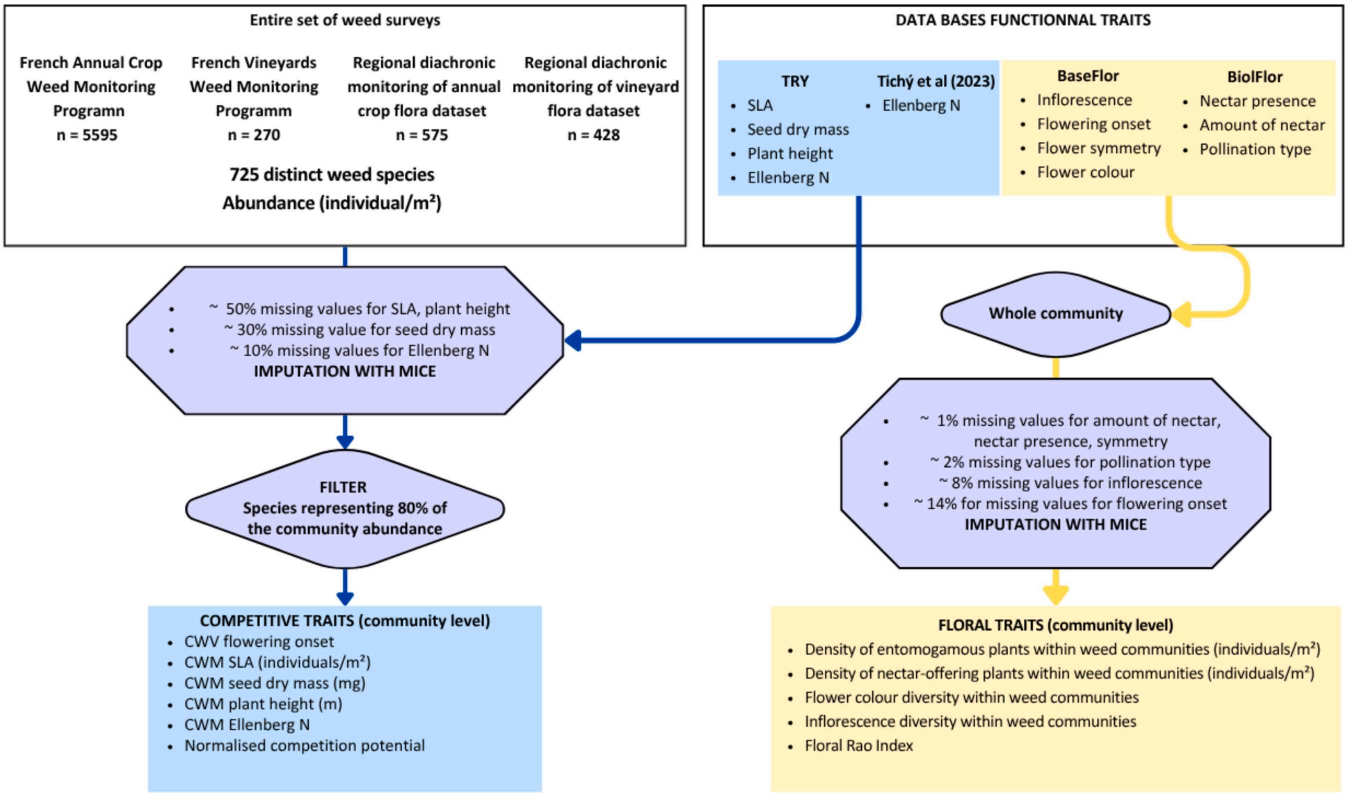

Figure A1. Pipeline of data collection

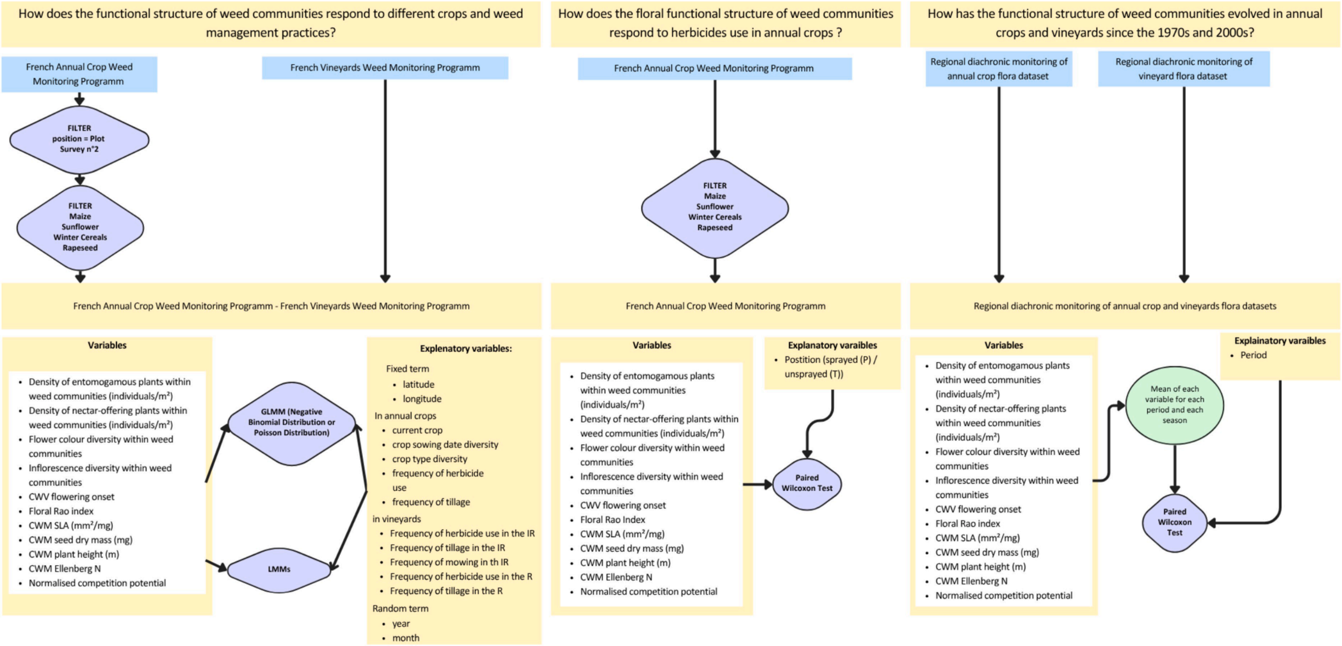

Figure A2. Pipeline of data analysis

Data availability

Data will be made available on request.

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