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Plant Species Better Adapted to Climate Change Need Agricultural Extensification to Persist

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ABSTRACT

Agricultural intensification and climate change have led to well-known vegetation shifts in agricultural landscapes. However, concomitant plant functional changes in agroecosystems, especially at large scales, have been seldom characterised. Here, we used a standardised yearly monitoring of > 400 agricultural field margins in France to assess the temporal response of vegetation diversity and functional traits to variations in climate and intensity of agricultural practices (herbicides, fertilisation and mowing) between 2013 and 2021. We observed clear temporal trends of increasing warming and aridity, but trends towards agricultural extensification were weak or nonsignificant. Our results showed functional changes in plant communities over time, driven mostly by climate change and suggested selective forces opposing climate change to agricultural intensification. This translated as a temporal decline of competitive and ruderal species in favour of stress-tolerant species, putting plant communities in agroecosystems in a difficult position to escape both climate and agricultural pressures at the same time.

1 | Introduction

Since the 1950s, agricultural intensification has been identified as one of the major causes of biodiversity decline (Emmerson et al. 2016), while climate change has caused notable changes in a wide range of taxa and habitats (Lovejoy 2006). However, since these two drivers operate simultaneously, disentangling their relative importance on community trajectories is challenging (Oliver and Morecroft 2014). The main changes linked to agricultural intensification in Europe (notably in terms of intensity in pesticide use and fertilisation) occurred between the 1950s and the 2000s and have already modified plant communities in agro-ecosystems (Lososová et al. 2004). For example, a meta-analysis covering the period from 1939 to 2011 in Europe showed that weed species richness declined up to the 1980s but has stabilised or even increased since then (Richner et al. 2015). More recently, the implementation of regulatory strategies aimed at curbing the utilisation of pesticides and nitrogen has not delivered a tangible decline of these chemical inputs in agricultural fields (Guichard et al. 2017; Poisvert, Curie, and Moatar 2017). Conversely, there has been an acceleration of climate change in recent years, with observable shifts in vegetation within a relatively short time frame (Martin et al. 2019). Early agricultural intensification, recent agricultural extensification efforts and accelerating climate change may interact as drivers of plant community changes in ways that have not yet been characterised at large scales.

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A taxonomic approach alone may not be enough to tease out the influences of agricultural and climatic drivers on vegetation. The functional approach offers a more mechanistic and hypothesis-driven method for two reasons. First, some specific plant traits relate to climate, resource levels and common perturbation regimes in agricultural systems (Garnier and Navas 2012). Agroecosystems are known for their resource (fertilisation) and disturbance (herbicides, tillage and mowing) gradients (Gaba et al. 2014; MacLaren et al. 2020), making the functional approach particularly relevant to understand drivers behind plant community structure. Second, trade-offs between traits of plants with different life strategies have been largely documented. These trade-offs are primarily defined at the physiological level within species and arise from limitations in resource availability (Reich 2014). They imply that achieving a benefit in one function of an individual's performance comes at the expense of another. From these individual-level constraints emerges a functional differentiation among species, evidencing combinations of traits that are more common than others, and thereby delimiting what are known as functional strategies (Díaz et al. 2016; Wright et al. 2004). For example, a species may invest more in its survival and longevity at the cost of its reproductive fitness, following a slow or conservative strategy (as opposed to a fast or acquisitive strategy). This fast–slow plant economics spectrum extends to leaves, stems and roots and is evident not only within species but also at the community level (Reich 2014). The acquisitive strategy parallels the ruderal strategy of weeds (low height and seed mass, long and early flowering, high specific leaf area, SLA), which are better adapted to agricultural disturbances, such as tillage, herbicides and mowing (Grime 2006; Fried et al. 2022). As a result, ruderal species increased their frequency between the 1970s and 2000s in French wheat fields, likely due to their ability to escape recurrent disturbances, such as herbicide applications (Fried, Kazakou, and Gaba 2012). Regarding climate, mean thermal preference and phenology of plant communities can vary over time in response to temperature changes, even over relatively short periods (Bellard et al. 2012; Martin et al. 2019). These temporal variations in functional traits reveal patterns that cannot be assessed solely through a taxonomic lens, highlighting the necessity of integrating functional traits to understand climate–agriculture interactions.

Grime (1977) explicitly recognised the existence of trait correlations between growth, lifespan, flower phenology, leaf, shoot and seed traits. These correlations form the basis of his CSR framework, which defines three plant ecological strategies (competitiveness, stress-tolerance and ruderality) along two axes of variation (resource and disturbance). Competitive species capitalise on resources for rapid growth, to outcompete other species in low-disturbed productive systems. Stress-tolerant species have slow growth, late reproduction and long lifespan, allowing them to survive in less productive and less disturbed settings. Finally, ruderal species favour fast growth, early reproduction and high dispersal ability to overcome frequent disturbances in productive habitats (Grime 1988). This framework has been widely documented in the literature (Fridley et al. 2023; Pierce et al. 2017) and has proven useful in understanding plant community dynamics in agroecosystems (Fried et al. 2022). Despite this, it has not been used for studying the interactions between agricultural and climate factors over time and the recent changes in plant communities in agroecosystems at the macroecological scale.

In this study, we aimed to decipher how interannual temporal variations and temporal trends in climate (temperature and soil moisture) and agricultural practices (frequency of herbicide use, margin mowing and nitrogen dose in fertilisers) in France structure species richness, above-ground trait composition, and ecological strategies of field margin plant communities. We studied the herbaceous field margin, that is, the uncultivated vegetated area located between the cultivated strip and the adjacent habitat. While arable plant communities are more directly affected by agricultural practices, their low diversity makes it difficult to detect functional responses, especially to climate change. In contrast, field margin plant communities, situated at the interface of field crops, experience weaker selective pressures and greater diversity, but are still influenced by management practices (Aavik et al. 2008). This makes field margins an excellent model for tracking both changes in climate and agricultural practices. Using a standardised national monitoring effort spanning 9 years (2013–2021) in > 400 agricultural field margins covering continental France, our study stands as one of the first to investigate the temporal trends in agricultural practices and climate, and explore the response of species richness, trait composition and ecological strategies to these trends at such an extensive spatial scale. Furthermore, we explored the connection between Grime's CSR strategies, climate and farming practices. Considering that these strategies are linked to resource and disturbance levels, we anticipated them to respond to climate (temperature and soil moisture) and agricultural practices (disturbance through margin mowing and herbicides, and resource provision through fertilisation). We wanted to answer two key questions: (i) Are there temporal trends in species richness, trait composition, ecological strategies, climatic and agricultural factors? And (ii) how have plant communities responded to changes in climate and agricultural practices over time?

2 | Materials and Methods

2.1 | Vegetation Surveys

We used vegetation data from the 500-ENI network, which is funded by the French Ministry of Agriculture (see details in Andrade et al. 2021) and monitored 555 agricultural field margins across continental France between 2013 and 2021 (with some sites added and others excluded over time, resulting in 429 to 481 sites by year) (Figure 1). These survey sites represented three main crop types (Appendix S1A, Figure S1): annual crops (with winter wheat or maize as the main crop production in the rotation), market gardening crops (mainly lettuce) and vineyards. The proportion of sites under organic farming was roughly 20%. On these organic sites, synthetic pesticides were banned, but other pesticides (typically from natural sources) were used, and agricultural practices cover a wide range of fertiliser intensities. Within each survey site, plant species were identified in ten 1 m^2 quadrats along the field margin (Appendix S1A, Figure S2). Presence–absence of each species was recorded for each quadrat, which provided a frequency of occurrence from 0 to 10 in each field margin, used here as an index of relative abundance. Surveys were

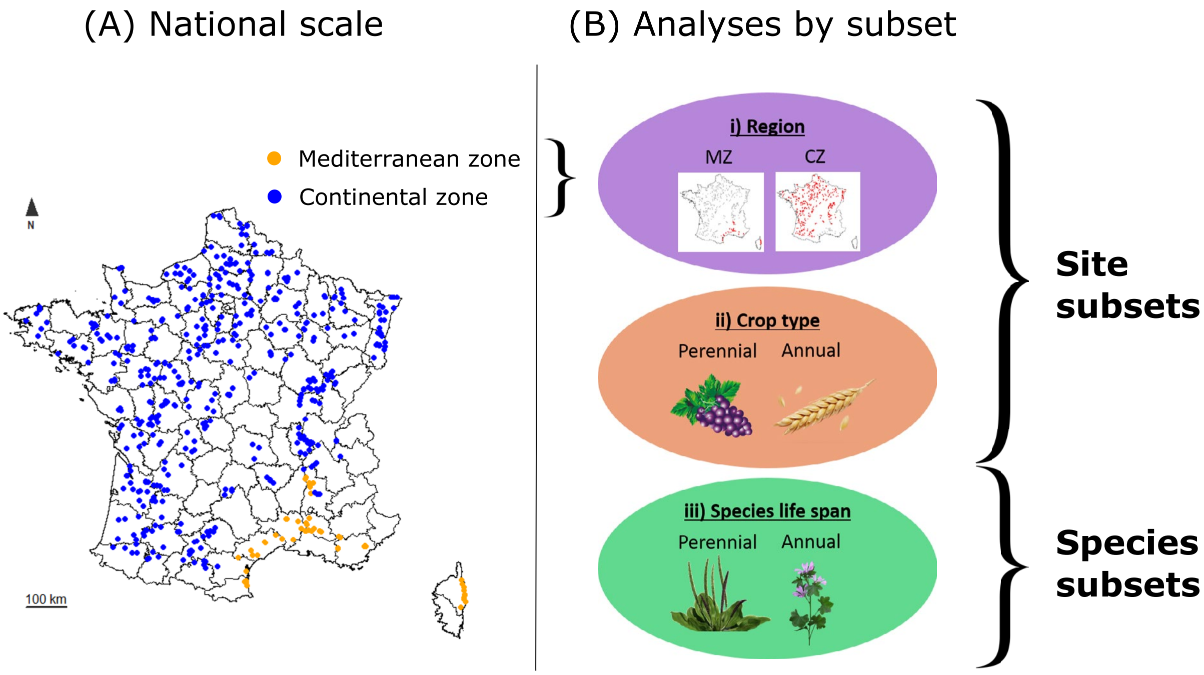


FIGURE 1 | (A) Distribution map of the 555 field margins monitored at least 1 year between 2013 and 2021 in France. The black lines represent the limits of French departments. Orange: Sites in the Mediterranean zone (MZ) ($n = 57$), blue: Sites in the Continental zone (CZ) ($n = 498$). The contours of the MZ were derived from the Mediterranean zone and Corsica as defined in the VégétalLocal map (Office français de la biodiversité 2021); the rest of France will be referred as the CZ. (B) Subsets of data used in additional analyses: (i) the regional scale splits the MZ from the CZ; (ii) annual crops included rotations based on wheat, maize and market gardening crops ($n = 450$); perennial crops only included vineyards ($n = 105$); (iii) annual plants ($n = 61$) opposed to perennials ($n = 79$).

performed once per year at peak flowering (between the end of April and the beginning of August, depending on the region). At the national scale, this represented 4172 observations (year × site), leading to the identification of 852 taxa. Because observers changed among sites and over time (312 observers in total, each observer following on average 5 distinct sites during 4 years) and did not have the same level of expertise, we constrained our analyses to a subset of 142 focal species (Andrade et al. 2021), which are expected to be known by all the observers (and thus removing 11% of the total abundances).

2.2 | Climatic and Agricultural Variables

We gathered two types of explanatory variables: The first came directly from the 500-ENI network and reflects agricultural practices assessed directly on the monitoring sites (fertilisation, herbicides, field margin mowing); the second one included meteorological data (temperature, soil moisture) from an external database (see below).

Agricultural practices were reported yearly from interviews of farmers in a standardised online database. Data collected relate to nitrogen dose in fertilisers (mean ± standard deviation: 101 ± 97 kg/ha per year), number of herbicide treatments (1.87 ± 2.42 treatments per year) and number of field margin management events (mowing of vegetation, 1.20 ± 0.89 events per year). Daily temperature and soil moisture were extracted from the SAFRAN climate model of Météo France, with a resolution of 8 km (Le Moigne 2002). Meteorological data were averaged over a one-year window prior to each floristic observation, while agricultural data were summed over the same period (Appendix S1C, Table S1C). We selected predictor variables that were weakly correlated (Spearman correlation < 0.65, Appendix S1B) and have previously been shown to influence plant communities (Table 1, see Appendix S1C for the choice of variables).

2.3 | Plant Functional Traits

We extracted from external databases five functional traits (specific leaf area, maximum plant height, seed mass, flowering onset and duration) and six species-level indices of ecological requirements (i.e., Ellenberg values for light, temperature, continentality, moisture, soil pH and nutrients; Ellenberg 1974), assumed to respond to agricultural or climatic factors (Table 1, Appendix S1B,C). These traits vary along resource and disturbance gradients, and Ellenberg values are indicators of ecological optima, reflecting variations in climate and practices affecting soil pH or nutrients. Functional traits were missing for four species, two of which (*Himantoglossum robertianum* and *Sedum sediforme*) could be imputed from an average over other species of the same genus (respectively, from one and two species for *H. robertianum* and *S. sediforme*). The remaining two species (*Brachypodium retusum* and *Gladiolus italicus*) were removed from the analysis (representing 0.01% of the total abundances).

To characterise plant communities, we calculated species richness, community-weighted means (CWM) and community-weighted variances (CWV) of traits and ecological requirements for observations with at least four species (59 out of 4172

TABLE 1 | List of explanatory factors (blue), functional traits and ecological requirements (green) and response variables (red) with their abbreviations and units. We have illustrated by arrows the expected link of each factor and trait to the agricultural resource (fertilisation) and disturbance gradient (herbicides and margin mowing), and to the climatic gradient (drought and increasing temperature). We also used arrows to illustrate the expected direction of variation of these gradients within a year (i.e., climatic and agricultural changes according to the date of observation). Horizontal arrows indicate contradictory findings in the literature. See Appendix S1C for the references and more detailed calculation of each factor.

Factors **Functional traits** **Response variables**	**Abbreviations**	**Units**	**Hypothesis of response to the temporal agricultural gradient: Disturbance (Di) and Resource (R)**	**Hypothesis of response to the temporal climatic gradient: Drought (Dr) and Temperature (T)**
Temperature	TEMP	°C		
Soil moisture	MOI	%		
Dose of nitrogen (fertilisation)	N_DOSE	kg/ha		
Number of herbicide treatments	HERB			
Number of field margin mowing events	MAN			
Date of observation	DATE	Julian days	↘ ↘	↗ ↗
Specific leaf area	SLA	$m^2 kg^{-1}$	↗ ↗	↘ →?
Maximum plant height	HEIGHT	m	↘ ↗	→? →?
Seed mass	SM	g	↘ ↗	↗ ↗
Flowering onset	FLOW_ON	months	↘	↗ ↗
Flowering duration	FLOW_DUR	Months	↗	↘ ↘
Ellenberg indicator for light, temperature, continentality, moisture, pH and nutrients	EIV_L, EIV_T, EIV_K, EIV_F, EIV_R, EIV_N		EIV_N: ↗	EIV_F: ↘ EIV_T: ↗ ↗
Species richness	S		→? →?	→? →?
Trait composition	See abbreviations above for each trait preceded by "CWM_"			

(Continues)

TABLE 1 | (Continued)

Factors **Functional traits** **Response variables**	**Abbreviations**	**Units**	**Hypothesis of response to the temporal agricultural gradient: Disturbance (Di) and Resource (R)**	**Hypothesis of response to the temporal climatic gradient: Drought (Dr) and Temperature (T)**
Trait divergence	See abbreviations above for each trait preceded by “CWV_”			
PCA traits—axis 1	PCA_1			
PCA traits—axis 2	PCA_2			
Scores of competitive, stress-tolerant and ruderal strategies	CWM_C, CWM_S, CWM_R	%	CWM_C: ↘ ↗ CWM_S: ↘ ↘ CWM_R: ↗ ↗	CWM_C: ↘ CWM_S: ↗

observations were excluded). The computation was performed using the R v.4.0.0 package *FD* with the function dbFD, with the following formulas:

$$\mathrm{CWM} = \sum_{i=0}^{n} p_i \times trait_i \qquad (1)$$

$$\mathrm{CWV} = \sum_{i=0}^{n} p_i \times \left(trait_i - CWM\right)^2 \qquad (2)$$

where p_i is the relative abundance, $trait_i$ is the value of trait for species i, and n is the total number of species. To correct for correlation between CWV and species richness, we used a null model approach, shuffling the abundances in the species matrix for species of the species pool, while keeping the species × trait matrix unchanged (Bopp et al. 2022). The species pool was defined by site, allowing us to investigate temporal variations. This procedure keeps trait correlations, species richness and total abundance in a site unchanged, while dissociating abundances from trait values (Bernard-Verdier et al. 2012). To quantify the difference between observed and null CWV, we computed effect sizes (Appendix S1D). A positive effect size denotes a divergence in trait values within the community (convergence for negative effect size). These effect sizes (and not the raw CWV) were used in our analyses and referred to as CWV in the subsequent sections. We performed a normed PCA on the CWM of traits to classify each community based on its average trait combination or ecological strategy.

2.4 | Plant Functional Strategies

According to Grime (1988), stress (i.e., shortage of resources such as nutrients, water and light) and disturbance (i.e., partial or total destruction of plant biomass) determine three main plant strategies representing combinations of traits that are viable under conditions of low disturbance and high resources (competitor, C), low disturbance and low resources (stress-tolerant, S) or high disturbance and high resources (ruderal, R). Originally developed to classify individual plant species into strategies, Grime's theory can be useful to interpret functional changes in plant communities, especially in the context of global changes where vegetation is subject to harsher climatic conditions (more droughts) and various levels of agricultural disturbances.

To assess these strategies, we extracted the CSR scores for 119 out of 142 focal species from Pierce et al. (2017). CWM of CSR scores were computed by observation and were added to the PCA on the CWM of traits as supplementary variables. They were plotted on a CSR triangle to illustrate temporal trends in plant strategies.

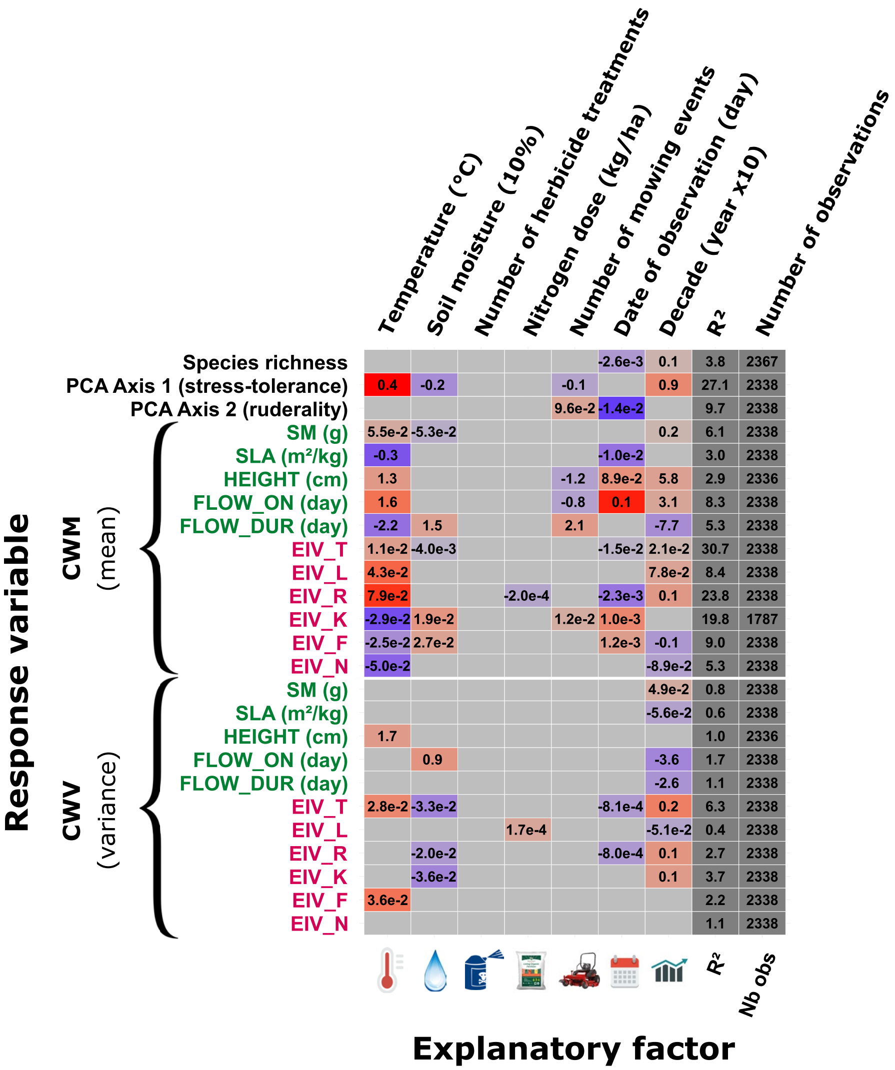
2.5 | Temporal Analyses of Plant Communities

The general framework of analyses is presented in Appendix S1E. First, we checked whether there was a temporal trend in the raw variables, and then used climate and agricultural practices as predictors for the different response variables. In all cases, we used generalised additive mixed models (GAMM) to account for repeated measures at a site, with a Gaussian distribution in most cases (but see Appendix S1F, Table S2F), and site identity as a random effect. Observer bias was accounted for by including the observer identity as a random term nested within sites. For each response variable (species richness, CWM, CWV and CSR strategies) and explanatory factor (temperature, soil moisture, nitrogen dose, herbicides and margin mowing), we built a first model with the year as a linear fixed effect. Then, a second model was built for each response variable, where climate, agricultural practices and observation date were linear explanatory factors. A first-order temporal autocorrelation structure within sites was included (Box et al. 2015). We removed observations with missing values in climatic and agricultural factors (1805 out of 4172 observations), and a few observations that distorted trait distributions (Appendix S1F), resulting in varying observation numbers across models. We repeated this analysis on subsets of data (Figure 1). As this data set includes the Mediterranean flora, which has been shown to respond more strongly to some agricultural filters (Poinas et al. 2023), we included analyses separating Mediterranean (MZ) from Continental zones (CZ). We also separated vineyards from annual crops, because vineyards include very different management practices and no crop rotation (Metay et al. 2022). Finally, we analysed annual plant species separately, as they may respond more rapidly to environmental changes (Martin et al. 2019; Fitter and Fitter 2002). For all analyses, we chose a *p* value threshold of 0.01 to focus on the effects for which our confidence level was highest.

3 | Results

3.1 | Temporal Trends in Climate, Agricultural Practices and Plant Communities

Temperatures have significantly increased by an average of 1.2°C over a decade (0.7°C in the MZ), while soil moisture has steadily declined (−14.1% by decade) (Figure 3A–C, and Appendix S1G). The MZ experienced a slower decline in soil moisture due to



Response variable		Temperature (°C)	Soil moisture (10%)	Number of herbicide treatments	Nitrogen dose (kg/ha)	Number of mowing events	Date of observation (day)	Decade (year x10)	R²	Number of observations
	Species richness						-2.6e-3	0.1	3.8	2367
	PCA Axis 1 (stress-tolerance)	0.4	-0.2			-0.1		0.9	27.1	2338
	PCA Axis 2 (ruderality)					9.6e-2	-1.4e-2		9.7	2338
CWM (mean)	SM (g)	5.5e-2	-5.3e-2					0.2	6.1	2338
	SLA (m²/kg)	-0.3					-1.0e-2		3.0	2338
	HEIGHT (cm)	1.3				-1.2	8.9e-2	5.8	2.9	2336
	FLOW_ON (day)	1.6				-0.8	0.1	3.1	8.3	2338
	FLOW_DUR (day)	-2.2	1.5			2.1		-7.7	5.3	2338
	EIV_T	1.1e-2	-4.0e-3				-1.5e-2	2.1e-2	30.7	2338
	EIV_L	4.3e-2						7.8e-2	8.4	2338
	EIV_R	7.9e-2			-2.0e-4		-2.3e-3	0.1	23.8	2338
	EIV_K	-2.9e-2	1.9e-2			1.2e-2	1.0e-3		19.8	1787
	EIV_F	-2.5e-2	2.7e-2				1.2e-3	-0.1	9.0	2338
	EIV_N	-5.0e-2						-8.9e-2	5.3	2338
CWV (variance)	SM (g)							4.9e-2	0.8	2338
	SLA (m²/kg)							-5.6e-2	0.6	2338
	HEIGHT (cm)	1.7							1.0	2336
	FLOW_ON (day)		0.9					-3.6	1.7	2338
	FLOW_DUR (day)							-2.6	1.1	2338
	EIV_T	2.8e-2	-3.3e-2				-8.1e-4	0.2	6.3	2338
	EIV_L				1.7e-4			-5.1e-2	0.4	2338
	EIV_R		-2.0e-2				-8.0e-4	0.1	2.7	2338
	EIV_K		-3.6e-2					0.1	3.7	2338
	EIV_F	3.6e-2							2.2	2338
	EIV_N								1.1	2338

FIGURE 2 | Results of temporal models (GAMM) on the whole dataset, with response variables in rows and explanatory factors in columns. The adjusted R^2, expressed as a percentage of variation, and the number of observations are reported. Significance is indicated by coloured cells, with a p-value threshold of 0.01. Positive estimates are in red, negative estimates are in blue, and the strength of the relationship (based on the standardised estimates) is reflected by the lightness of the colour (weaker when lighter). It is important to note that the strength of the relationship can only be compared among explanatory factors for the same response variable. Reported values are the raw estimates and can be interpreted in the units of response and explanatory variables (e.g., an increase of 1°C in temperature leads to an increase of 1.6 days in the CWM of flowering onset). Models with the year as an explanatory factor were run separately. Abbreviations are in Table 1.

higher cumulative precipitation in 2019 (Figure 3D). Regarding agricultural practices, herbicide use slightly decreased over time in vineyards (−0.9 application by decade; Figure 3E), and more weakly in annual crops (−0.2 application by decade). Fertilisation showed no significant temporal trend, except in vineyards where the cumulative dose of nitrogen has recently slightly increased (Figure 3F). The number of margin mowing events has decreased and particularly in the MZ (−0.5 by decade). Floristic surveys were conducted increasingly earlier in the season in the CZ (10.4 days earlier by decade) (Appendix S1G). Overall, there was a clear warming and drying trend in climate, but agricultural trends were weaker.

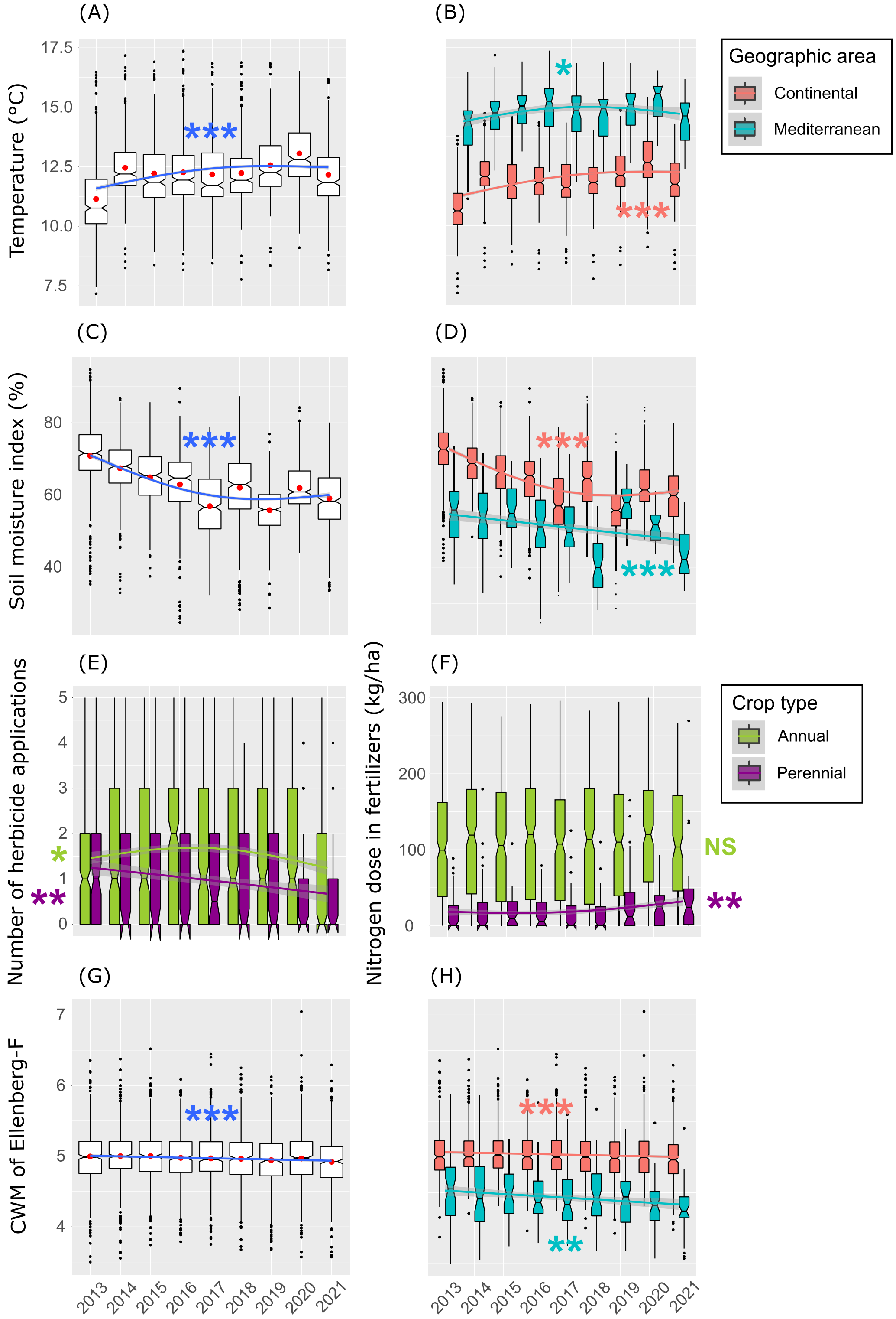


FIGURE 3 | Temporal changes in temperature, soil moisture, number of herbicide applications, nitrogen dose in fertilisers and CWM of Ellenberg-F (moisture requirement). Red dots represent mean values. The curves are from a GAM, with a smooth term on the year restricted to three effective degrees of freedom. (A, C, E) National trend. (B, D, F) Trend by geographic area: CZ and MZ. (G, H) Trend by crop type: Annual (wheat, maize, lettuce) and perennial (vineyard). Significance of smooth terms is referred as following: NS $p \geq 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Plant species richness has slightly increased over time at the national scale (+0.1 species by decade, Figure 2), even more in the MZ (+0.4 species by decade) and vineyards (+0.3 species by decade) and only for annual species (Appendix S1I). We saw an increase in the CWM of maximum height (+5.8 cm by decade), seed mass (+0.2 g by decade), flowering onset (+3.1 days by decade) and a decrease in flowering duration (−7.8 days by decade, Figure 2). The requirements (Ellenberg values) for light, temperature and pH have increased, while those for moisture and nitrogen have declined. CWV (i.e., computed by comparison with expected CWV in a community of same richness) have decreased for most traits, indicating trait convergence, and particularly for phenological traits such as flowering onset and flowering duration (−3.6 and −2.6 days by decade, respectively); while they have increased for the requirements for temperature, pH and continentality, indicating trait divergence.

Changes in functional traits were more pronounced in the MZ, particularly for the flowering onset (+8.8 days by decade) and duration (−18.9 days by decade; Appendix S1G). Conversely, changes in ecological requirements were only significant in the CZ and annual crops. One exception was the temperature (Ellenberg-T) and moisture (Ellenberg-F) requirements, which have significantly changed in both the MZ and CZ (Figure 3H). Interestingly, functional traits (and not environmental requirements) showed a temporal trend mainly for annual species (Appendix S1G).

3.2 | Functional Strategies

The first PCA axis (named hereafter stress-tolerance axis, see Appendix S1H, Figure S1H for the correlation of each trait and each CSR strategy with each axis) explained 29.6% of the variation in traits and revealed a gradient from continental hygrophilous communities (high Ellenberg-K and F) associated with moist and resource-rich environments (high Ellenberg-N), to Mediterranean xero-thermophilous stress-tolerant communities (high Ellenberg-T and L, low Ellenberg-F) adapted to warm, arid and resource-poor environments (Figure 4). Communities with continental species were more nitrophilous (high Ellenberg-N), while Mediterranean communities had a higher seed mass. The second PCA axis (named hereafter ruderal axis) explained 19.7% of the variation and contrasted stress-tolerant/conservative communities adapted to low disturbance (low SLA, high stature, late and short flowering) with ruderal/acquisitive communities adapted to high disturbance (high SLA, short stature, early and long flowering). The PCA in Appendix S1H, Figure S2A illustrates that these functional covariations identified at the community level were also evident at the species-level.

3.3 | Temporal Analyses of Plant Communities

Climatic factors were the predominant drivers of changes in community trait composition, with high R^2 for the temperature requirement ($R^2=0.33$) and stress-tolerance axis (see previous section, $R^2=0.27$, Figure 2). Associations between each Ellenberg value and climatic factors opposed in a consistent way Mediterranean communities to nitrophilous continental ones along the stress-tolerance axis (Figure 2). Increasing temperature increased the CWM of seed mass and Ellenberg-T (requirement for temperature) and decreased the CWM of SLA. Increasing temperature led to more divergence in the requirement for temperature and moisture (compared with a community of same richness). Conversely, increasing soil moisture brought convergence in the requirement for temperature, continentality and soil pH. Increasing temperature and drought were also associated with shorter flowering duration (−2.2 days by°C and + 0.15 days by % of soil moisture), and later flowering onset (+1.6 days by°C; Figure 2).

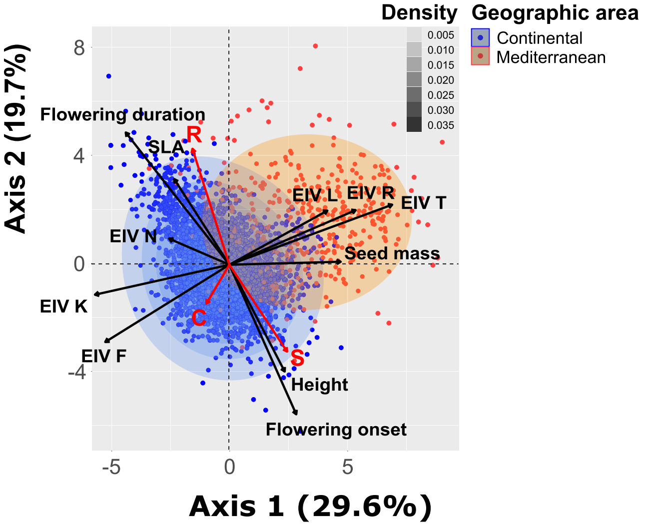


FIGURE 4 | Normed PCA on CWM (first two axes) of functional traits and ecological requirements computed by observation. The colour of the dots indicates the region to which they belong and the density curve highlights the concentration of data points in a given area. The correlations of traits to the PCA axes are in Appendix S1G, Figure S1 and the PCA for annual and perennial species is in Figure S3. The CWM of strategies (in red) were added as supplementary variables. Abbreviations for CWM: SLA, specific leaf area; Height, maximum plant height; EIV L, T, K, F, R, N, requirement for light, temperature, continentality, moisture, pH, nitrogen; C, competitive strategy; S, stress-tolerant strategy; R, ruderal strategy.

Margin mowing was the agricultural practice with the largest impact on changes in community trait composition, with an increase in its frequency associated with more ruderality (−1.2 cm in maximum height, −0.8 days in flowering onset and + 2.1 days in flowering duration by mowing event). The date of observation also influenced changes in community trait composition, with a later observation related to more conservative, competitive and continental communities, and to a decrease in species richness. Changes in the frequency of herbicide treatments had no significant effect, while an increasing annual nitrogen dose in fertilisers only slightly decreased the pH requirement (Figure 2).

Results differed depending on the region, crop type and species life span (Figure 1). In vineyards and the MZ, changes in soil moisture did not have any influence on changes in species richness or community trait composition (Appendix S1I) and temperature only increased the requirement for temperature (Ellenberg-T) and decreased SLA. When margins were more frequently mowed in the MZ, Mediterranean species declined (decrease of temperature requirement and convergence towards higher values of continentality, Appendix S1I). Increasing nitrogen dose tended to decrease species richness in the MZ, an effect also found on annual species. In vineyards, no agricultural effect was detected at the national scale. Communities of annual species were more impacted by climatic variations and seasonal effects (observation date) than perennials, with high R^2 for temperature ($R^2 = 0.39$) and moisture ($R^2 = 0.32$) requirements.

4 | Discussion

Our study provides empirical evidence that climate change is already resulting in detectable functional changes in plant communities over a relatively short time interval of 10 years (see also Martin et al. 2019) (Figure 5A). Climate change tended to favour the stress-tolerance strategy at the expense of ruderality. These contrasting strategies might indicate functional trade-offs that prevent field margin plants from simultaneously adapting to climate change and intensive agricultural practices. Interestingly, a reduced frequency of margin mowing mimicked the impact of climate change on community trait composition, although the trend was less pronounced. Changes in agricultural practices in adjacent fields, including herbicide use and fertilisation, had almost no effect on changes in community trait composition.

4.1 | Climate Is the Main Driver of Temporal Variations in Plant Communities

Our analyses revealed a temporal shift towards more stress-tolerant and less ruderal communities, primarily driven by

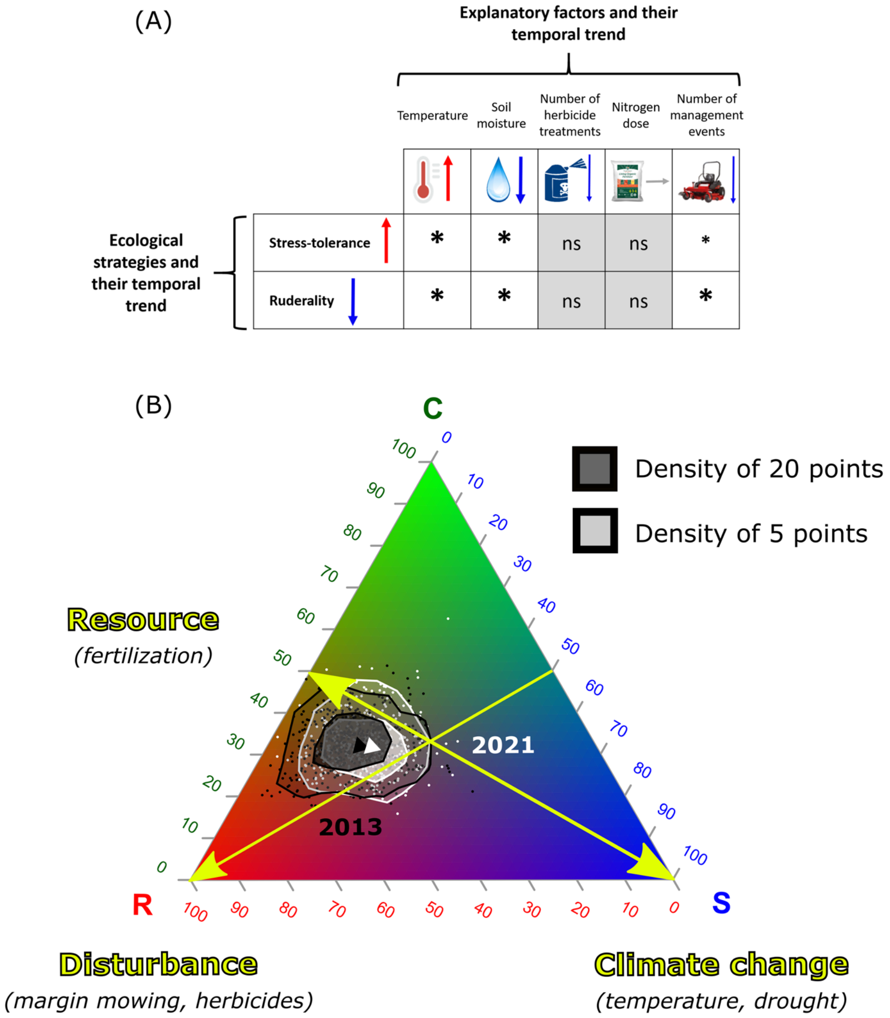


FIGURE 5 | (A) Synthesis of results based on temporal trends and temporal analyses of community response to changes in climate and practices. Ecological strategies are based on PCA axes (Axis 1 for stress-tolerance and Axis 2 for ruderality) and their associated traits. Explanatory factors and ecological strategies are depicted with their temporal trend over a decade (arrows). The asterisks illustrate the significant relationships between temporal trends in climate and practices and the resulting trends in communities, inferred from the coefficients in Figure 2 (ns = non-significant). The size of the asterisks represents the strength of the relationship, estimated from the number of impacted traits and standardised estimates in models. (B) Grime's CSR triangle depicting the temporal trajectory of community strategies between 2013 and 2021. To enhance clarity, we only show two levels of density curves, with each point representing a specific site. The relative percentages of each strategy are depicted through the use of green, blue and red colours (C = competitor, S = stress-tolerant and R = ruderal). Arrows indicate the expected impacts of climate change, disturbance, and resource levels. Temporal models (GAMM) applied to the CWM of each strategy revealed significant decreases in ruderality (−1.14% by decade) and competitiveness (−0.81% by decade) scores of communities, and a significant increase in stress-tolerance scores (+1.80% by decade).

climate (Díaz et al. 2016; Pakeman et al. 2009). Increasing temperature and drought favoured more xerophilous and thermophilous species, with higher seed mass and lower nitrogen requirement, thus shifting the position of communities along the stress-tolerance axis. Our results also indicated that sites increasingly warmer and drier allowed for coexistence of a wider functional set of species, suggesting an increased abundance of thermophilous species without any loss of cold-adapted species so far. The increase in species richness over time provided additional support for this hypothesis.

The increase in community temperature requirement with rising temperatures has already been documented, but mainly by studies covering entire floras (regional or local species pool) and time scales of several decades to a century (Salinitro et al. 2019; Tamis et al. 2005). We found that this trend is now detectable over a short-term period of only 9 years (Martin et al. 2019). Interestingly, as in other recent studies (Duchenne, Martin, and Porcher 2021; Martin et al. 2019), this trend was more pronounced in northern France, while Mediterranean communities responded less to climate change (Appendix S1I). This might be attributed to the adaptation of Mediterranean species to drought and heat stress, which enhances their resilience to extinction risks (Thuiller et al. 2005). Also, their geographic position north of the Mediterranean Sea might result in competitive release, due to the lack of immigrant species coming from the south, and the northward shift of temperate species (Duchenne, Martin, and Porcher 2021).

Beyond the increase in temperature requirement, we revealed additional temporal changes related to climate change that align well with the existing literature, including a decrease in mean SLA and an increase in mean seed mass and maximum height (Alarcón Víllora et al. 2019; Kühn et al. 2021). These trait values (low SLA, high seed mass and height) are also known to be linked to less intensive agriculture (Fried, Kazakou, and Gaba 2012; Richner et al. 2015). In our models, we observed a similar pattern, with less frequent margin mowing associated with a decrease along the ruderality axis and an increase along the stress-tolerance axis. All of this suggests that climate change and the evolution towards more extensive agricultural practices will select the same trait values towards more stress-tolerant and less ruderal strategies (Bopp et al. 2024; MacLaren et al. 2020).

Finally, temporal analyses showed phenological changes, suggesting that climate change could increase the occurrence or abundance of late-flowering species, that is, species that have high temperature requirement to complete their life cycle (Peters, Breitsameter, and Gerowitt 2014). These phenological shifts coincided with a decrease in trait variance, leading to trait convergence within communities. Critically, such changes can reduce the ability of species to escape field margin mowing, which typically favours species able to flower all-year-round, as expected with a ruderal strategy. As species will not be able to advance their phenology indefinitely, this can ultimately result in species losses in the long term. However, farmers are likely to adapt the temporality of their practices to climate change, mitigating some of these impacts.

4.2 | Agricultural Practices Have a Weaker Impact on Temporal Plant Dynamics

Temporal variations in agricultural practices had a weaker influence on field margin plant communities than climatic variations (Alarcón Víllora et al. 2019; Fried et al. 2019). Field margin mowing was the most impactful practice, affecting traits related to the ruderal syndrome in a consistent way. This supports the idea that field margin mowing, as the only practice applied directly in the margin, has a greater impact than herbicides and fertilisation applied in adjacent agricultural fields.

The lack of herbicide effect on community trait composition might be due to the relatively constant number of herbicide applications or because we omitted some traits reflecting herbicide tolerance (e.g., leaf cuticle thickness, hairiness). Also, reducing the intensity of agricultural practices may not necessarily influence community trait composition, because agricultural intensification has already greatly reduced functional diversity, and diverse landscapes would be required for some species to recolonize field margins.

Fertilisation had minimal influence on changes in community trait composition, but reduced species richness (Kleijn and Verbeek 2000), an effect detected in the MZ and leading to the loss of some annual Mediterranean species (Poinas et al. 2023). With trait covariations, we saw that nitrophilous plant species were less thermophilous and more acidiphilous, which explains why nitrogen dose was related to affinity for acidic soils in our models. Nitrogen dose remained constant over time, which aligns with the weak change in global nitrophily levels in plant communities, suggesting that eutrophication may no longer be the primary driver of changes in arable vegetation (Alignier 2018; Duchenne, Martin, and Porcher 2021).

4.3 | Functional Strategies and Implications for Community Responses to Global Changes

Our findings revealed that resource level (driven by fertilisation) and climate shift the position of communities along the stress-tolerance axis (see Appendix S1J for more results on the effect of fertilisation), while disturbance level (driven by field margin mowing) and climate shift the position of communities along the ruderal axis (Figure 5B). As a result, agricultural intensification and climate change act in opposite ways on the trait composition of field margin plant communities. Climate change favours species that are adapted to high temperatures and drought, but not to intensive agriculture. It tends to expand the functional range for traits related to stress-tolerance within communities (divergence), but reduces it for traits associated with ruderality (convergence). Conversely, agricultural disturbances select species that are more sensitive to current climatic trends, without any particular trend in trait variance.

These potential trade-offs, highlighted by the shift towards species that are better adapted to climatic stress and less ruderal, emphasise the need to consider the interactions between climate and agricultural practices when predicting future community trajectories (Garnier et al. 2019; Pakeman et al. 2009). We acknowledge the difficulty in quantifying these interactions without experimental study, given the limited changes observed in practices over time. However, the effects of practices were more perceptible with analyses focused on spatial effects (Appendix S1J, and see also Poinas et al. 2023), allowing us to hypothesize which would be the main trends in community trajectories according to several scenarios (Figure 5B). Accelerating climate change coupled with an agricultural abandonment and extensive practices in Europe (Miller et al. 2022; Peeters, Lefebvre, and Balogh 2020) would likely increase xerothermophilous and conservative species. However, a large part of these species are habitat specialists (e.g., Mediterranean species as found in Munoz et al. 2017; Fried, Chauvel, and Reboud 2009) and exhibit a strong affinity for calcareous soils. This will likely restrict their expansion towards the CZ to limited calcareous areas, such as well-exposed hillsides in the Parisian Basin. Areas where they are unable to colonise might suffer a decrease in species richness, and this scenario could worsen if current levels of agricultural intensification are maintained or increased. Mediterranean species expanding in the northern half of France could face severe agricultural intensification that would likely limit their expansion, while ruderal species would become less frequent mostly because of drought. This highlights the need to consider the conjunction of climate change and intensive agriculture when making future predictions.

5 | Conclusion

Climate is the primary factor affecting changes in field margin plant communities in France, with increasing temperatures and decreasing soil moisture fostering Mediterranean, stress-tolerant and conservative species, while negatively affecting ruderal species. In comparison, agricultural practices had limited effects on changes in species richness and trait composition, with field margin mowing having the greatest impact. Our study suggests that species selected by climate change are poorly adapted to intensive farming, while species colonising field margins are restricted to a limited functional range adapted to agricultural practices. The persistence of intensive agricultural practices and accelerating climate change could thus have critical consequences for the conservation of floristic diversity in agroecosystems. However, it is important to consider the potential of adaptation of species, through intraspecific trait variability and phenotypic plasticity (known to be particularly high in ruderal species, Baker 1974), as it may enhance their resilience to changing conditions. Our findings suggest a reduction in ruderality and an increase in stress-tolerance according to Grime's strategies. Bopp et al. (2024) highlighted a similar increase in stress-tolerance for weeds in response to climate change, but did not observe a corresponding decrease in ruderality. Further investigations are thus necessary to assess the generalizability of these results across different habitats, including communities with broader or narrower functional niches, such as weeds. Long-term monitoring programs are necessary to address other important research questions, such as the potential time-lag in flora's response to environmental changes, the non-linearity in temporal trends and the interactive effects between climate and agricultural changes. Finally, this study calls for rethinking our current agricultural model, urging us to prioritise the development of agricultural practices that create favourable microclimates while minimising local intensification. Promising approaches, such as agroforestry, hold the potential to align agricultural production with biodiversity conservation goals by providing refuge habitats and microclimate regulation.

Author Contributions

I.P., G.F. and C.N.M. planned and designed the research. I.P. analysed the data and wrote the first draft of the manuscript. G.F. and C.N.M. contributed substantially to revisions. All authors gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and scripts available via Zenodo at 10.5281/zenodo.14191328

Peer Review

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References

Aavik, T., I. Augenstein, D. Bailey, F. Herzog, M. Zobel, and J. Liira. 2008. "What Is the Role of Local Landscape Structure in the Vegetation Composition of Field Boundaries?" *Applied Vegetation Science* 11, no. 3: 375–386. https://doi.org/10.3170/2008-7-18486.

Alarcón Víllora, R., E. Hernández Plaza, L. Navarrete, M. J. Sánchez, and A. M. Sánchez. 2019. "Climate and Tillage System Drive Weed communities' Functional Diversity in a Mediterranean Cereal-Legume Rotation." *Agriculture, Ecosystems & Environment* 283: 106574. https://doi.org/10.1016/j.agee.2019.106574.

Alignier, A. 2018. "Two Decades of Change in a Field Margin Vegetation Metacommunity as a Result of Field Margin Structure and Management Practice Changes." *Agriculture, Ecosystems & Environment* 251: 1–10. https://doi.org/10.1016/j.agee.2017.09.013.

Andrade, C., A. Villers, G. Balent, et al. 2021. "A Real-World Implementation of a Nationwide, Long-Term Monitoring Program to Assess the Impact of Agrochemicals and Agricultural Practices on Biodiversity." *Ecology and Evolution* 11, no. 9: 3771–3793. https://doi.org/10.1002/ece3.6459.

Baker, H. G. 1974. "The Evolution of Weeds." *Annual Review of Ecology and Systematics* 5, no. 1: 1–24. https://doi.org/10.1146/annurev.es.05.110174.000245.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. "Impacts of Climate Change on the Future of Biodiversity." *Ecology Letters* 15, no. 4: 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x.

Bernard-Verdier, M., M.-L. Navas, M. Vellend, C. Violle, A. Fayolle, and E. Garnier. 2012. "Community Assembly Along a Soil Depth Gradient: Contrasting Patterns of Plant Trait Convergence and Divergence in a Mediterranean Rangeland." *Journal of Ecology* 100, no. 6: 1422–1433. https://doi.org/10.1111/1365-2745.12003.

Bopp, M.-C., E. Kazakou, A. Metay, and G. Fried. 2022. "Relative Importance of Region, Seasonality and Weed Management Practice Effects on the Functional Structure of Weed Communities in French Vineyards." *Agriculture, Ecosystems & Environment* 330: 107892. https://doi.org/10.1016/j.agee.2022.107892.

Bopp, M.-C., E. Kazakou, A. Metay, et al. 2024. "Climate and Management Changes in 40 Years Drove More Stress-Tolerant and Less Ruderal Weeds Communities in Vineyards." *Ecological Monographs*, e1631. https://doi.org/10.1002/ecm.1631.

Box, G. E. P., G. M. Jenkins, G. C. Reinsel, and G. M. Ljung. 2015. *Time Series Analysis: Forecasting and Control*. Hoboken, New Jersey, USA: John Wiley and Sons.

Díaz, S., J. Kattge, J. H. C. Cornelissen, et al. 2016. "The Global Spectrum of Plant Form and Function." *Nature* 529, no. 7585: 167–171. https://doi.org/10.1038/nature16489.

Duchenne, F., G. Martin, and E. Porcher. 2021. "European Plants Lagging Behind Climate Change Pay a Climatic Debt in the North, but Are Favoured in the South." *Ecology Letters* 24, no. 6: 1178–1186. https://doi.org/10.1111/ele.13730.

Ellenberg, H. 1974. "Indicator Values of Vascular Plants in Central Europe." *Scripta Geobotanica* 9: 97.

Emmerson, M., M. B. Morales, J. J. Oñate, et al. 2016. "How Agricultural Intensification Affects Biodiversity and Ecosystem Services." In *Advances in Ecological Research*, vol. 55, 43–97. Cambridge, MA: Elsevier Ltd. https://linkinghub.elsevier.com/retrieve/pii/S0065250416300204.

Fitter, A. H., and R. S. R. Fitter. 2002. "Rapid Changes in Flowering Time in British Plants." *Science* 296, no. 5573: 1689–1691. https://doi.org/10.1126/science.1071617.

Fridley, J. D., X. Liu, N. Pérez-Harguindeguy, et al. 2023. "Perspectives on the Scientific Legacy of J. Philip Grime." *Journal of Ecology* 111, no. 9: 1814–1831. https://doi.org/10.1111/1365-2745.14177.

Fried, G., C. Blanchet, L. Cazenave, et al. 2022. "Consistent Response of Weeds According to Grime's CSR Strategies Along Disturbance and Resource Gradients in Bordeaux Vineyards." *Weed Research* 62, no. 5: 347–359. https://doi.org/10.1111/wre.12549.

Fried, G., B. Chauvel, and X. Reboud. 2009. "A Functional Analysis of Large-Scale Temporal Shifts From 1970 to 2000 in Weed Assemblages of Sunflower Crops in France." *Journal of Vegetation Science* 20, no. 1: 49–58. https://doi.org/10.1111/j.1654-1103.2009.05284.x.

Fried, G., S. Cordeau, A. Metay, and E. Kazakou. 2019. "Relative Importance of Environmental Factors and Farming Practices in Shaping Weed Communities Structure and Composition in French Vineyards." *Agriculture, Ecosystems & Environment* 275: 1–13. https://doi.org/10.1016/j.agee.2019.01.006.

Fried, G., E. Kazakou, and S. Gaba. 2012. "Trajectories of Weed Communities Explained by Traits Associated With species' Response to Management Practices." *Agriculture, Ecosystems & Environment* 158: 147–155. https://doi.org/10.1016/j.agee.2012.06.005.

Gaba, S., G. Fried, E. Kazakou, B. Chauvel, and M.-L. Navas. 2014. "Agroecological Weed Control Using a Functional Approach: A Review of Cropping Systems Diversity." *Agronomy for Sustainable Development* 34, no. 1: 103–119. https://doi.org/10.1007/s13593-013-0166-5.

Garnier, E., and M.-L. Navas. 2012. "A Trait-Based Approach to Comparative Functional Plant Ecology: Concepts, Methods and Applications for Agroecology. A Review." *Agronomy for Sustainable Development* 32, no. 2: 365–399. https://doi.org/10.1007/s13593-011-0036-y.

Garnier, E., D. Vile, C. Roumet, et al. 2019. "Inter- and Intra-Specific Trait Shifts Among Sites Differing in Drought Conditions at the North Western Edge of the Mediterranean Region." *Flora* 254: 147–160. https://doi.org/10.1016/j.flora.2018.07.009.

Grime, J. P. 1977. "Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory." *American Naturalist* 111, no. 982: 1169–1194.

Grime, J. P. 1988. "The C-S-R Model of Primary Plant Strategies—Origins, Implications and Tests." In *Plant Evolutionary Biology*, edited by L. D. Gottlieb and S. K. Jain, 371–393. Netherlands: Springer. https://doi.org/10.1007/978-94-009-1207-6_14.

Grime, J. P. 2006. "Trait Convergence and Trait Divergence in Herbaceous Plant Communities: Mechanisms and Consequences." *Journal of Vegetation Science* 17, no. 2: 255–260. https://doi.org/10.1111/j.1654-1103.2006.tb02444.x.

Guichard, L., F. Dedieu, M.-H. Jeuffroy, J.-M. Meynard, R. Reau, and I. Savini. 2017. "Le plan Ecophyto de réduction d'usage des pesticides en France: Décryptage d'un échec et raisons d'espérer." *Cahiers Agricultures* 26, no. 1: 14002. https://doi.org/10.1051/cagri/2017004.

Kleijn, D., and M. Verbeek. 2000. "Factors Affecting the Species Composition of Arable Field Boundary Vegetation." *Journal of Applied Ecology* 37, no. 2: 256–266. https://doi.org/10.1046/j.1365-2664.2000.00486.x.

Kühn, N., C. Tovar, J. Carretero, V. Vandvik, B. J. Enquist, and K. J. Willis. 2021. "Globally Important Plant Functional Traits for Coping With Climate Change." *Frontiers of Biogeography* 13, no. 4: e53774. https://doi.org/10.21425/F5FBG53774.

Le Moigne, P. 2002. "*Description de l'analyse des champs de surface sur la France par le système SAFRAN*." [Note de centre GMME]. Météo-France 1–30.

Lososová, Z., M. Chytrý, S. Cimalová, et al. 2004. "Weed Vegetation of Arable Land in Central Europe: Gradients of Diversity and Species Composition." *Journal of Vegetation Science* 15, no. 3: 415–422. https://doi.org/10.1111/j.1654-1103.2004.tb02279.x.

Lovejoy, T. E. 2006. *Climate Change and Biodiversity*. New Haven, USA: Yale University Press.

MacLaren, C., J. Storkey, A. Menegat, H. Metcalfe, and K. Dehnen-Schmutz. 2020. "An Ecological Future for Weed Science to Sustain Crop Production and the Environment." *A Review. Agronomy for Sustainable Development* 40, no. 4: 24. https://doi.org/10.1007/s13593-020-00631-6.

Martin, G., V. Devictor, E. Motard, N. Machon, and E. Porcher. 2019. "Short-Term Climate-Induced Change in French Plant Communities." *Biology Letters* 15, no. 7: 20190280. https://doi.org/10.1098/rsbl.2019.0280.

Metay, A., L. Garcia, E. Kazakou, and G. Fried. 2022. "Effet des couverts sur la flore en viticulture." *Agronomie, Environnement & Sociétés* 12, no. 1: 1–19. https://doi.org/10.54800/prt789.

Miller, D., S. Legras, A. Barnes, et al. 2022. "Creating Conditions for Harnessing the Potential of Transitions to Agroecology in Europe and Requirements for Policy." *EuroChoices* 21, no. 3: 72–79. https://doi.org/10.1111/1746-692X.12374.

Munoz, F., G. Fried, L. Armengot, et al. 2017. "Database of Weeds in Cultivation Fields of France and UK, With Ecological and Biogeographical Information [Dataset]." https://doi.org/10.5281/zenodo.1112342.Zenodo.

Office français de la biodiversité. 2021. “Carte Des régions d'origine—Référentiel Technique de la Marque Végétal Local—Version 2021.” www.vegetal-local.fr.

Oliver, T. H., and M. D. Morecroft. 2014. “Interactions Between Climate Change and Land Use Change on Biodiversity: Attribution Problems, Risks, and Opportunities.” *WIREs Climate Change* 5, no. 3: 317–335. https://doi.org/10.1002/wcc.271.

Pakeman, R. J., J. Lepš, M. Kleyer, S. Lavorel, E. Garnier, and Consortium, the V. 2009. “Relative Climatic, Edaphic and Management Controls of Plant Functional Trait Signatures.” *Journal of Vegetation Science* 20, no. 1: 148–159. https://doi.org/10.1111/j.1654-1103.2009.05548.x.

Peeters, A., O. Lefebvre, and L. Balogh. 2020. “A Green Deal for Implementing Agroecological Systems: Reforming the Common Agricultural Policy of the European Union.” *Journal of Sustainable and Organic Agricultural Systems* 70: 83–93. https://doi.org/10.3220/LBF1610123299000.

Peters, K., L. Breitsameter, and B. Gerowitt. 2014. “Impact of Climate Change on Weeds in Agriculture: A Review.” *Agronomy for Sustainable Development* 34, no. 4: 707–721. https://doi.org/10.1007/s13593-014-0245-2.

Pierce, S., D. Negreiros, B. E. L. Cerabolini, et al. 2017. “A Global Method for Calculating Plant CSR Ecological Strategies Applied Across Biomes World-Wide.” *Functional Ecology* 31, no. 2: 444–457. https://doi.org/10.1111/1365-2435.12722.

Poinas, I., G. Fried, L. Henckel, and C. N. Meynard. 2023. “Agricultural Drivers of Field Margin Plant Communities Are Scale-Dependent.” *Basic and Applied Ecology* 72: 55–63. https://doi.org/10.1016/j.baae.2023.08.003.

Poisvert, C., F. Curie, and F. Moatar. 2017. “Annual Agricultural N Surplus in France Over a 70-Year Period.” *Nutrient Cycling in Agroecosystems* 107, no. 1: 63–78. https://doi.org/10.1007/s10705-016-9814-x.

Reich, P. B. 2014. “The World-Wide ‘Fast–Slow’ Plant Economics Spectrum: A Traits Manifesto.” *Journal of Ecology* 102, no. 2: 275–301. https://doi.org/10.1111/1365-2745.12211.

Richner, N., R. Holderegger, H. P. Linder, and T. Walter. 2015. “Reviewing Change in the Arable Flora of Europe: A Meta-Analysis.” *Weed Research* 55, no. 1: 1–13. https://doi.org/10.1111/wre.12123.

Salinitro, M., A. Alessandrini, A. Zappi, and A. Tassoni. 2019. “Impact of Climate Change and Urban Development on the Flora of a Southern European City: Analysis of Biodiversity Change Over a 120-Year Period.” *Scientific Reports* 9, no. 1: 9464. https://doi.org/10.1038/s41598-019-46005-1.

Tamis, W. L. M., M. V. Zelfde, R. V. Der Meijden, and H. A. U. De Haes. 2005. “Changes in Vascular Plant Biodiversity in The Netherlands in the 20th Century Explained by Their Climatic and Other Environmental Characteristics.” *Climatic Change* 72, no. 1: 37–56. https://doi.org/10.1007/s10584-005-5287-7.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. “Climate Change Threats to Plant Diversity in Europe.” *Proceedings of the National Academy of Sciences* 102, no. 23: 8245–8250. https://doi.org/10.1073/pnas.0409902102.

Wright, I. J., P. B. Reich, M. Westoby, et al. 2004. “The Worldwide Leaf Economics Spectrum.” *Nature* 428, no. 6985: 821–827. https://doi.org/10.1038/nature02403.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.