Functional trade-offs: exploring the effects of climate change and agricultural practices as drivers of field margin plant communities

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Abstract

Over the past decades, agricultural intensification and climate change have led to vegetation shifts in Europe. However, functional trade-offs linking traits responding to climate and farming practices are rarely analyzed, especially on large-scale empirical studies. Here we used a standardized yearly monitoring effort of agricultural field margin flora at the national scale to assess the spatio-temporal response of diversity and functional traits to climatic and agricultural variations. We examined temporal trends in climate (temperature, soil moisture), intensity of agricultural practices (herbicides, fertilization, margin management), plant species richness, and community-weighted means and variances of traits expected to vary both with climate and practices (e.g. seed mass, specific leaf area), across 555 sites in France between 2013 and 2021. We found that temperatures have increased while soil moisture has decreased, reflecting current climate change, whereas the intensity of agricultural practices did not show clear temporal trends over the past decade. Functional changes in plant communities were significant, showing an increase of thermophilic species with a conservative resource acquisition strategy mainly explained by climate change. The impact of agricultural practices was more limited and mainly exerted through field margin management and fertilization that shifted vegetation towards species with a ruderal syndrome. Responses to climate change differed according to crop type (vineyards versus annual crops), region (Mediterranean versus continental), and species life cycle (annual versus perennial). Our findings suggest that species adapted to climate change (including Mediterranean and conservative species) have increased in proportion. Importantly, we identified functional trade-offs indicating that these species are also the most vulnerable to intensive agricultural practices, as they are less adapted to high levels of resources and disturbances. We put these results into the conceptual framework of Grime's CSR triangle and revealed a decline of competitive and ruderal species in favor of stress-tolerant species better adapted to climate change. By choosing less intensive management, we can promote diverse communities with a wide range of CSR strategies, thereby increasing the presence of species adapted to climate change.

Keywords: functional trade-offs, climate change, temporal variation, field margin, plant diversity, agricultural practices, CSR strategies, Mediterranean species, phenology

Introduction

Since the 1950s, agricultural intensification has led to declining biodiversity (Emmerson et al., 2016), while climate change has caused notable changes in a wide range of taxa and habitats (Lovejoy, 2006). However, teasing out the relative importance of these two drivers on community trajectories can be quite challenging (Oliver & Morecroft, 2014). Since agricultural intensification took place in the 1950s in Europe, the main changes linked to agricultural practices (notably in terms of intensity in pesticide use and fertilization) in plant communities have likely already occurred (Lososová et al., 2004). For example, a meta-analysis considering 32 studies across Europe and covering the time period from 1939 to 2011 showed that weed species richness declined up to the 1980s, but has stabilized or even increased since then (Richner et al., 2015). Pesticide reduction plans have had so far little effect in France (Guichard et al., 2017), hindering the detection of temporal changes in biodiversity linked to changes in pesticide use. Conversely, short-term declines in species diversity due to climate change are observable (e.g. Fonty et al., 2009), and recent temperature increases in France may impact plant communities similarly (Baude et al., 2022; Martin et al., 2019). Given this clear trend in climate, contrasted with a lack of recent temporal trend in pesticides, combining spatial and temporal analyses seems necessary to understand the effects of these two drivers on plant communities around agricultural fields.

Changes in plant communities cannot be discerned solely by taxonomic diversity due to the differing traits affected by resource availability and disturbance levels (Garnier & Navas, 2012); therefore, a functional dimension provides an additional perspective to accurately understand these changes. This is particularly important in agroecosystems, where both resource (fertilization) and disturbance (herbicides, field margin management) gradients play crucial roles in shaping communities (Gaba et al., 2014; MacLaren et al., 2020). For instance, weeds with a ruderal strategy are better adapted to agricultural disturbances, such as tillage, herbicides or management by mowing (Grime, 2006; Fried et al., 2022). At the same time, traits responding to agricultural practices can co-vary with other traits

that are linked to resource acquisition, competitive ability, or climate. For example, seed mass, which is often used as a proxy for competitive ability, increases along soil fertility, temperature and solar radiation gradients (Fried et al., 2022; Murray et al., 2004). Furthermore, correlations among different traits may represent trade-offs that impact community adaptation (Díaz et al., 2016; Wright et al., 2004). In this context, Grime (1977) proposed a framework called the CSR triangle, which defines two axes of variation - resource and disturbance - along which three strategies are distributed - competitiveness, stress-tolerance, and ruderality - that are correlated to multiple traits and have proven useful to understand plant community dynamics in agrosystems (Fried et al., 2022). As traits responding to climate and agricultural practices may co-vary (Garnier & Navas, 2012), it can be difficult to identify the main drivers behind community changes.

To understand the complex interactions between climate change and agricultural practices, it is thus essential to examine the temporal dimension of functional inter-specific trait variations. For example, in French wheat fields, small species with low seed mass and long germination and flowering periods increased their frequency between the 1970s and 2000s, potentially due to their ability to escape recurrent disturbances, such as herbicide applications (Fried et al., 2012). Inter-annual variations in specific leaf area, leaf dry matter content and plant height are related to nitrogen supply, while increased precipitations push the foliar economic spectrum towards more acquisitive species (Wheeler et al., 2023). Additionally, mean thermal preference of plant communities, as well as their phenology, 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 with a space-for-time approach.

In this study, we aimed at deciphering how spatio-temporal variations of climate (temperature, soil moisture) and agricultural practices (frequency of herbicide use, margin management and nitrogen dose in fertilizers) in France structure species richness, trait composition and ecological strategies of field margin plant communities. We studied the herbaceous field margin, which represents the

uncultivated vegetated area located between the cultivated strip and the adjacent habitat. Using a standardized national monitoring effort spanning 9 years (2013-2021) in 555 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 spatial and temporal drivers of species richness and functional traits at such extensive scales. We hypothesized that plant traits sensitive to temperature and soil moisture will co-vary with both spatial climatic gradients and temporal warming trends while agricultural practices would have a greater spatial than temporal influence on plant communities, as we did not expect clear temporal trends in these practices. We also assumed that the impact of agricultural practices on margin plant communities would likely be limited, as field margins only receive a small amount of nitrogen and herbicides drifting from neighboring plots. 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 hypothesized that they would respond to climate factors (particularly reduced water resource) and agricultural practices (disturbance and resource provision through fertilization). On top of the national analyses, and because this dataset includes the Mediterranean flora, which has been shown to respond more strongly to some agricultural filters (Poinas et al., 2023), we included analyses separating this region from the rest of France. We also separated vineyards from annual crops, because vineyards include very different management practices and no crop rotation (Metay et al., 2022). Finally, we also analyzed annual plant species separately, as they may respond more rapidly to environmental changes (Martin et al., 2019; Fitter & Fitter, 2002).

Materials and methods

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 site turnover) (**Fig. 1**). These survey sites represented three main crop types **(Appendix A, Fig. SA. 1)**: 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%, but agricultural practices covered a wide range of pesticide application, fertilizers and soil management. Within each survey site, plant species were identified in ten 1 m² quadrats along the field margin (**Appendix A**, **Fig. SA.2**). 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 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 x 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).

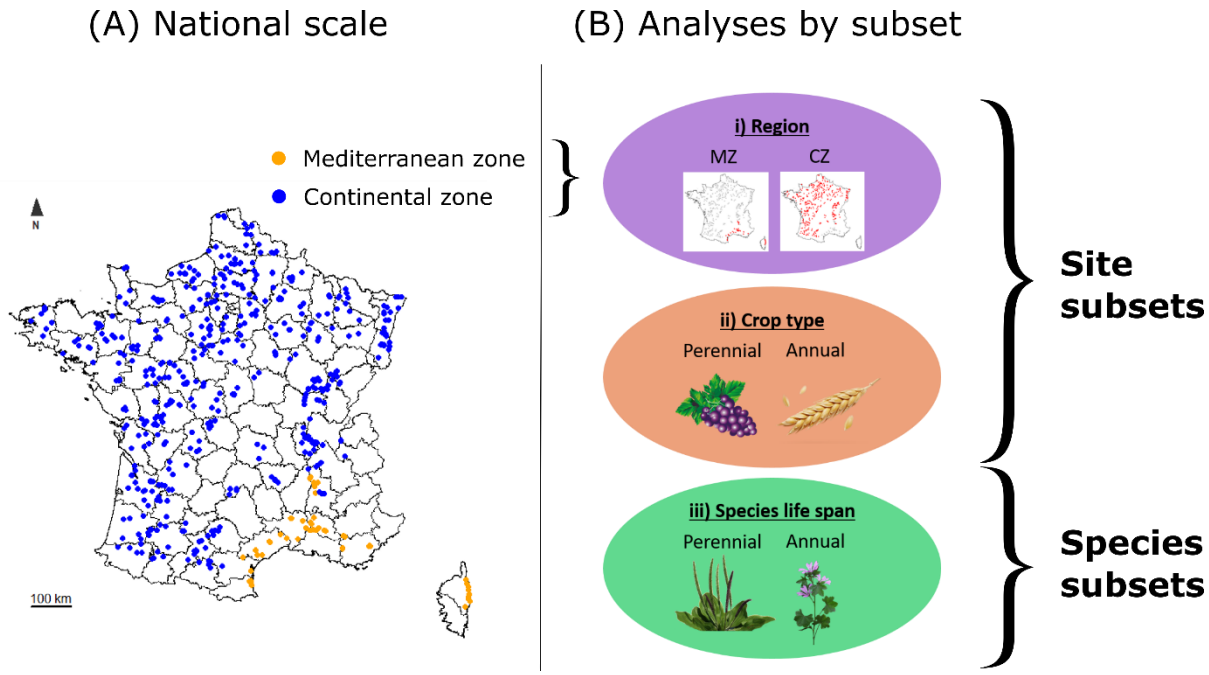

Fig. 1. (A) Distribution map of the 555 field margins monitored at least one year between 2013 and 2021 in France. The black lines represent the limits of French departments. Orange: sites in Mediterranean zone (n = 57), blue: sites in Continental zone (n = 498). The contours of the Mediterranean zone (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 to here as Continental zone (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).

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; the second one included meteorological data from an external database (see below). Here, we chose not to include landscape

factors, as a previous study on the same dataset demonstrated that landscape variables account for a negligible proportion of variance at the national scale, in contrast to climate (Poinas et al., 2023).

Agricultural practices were reported yearly from interviews of farmers into a standardized online database. Data collected relate to fertilization, herbicide use and field margin management (mainly mowing of vegetation). Daily meteorological data 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 (**Table 1**). We selected variables that were weakly correlated (Spearman correlation < 0.65, **Appendix B**) and have been shown to influence plant communities in previous studies (**Table 1,** see **Appendix C** for the choice of variables).

Table 1. List of explanatory factors (blue), functional traits (green) and response variables (red) with their abbreviations, units and calculation. The variables only used in temporal models are underlined, while those only used in spatial ones are in italic. We have illustrated by arrows the expected link of each factor and trait to the agricultural resource and disturbance gradient, and to climate change. Horizontal arrows indicate contradictory findings in the literature (see **Appendix C** for the references).

Factors	Abbreviations	Units	Index used	Hypothesis of response to the Agricultural gradient: Disturbance (Di) and Resource (R)	Hypothesis of response to the Climatic gradient: Drought (Dr) and Increasing temperature (T)
Temperature	TEMP	°C	Annual mean of daily values		↗
Soil moisture	MOI	%	Annual mean of daily values		↘
Dose of nitrogen (fertilization)	N_DOSE	kg/ha	For each application: $Dose = \frac{Quantity \times N\ of\ the\ formulation}{100}$ Doses were summed one year before observation	↗	
Number of herbicide treatments	HERB		Treatments were summed one year before observation	↗	
Number of management events	MAN		An event corresponds to the occurrence of vegetation management at a given time, most often by mowing or grinding. Management events were summed one year before observation.	↗	
Date of observation	DATE	Julian days		↘ ↘	↗ ↗

Number of observers	OBS			
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	High values of Ellenberg-L reflect heliophilous species (preference for light), Ellenberg-T, thermophilous species (preference for high temperatures), Ellenberg-K, continental species (opposed to oceanic and Mediterranean species), Ellenberg-F, hygrophilous species (preference for moisture), Ellenberg-R, calcareous species (preference for calcareous soils), Ellenberg-N, nitrophilous species (preference for fertile soils) (Ellenberg, 1974)	EIV_N: ↗	EIV_F: ↘ EIV_T: ↗ ↗
Species richness	S	Number of species	→? →?	→? →?
Functional composition	See abbreviations above for each trait preceded by "CWM_"	Community weighted means (CWM) : community trait values weighted by species abundance (Lavorel et al., 2008)		
Functional divergence	See abbreviations above for each trait preceded by "CWV_"	Community weighted variances (CWV) : community trait variability around the average value (Sonnier et al., 2010)		
PCA traits - axis 1	PCA_1	Scores of sites or observations on the 1st axis of the PCA including CWM of all traits		
PCA traits - axis 2	PCA_2	Scores of sites or observations on the 2nd axis of the PCA including CWM of all traits		

Scores of competitive, stress-tolerant and ruderal strategies	CWM_C, CWM_S, CWM_R	%	Community weighted means (CWM) : community strategy values weighted by species abundance (Lavorel et al., 2008). Species scores for each strategy are computed from the leaf area, leaf dry matter content and specific leaf area (see the algorithm of Pierce et al., 2017).	CWM_C: ↘ ↗ CWM_S: ↘ ↘ CWM_R: ↗ ↗	CWM_C: ↘ CWM_S: ↗

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Plant functional traits

We extracted from external databases five functional traits and six species-level indices of ecological requirements, assumed to respond to agricultural or climatic factors (**Table 1**, **Appendix B-C**). Functional traits were missing for four species, two of which could be imputed from an average over other species of the same genus. The remaining two species were removed from the analysis (representing 0.01% of the total abundances among the 142 species considered). In the following analyses, maximal height and seed mass were log-transformed to ensure normality and reduce the influence of extreme values.

To characterize plant communities, we calculated species richness, community-weighted means (CWM) and community-weighted variances (CWV) of traits for sites and observations with at least three species (59 out of 4172 observations were excluded). The computation was performed using the R v.4.0.0 package FD, function *dbFD* for CWM, with the following formulas:

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

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

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 x trait matrix unchanged (Bopp et al., 2022). 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).

For CWV by site, the species pool was defined by the biogeographic region, allowing us to examine spatial variations. For CWV by observation, the species pool was defined by the site itself, allowing us to investigate temporal variations. To determine the biogeographic regions of each site, we used the VégétalLocal map (Office français de la biodiversité, 2021). To quantify the difference between

observed and null CWV, we computed effect sizes (**Appendix D**). 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 (by site for spatial analyses, by observation for temporal analyses) to classify each community based on its average trait combination or ecological strategy, which is reflected by its position on the first two axes.

Plant functional 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 by site and were added to the PCA on the CWM of traits as supplementary variables. The CWM of CSR scores computed by observation were plotted on a CSR triangle to illustrate temporal trends in strategies.

Spatial analyses of plant communities

The general framework of analyses is presented in **Fig. 2**. To analyze the effects of spatial variations in climate and agricultural practices while ignoring temporal patterns, explanatory factors and species abundances were averaged across years within sites having at least five years of data, leaving a total of 349 sites. Spatial simultaneous autoregressive models (SAR; package SPDEP, function *errorsarlm*; Cressie, 2015) were implemented to model linear relationships that take into account spatial autocorrelation in the data, i.e. the tendency of nearby points to have more similar values than expected by chance. We examined the relationship between each response variable (species richness, functional composition, divergence and strategies) and the explanatory factors (temperature, soil moisture, nitrogen dose, herbicides and margin management). The Nagelkerke pseudo-R^2 (which can be interpreted similarly to a conventional R^2) was used to assess the model's explanatory power, and

we controlled for the observer bias by adding the number of successive observers in a site as a fixed effect. For all analyses, we chose a p-value threshold of 0.01 to focus on the effects for which our confidence level was highest.

Temporal analyses of plant communities

In a second stage, we wanted to assess the extent to which spatial patterns on climate and agricultural practices were also reflected on temporal trends. We checked first if there was a temporal trend on the raw variables, and then we used climate and agricultural practices as predictors for the different response variables. In all cases, we used generalized additive mixed models (GAMM) to account for repeated measures at a site, with a Gaussian distribution in most cases (but see **Appendix E**, **Table SE.2**), 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, functional composition, divergence and CSR strategies) and explanatory factor (temperature, soil moisture, nitrogen dose, herbicides and margin management), 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 E**), resulting in varying observation numbers across models (see **Fig. 5**). We repeated this analysis on subsets of data, including Mediterranean (MZ) vs Continental (CZ) zones, margins adjacent to annual crops vs vineyards, and annual vs perennial plant species (**Fig. 1**).

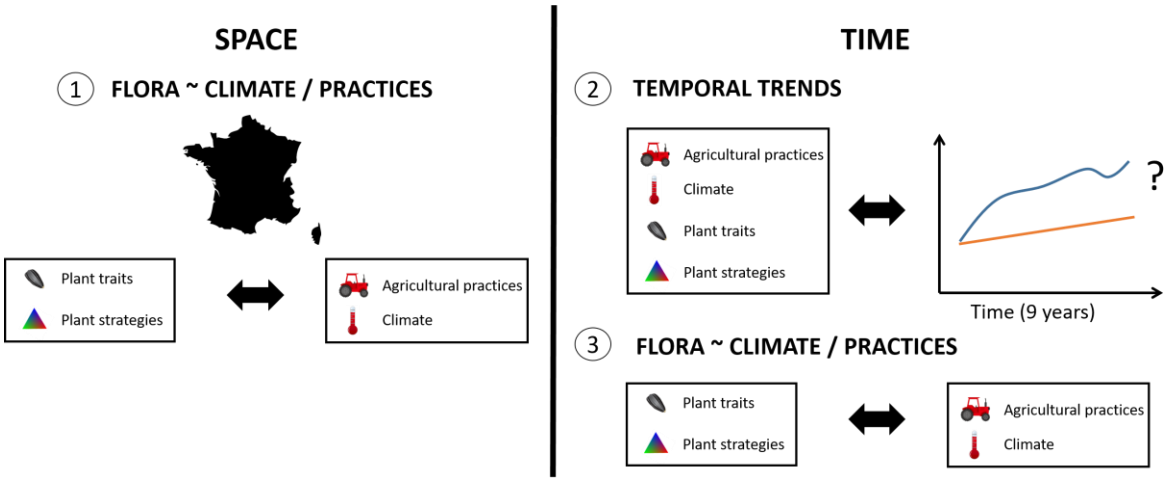

Fig. 2. General framework of our analyses involved three main steps. (1) Firstly, we ignored temporal trends and examined the spatial response of plant communities, primarily in terms of functional traits and strategies, to climatic and agricultural factors. (2) Secondly, we investigated the presence of any temporal trends in these factors (both communities and environment), as this provides crucial insights for the subsequent analysis. Indeed, given that we expected minimal temporal trends in agricultural practices, we did not expect significant temporal changes in flora in response to practices. (3) Finally, we explored how plant communities have responded to the temporal changes in climate and agricultural practices.

Results

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 Mediterranean Zone), while soil moisture has steadily declined (-14.1% by decade) (**Fig. 3**, and **Appendix F**). These trends differed between the Mediterranean Zone (MZ) and the Continental Zone (CZ), with the MZ experiencing a slower decline in soil moisture due to a high cumulative precipitation in 2019 (**Fig. 3**). Regarding agricultural practices, herbicides slightly decreased over time in vineyards (-0.9 application by decade; **Fig. 3**), with an even weaker trend in annual crops (-0.2 application by

258 decade). Fertilization showed no significant temporal trend, except in vineyards where the cumulative
259 dose of nitrogen has recently slightly increased (**Fig. 3**). The number of margin management events
260 has decreased and particularly in the MZ (-0.5 by decade). Floristic surveys were conducted
261 increasingly earlier in the season in the CZ (10.4 days earlier by decade) (**Appendix F**). Overall, there
262 was a clear warming and drying trend in climate, but agricultural trends remained more uncertain.

263 Plant species richness has slightly increased over time at the national scale (+0.1 species by decade),
264 even more in the MZ (+0.4 species by decade) and vineyards (+0.3 species by decade) and only for
265 annual species (**Appendix H**). In France, we saw an increase in the CWM of maximum height (+5.8 cm
266 by decade), seed mass (+0.2 g by decade), flowering onset (+3.1 days by decade) and a decrease in
267 flowering duration (-7.8 days by decade) (**Appendix F**). The requirements for light, temperature and
268 pH have increased, while those for moisture and nitrogen have declined. CWV (i.e. computed by
269 comparison with expected CWV in a community of equal richness) have decreased for most of traits
270 (convergence), and particularly for phenological traits such as flowering onset and flowering duration
271 (-3.6 and -2.6 days by decade respectively), while they have increased for the requirements for
272 temperature, pH and continentality (divergence).

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

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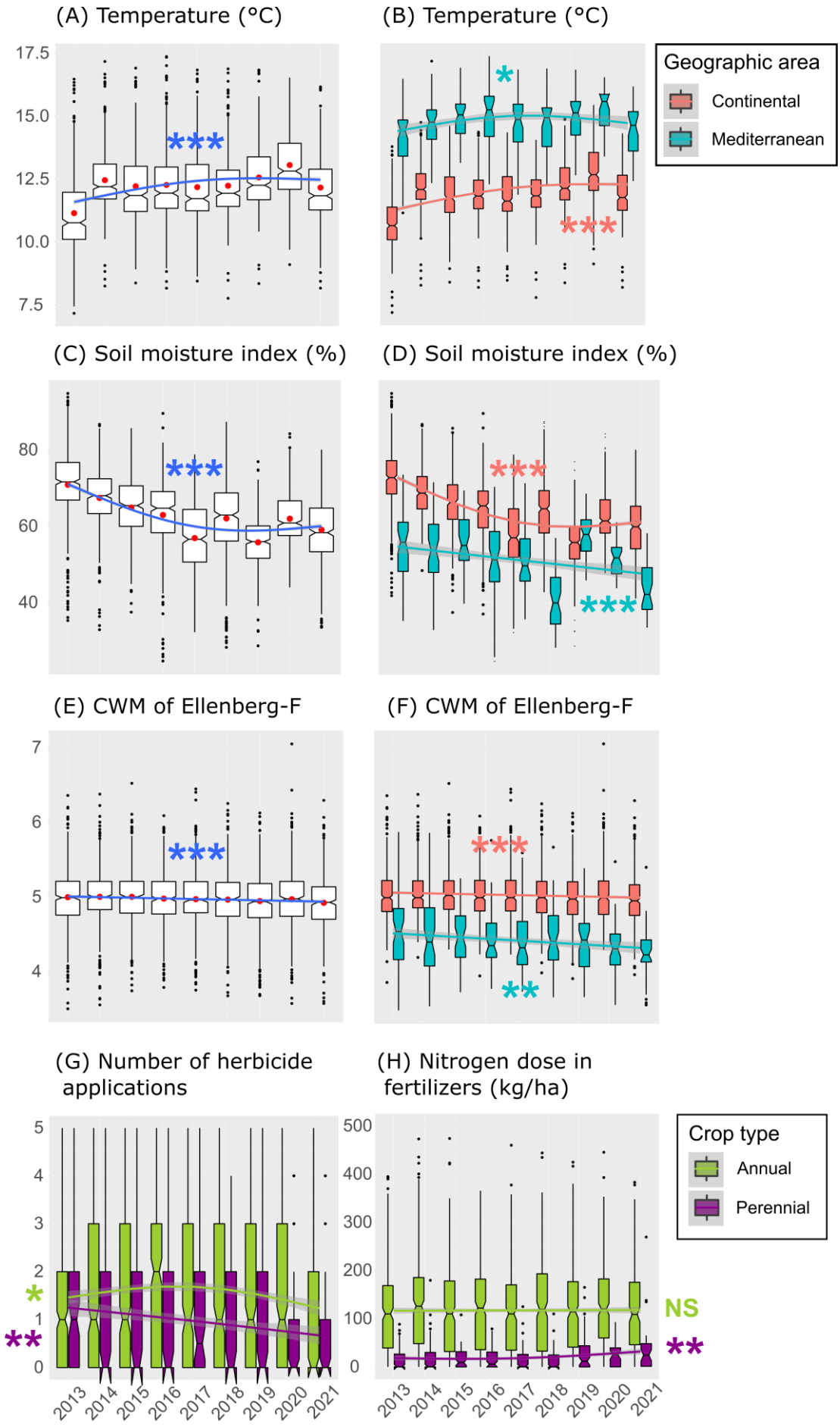

(A) Temperature (°C)
(B) Temperature (°C)
Geographic area
Continental
Mediterranean
(C) Soil moisture index (%)
(D) Soil moisture index (%)
(E) CWM of Ellenberg-F
(F) CWM of Ellenberg-F
(G) Number of herbicide applications
(H) Nitrogen dose in fertilizers (kg/ha)
Crop type
Annual
Perennial
NS
2013
2014
2015
2016
2017
2018
2019
2020
2021

280

Fig. 3. Temporal changes in temperature, soil moisture, CWM of Ellenberg-F (moisture requirement), number of herbicide and nitrogen dose in fertilizers. 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 $p \geq 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Spatial analyses of plant communities

The first PCA axis (named thereafter stress-tolerance axis, see **Appendix G, Fig. SG.1** for the correlation of each strategy with each axis) explained 36.4% of the variation and revealed a gradient from continental hygrophilous, ruderal and competitive communities associated with resource-rich environments, to Mediterranean xero-thermophilous stress-tolerant communities adapted to resource-poor and arid environments (**Fig. 4, Appendix G, Fig. SG.2**). Communities with continental species were more nitrophilous, had a higher SLA and flowering duration, while Mediterranean communities had a higher seed mass. The second PCA axis (named thereafter ruderal axis) explained 19.7% of the variation and contrasted stress-tolerant/conservative communities adapted to low disturbance (high stature, late and short flowering) with ruderal/acquisitive communities adapted to high disturbance (short stature, early and long flowering).

Spatial models revealed that climate had a predominant impact on functional composition and particularly on Ellenberg values, opposing in a consistent way Mediterranean communities to nitrophilous continental ones along the stress-tolerance axis (**Fig. 5**). Temperature increased the CWM and CWV of seed mass (divergence) and decreased the CWM and CWV of SLA (convergence). High temperatures lead to more divergence in all environmental requirements (compared to a community of equal richness), except for the requirement for light (Ellenberg-L). Conversely, soil moisture brought convergence in the requirement for temperature and continentality (Ellenberg-T and K). Field margin

management favored ruderal communities with higher SLA and/or lower seed mass (PCA Axis 1), shorter stature (-7.1 cm by management event) and longer flowering duration (+3.7 days by management event; PCA Axis 2). Herbicide applications had no significant effect, while the average annual nitrogen dose in fertilizers slightly decreased the species richness (-3.2x10^{-2} species by kg/ha) and pH requirement, and increased the nitrogen requirement, SLA and divergence in flowering duration (**Fig. 5**). The number of observers surveying a site over the 9-year period was positively correlated with species richness (average increase of 1.7 species by observer) and with the CWM and CWV of flowering duration (divergence).

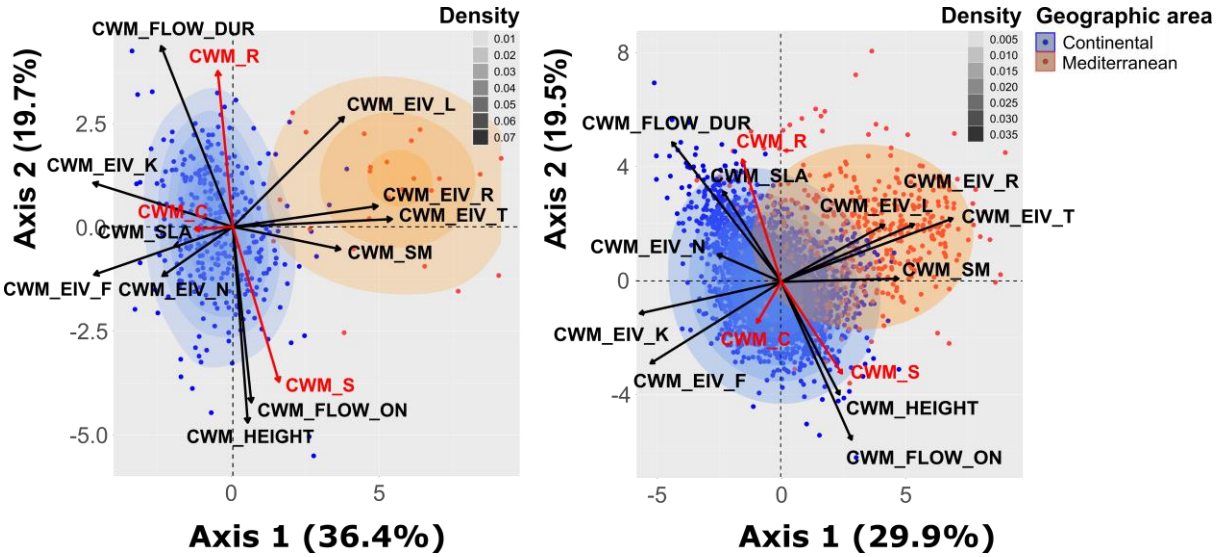


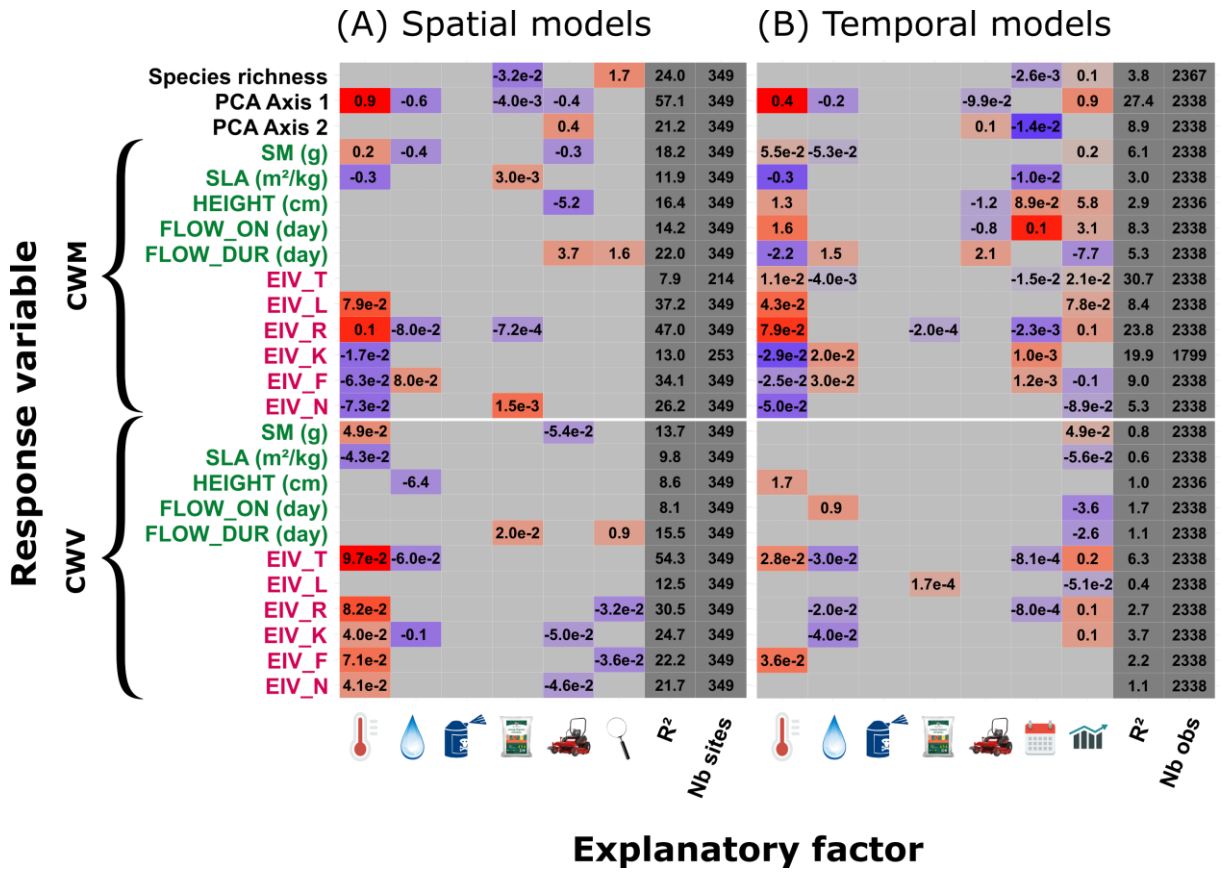
Fig. 4. Normed PCA on CWM (first two axes). (A) Scores of CWM of functional traits computed by site. (B) Scores of CWM of functional traits computed by observation. The color of the dots indicates the region to which they belong and the density curve highlights the concentration of data points in a given area. The correlations of traits to the PCA axes are in **Appendix G**, **Fig. SG.1** and the PCA for annual and perennial species in **Fig. SG. 3**. The CWM of strategies (in red) were added as supplementary variables. Abbreviations for CWM: CWM_SLA, specific leaf area; CWM_HEIGHT, maximum plant height; CWM_SM, seed mass; CWM_FLOW_ON, flowering onset; CWM_FLOW_DUR, flowering duration;

CWM_EIV_L/T/K/F/R/N, requirement for light/temperature/continentality/moisture/pH/nitrogen; CWM_C, competitive strategy; CWM_S, stress-tolerant strategy; CWM_R, ruderal strategy.

Temporal analyses of plant communities

PCA on CWM by observation closely mirrored PCA on CWM by site (**Fig. 4**). The first two axes represented the same ecological strategies, explaining 29.9% and 19.5% of the variation, respectively. However, one difference was that SLA was more correlated to the ruderal rather than the stress-tolerance axis in the PCA based on observations. The competitive strategy was also more tightly associated with Axis 2 than Axis 1 (**Appendix G, Fig. SG.1**).

Climatic factors were also the most influential in temporal models, with high R^2 for the temperature requirement (R^2 = 0.33) and stress-tolerance axis (R^2 = 0.27, **Fig. 5**). Regressions between each Ellenberg value and climatic factors remained consistent across spatial and temporal models, with increasing temperature leading to an increase and divergence in Ellenberg-T values (requirement for temperature). However, new patterns emerged in temporal models, with increasing temperature and drought associated with shorter flowering duration (-2.2 days by °C and +0.15 days by % of soil moisture), and later flowering onset only for increasing temperature (+1.6 days by °C; **Fig. 5**). Margin management was the agricultural practice with the largest impact on community changes, 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 management event). The date of observation also influenced community changes, as a later observation was related to more conservative, competitive and continental communities, and to a decrease in species richness.



Legend

Column

- Temperature (°C)
- Soil moisture (10%)
- Number of herbicide treatments
- Nitrogen dose (kg/ha)
- Number of management events
- Number of observers
- Date of observation (day)
- Decade (yearx10)
- **Nb sites** Number of sites
- **Nb obs** Number of observations

Row

CWM of functional traits

- SM = Seed mass
- SLA = Specific leaf area
- HEIGHT = Maximum plant height
- FLOW_ON = Flowering onset
- FLOW_DUR = Flowering duration

CWM of Ellenberg values

- EIV_T = Ellenberg-T
- EIV_L = Ellenberg-L
- EIV_R = Ellenberg-R
- EIV_K = Ellenberg-K
- EIV_F = Ellenberg-F
- EIV_N = Ellenberg-N

Fig. 5. Results of (A) spatial (SAR) and (B) 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 colored cells, with a p-value threshold of 0.01. Positive estimates are in red, negative estimates in blue, and the strength of the relationship (based on the standardized estimates) is reflected by the lightness of the color (weaker when lighter). It is important to note that the strength of the relationship can only be compared among explanatory factors for a 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 in 1.6 days in the CWM of flowering onset). Models with the year as explanatory factor were run separately.

Results differed depending on the subset of data used (**Fig. 1**). In vineyards and the MZ, soil moisture did not have any influence on diversity or functional composition (**Appendix H**) and temperature only increased the requirement for temperature (Ellenberg-T) and decreased SLA in the MZ. In frequently managed margins of the MZ, Mediterranean species declined (decrease of temperature requirement and convergence towards higher values of continentality, **Appendix H**). Nitrogen dose tended to decrease the number of species in the MZ, an effect also found on annual species. In vineyards, no agricultural effect was detected. Annuals were more impacted by climatic variations and seasonal effects than perennials, with high R^2 for temperature ($R^2 = 0.39$) and moisture ($R^2 = 0.32$) requirements.

Discussion

The changes observed in both spatial and temporal analyses can be interpreted through the lens of Grime's competitor, stress-tolerant, ruderal (CSR) framework (**Fig. 6**; Grime, 1988). According to Grime, stress (i.e. a shortage of resources such as nutrients, water and light) and disturbance (i.e. the partial or total destruction of plant biomass) determine three main plant strategies representing combinations of traits that are viable under conditions of low disturbances and high resources (competitor, C), low disturbances and low resources (stress-tolerant, S) or high disturbances 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 (**Fig. 6**). Below, we use this framework to contextualize our results.

Climate as the main driver of spatial and temporal variations in field margin plant communities

Our analyses revealed a shift towards more stress-tolerant and less ruderal communities, primarily driven by climate (Díaz et al., 2016; Pakeman et al., 2009). Since meteorological variables were extracted at a 8 km resolution, changes in soil moisture can be confidently attributed to climate change and not to the effect of soil compaction due to cultivation. Increasing temperature and drought favored more xerophilous (Ellenberg-F) and thermophilous (Ellenberg-T) 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 or already warmer and drier allowed for coexistence of a wider functional variety of species, suggesting a potential dominance of generalist species with a wider temperature tolerance range, or an increased abundance of thermophilic species without any loss of cold-adapted species. The increase in species richness over time provided additional support for this latter hypothesis.

Our study is one of the first to provide 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). The increase in mean thermal preference at the community-level with rising temperatures was already 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 nine years (Martin et al., 2019). Interestingly, as in other recent studies (Duchenne et al., 2021; Martin et al., 2019), this trend was more pronounced in northern France, while Mediterranean communities responded less to climate change (**Appendix H**). On top of the fact that climatic trends observed in the MZ were weaker than in the CZ, Mediterranean species are already adapted to dry and heat stress, and might be more resilient to extinction risks (Thuiller et al., 2005). Because of their geographic position north of the Mediterranean Sea, they might also experience some competitive release due to the lack of immigrants coming from the south, and the northward shift of more temperate species (Duchenne et al. 2021).

Beyond the increase in mean thermal preference, our temporal models 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 et al., 2012; Richner et al., 2015). In our models, we observed a similar pattern, with less intensive margin management 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. However, we cannot entirely rule out the possibility that plant communities are also responding to past landscape diversification, which could have generated a functional response similar to the one observed for climate change, leading to a decrease in ruderal species as arable lands decrease.

Finally, temporal analyses showed additional phenological changes, suggesting that climate change could increase the occurrence or abundance of late-flowering species, i.e. species that have high thermal requirements to complete their life cycle (Peters et al., 2014). These phenological shifts coincided with a decrease in trait variance, leading to a reduction in functional diversity. Critically, such changes can reduce the ability of species to escape field margin management, which typically favors 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, unless farmers may also adapt the temporality of their practices to climate change.

Agricultural practices have a weaker impact on diversity and species assembly

Temporal variations in agricultural practices over the short-term had a weaker influence on diversity and species assembly than climatic variations (Alarcón Víllora et al., 2019; Fried et al., 2019). Field margin management was the most impactful practice, affecting traits related to the ruderal syndrome in a consistent way. This supports the idea that field margin management, as the only practice applied directly in the margin, has a greater impact than herbicides and fertilization applied in the adjacent agricultural fields, which can only have collateral effects. The lack of herbicide effect on the functional structure of communities could arise because communities affected by herbicides represent a functionally similar subset of communities without herbicide application or because we have omitted traits that reflect herbicide tolerance (leaf cuticle thickness, hairiness…). Also, reducing the intensity of agricultural practices may not necessarily influence the functional composition of communities, because agricultural intensification has already greatly reduced functional diversity, and highly diverse landscapes would be required for some species to recolonize field margins.

Fertilization had a weaker but very consistent impact on floristic communities, increasing the nutrient requirement (Ellenberg-N) and acquisitive capacity (SLA), indicating higher levels of competition among species (Andrade et al., 2021; Pellissier et al., 2014). This can reduce species richness (Kleijn &

Verbeek, 2000), an effect detected in the MZ and leading to the loss of some annual Mediterranean species (Poinas et al., 2023). Due to functional trade-offs, high nitrogen levels can favor nitrophilous plant species, which are often less thermophilous and more acidiphilous, explaining that nitrogen dose was related to affinity for acidic soils in our models. Nitrogen application levels 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 vegetation (Alignier, 2018; Duchenne et al., 2021).

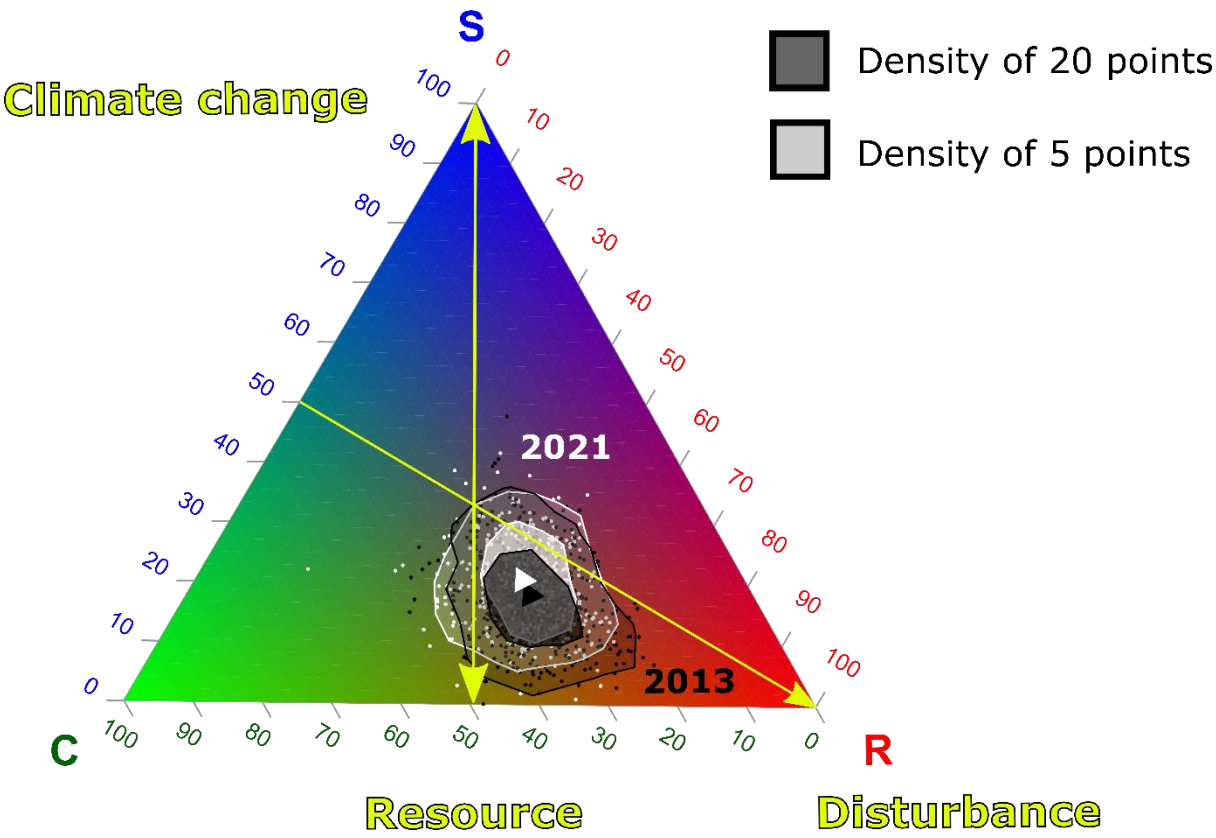


Fig. 6. Grime's CSR triangle depicting the temporal trajectory of community strategies between 2013 and 2021. To enhance clarity, we show only two levels of density curves, with each point representing a specific site. The relative percentages of each strategy are depicted through the use of green, blue and red colors (C = competitor, S = stress-tolerant and R = ruderal). Arrows indicate expected impacts

459 of climate change, disturbance, and resource levels. Temporal models (GAMM) applied to the CWM of
460 each strategy revealed significant decreases in the ruderality and competitiveness of communities, and
461 a significant increase in the stress-tolerance.

462

463 *Functional trade-offs and future implications for communities response to global changes*

464 Our findings revealed that resource level (driven by fertilization) and climate vary the position of
465 communities along the stress-tolerance axis, while disturbance level (driven by field margin
466 management) and climate vary the position of communities along the ruderal axis. This supports the
467 view that functional trade-offs are not only evident on a global scale as found by Wright et al. (2004)
468 and Díaz et al. (2016), but can also occurred within a narrower functional range (such as plants
469 colonizing agricultural field margins). As a result, agricultural intensification and climate change act in
470 opposite ways on the functional composition of communities. Climate change favors species that are
471 adapted to high temperatures and drought, but not to intensive agriculture. It tends to expand the
472 functional range for traits related to stress-tolerance within communities, but reduces the functional
473 range for traits associated to ruderality. Conversely, agricultural disturbances select species more
474 sensitive to current climatic trends, without any particular trend in trait variance.

475 These trade-offs emphasize the need to consider the existing interactions between climate and
476 agricultural practices when predicting future community trajectories (Garnier et al., 2019; Pakeman et
477 al., 2009). Here, we acknowledge the difficulty in quantifying these interactions between climate and
478 agricultural practices, particularly given the limited changes observed in these practices over time.
479 However, the effects of practices were more perceptible in space, allowing us to identify main trends
480 in community trajectories according to several scenarios (**Fig. 6**). Accelerating climate change coupled
481 with an agricultural abandonment and more extensive practices in Europe (Miller et al., 2022; Peeters
482 et al., 2021) will likely result in an increase in xero-thermophilous and conservative species. However,
483 a large part of these species are specialized to their habitat (e.g. Mediterranean species as found in

Munoz et al. (2017); Fried, Chauvel, et al., 2009) and have a high affinity for calcareous soils, which will probably limit their expansion towards the CZ to restricted areas. Areas where they are unable to colonize might suffer a decrease in species richness, and this scenario could be 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 at the same time ruderal species would become less frequent mostly because of drought. This highlights the need to consider the conjunction of climate change and intensive agriculture.

Conclusion

Our study highlights climate as the primary factor affecting 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 a limited effect on species richness and assembly at the national level, with field margin management having the greatest impact. The species selected by climate change are poorly adapted to intensive farming, while the pool of species currently able to colonize field margins is 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 likely reduction in ruderality and an increase in stress-tolerance according to Grime's strategies. Bopp (2023) highlighted a similar increase of stress-tolerance in 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 niche, such as weeds. Long-term monitoring programs are necessary to address some perspectives, 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, the findings presented in this study call for a rethink of our current agricultural model, urging us to prioritize the development of agricultural practices that foster the creation of favorable microclimates while minimizing local intensification. Promising approaches, such as agroforestry, hold the potential to align agricultural production with biodiversity conservation goals by providing habitat diversity, microclimate regulation, and maintenance of ecosystem services.

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Conflict of interest disclosure

All authors of this preprint declare that they have no financial conflict of interest with the content of this article.

Appendix A-H. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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