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

Isis Poinas[1,2*], Christine N Meynard[1], Guillaume Fried[2]

[1] CBGP, INRAE, CIRAD, Institut Agro, IRD, Univ Montpellier, Montpellier, France

[2] Anses, Laboratoire de la Santé des Végétaux, Unité Entomologie et Botanique, 755 avenue du campus Agropolis, CS30016, 34988 Montferrier-sur-Lez Cedex, France

* Corresponding author: Isis Poinas (isis.poinas@inrae.fr)

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Abstract

Over the past decades, agricultural intensification and climate change have led to vegetation shifts in Europe. However, these impacts are often studied using meta-analyses at large scales, or using taxonomic diversity. 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, agricultural practices, plant species richness, and trait community-weighted means and variances 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. Changes in plant communities were noticeable, especially as they relate to climate change, while the impact of agricultural practices was limited and mainly exerted through field margin management and to a lesser extent, fertilization. Mediterranean sites, vineyards and perennial species demonstrated reduced response to climatic variations. Our findings suggest that species adapted to climate change (including Mediterranean species) have increased in proportion and are spreading northward. Importantly, we identified functional trade-offs suggesting that these species are also the most vulnerable to intensive agricultural practices. We put these results into the conceptual framework of Grime's CSR triangle and suggest that the convergence of climate change and the maintenance of a highly intensive agriculture could carry a risk of abrupt declines in floristic diversity of field margins, a concern that merits further attention.

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 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 increased since then (Richner et al., 2015). Pesticide reduction plans have had little effect in France (Guichard et al., 2017), hindering the detection of temporal changes in biodiversity linked to 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 agricultural practices, combining spatial and temporal analyses seems necessary to study 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 is required to accurately understand these changes. This is particularly important in an agroecological context, where both resource (fertilization) and disturbance (herbicides, field management) gradients play crucial roles (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 frequent margin management (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 resources, 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 (1988) proposed a framework called the CSR triangle, which defines three axes of variation - competitive, stress-tolerance, and ruderal adaptations - that are correlated to multiple traits and have proven useful to understand plant community dynamics (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 traits variations. For example, in French wheat fields, species with small height, 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 and agricultural practices in France structure the diversity and trait composition 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, we aimed to determine temporal trends in agricultural practices and climate, and explore the spatial and

temporal drivers of species diversity and functional traits. 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 . 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., under review), we included analyses separating this region from the others. 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 survey

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 yearly monitored 555 agricultural field margins across continental France between 2013 and 2021 (with some site turnover) (**Fig. 1**). These survey sites represented four 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 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 855 taxa. As 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).

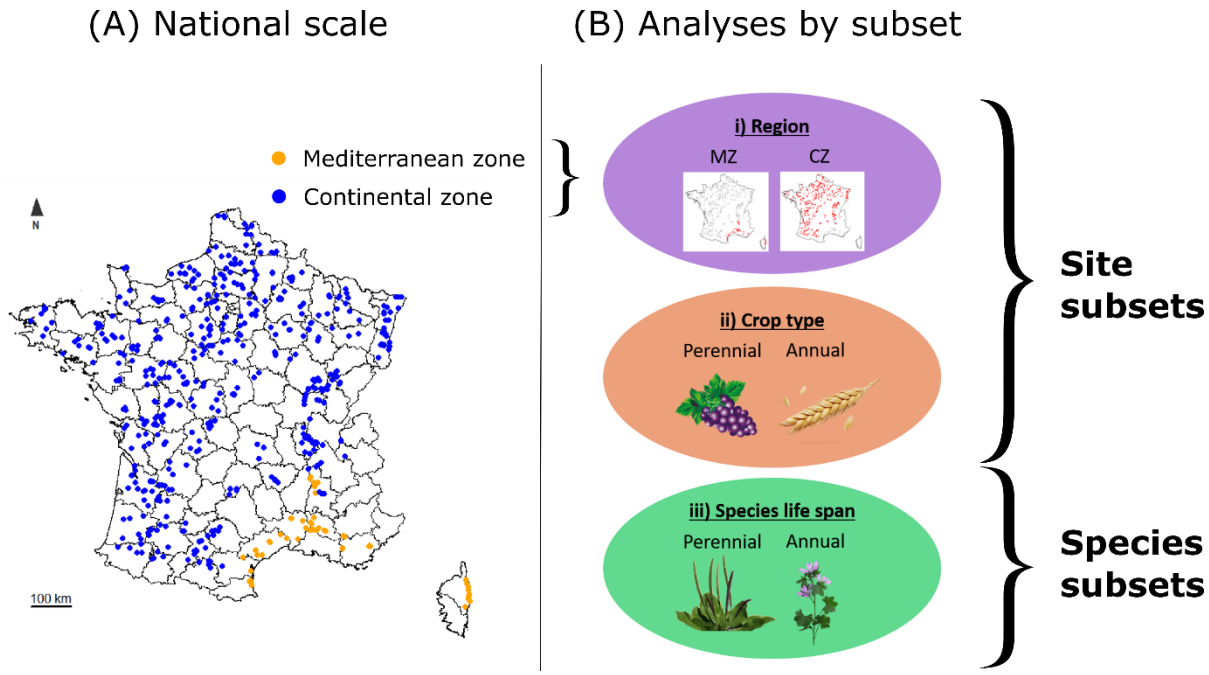


Fig. 1. (A) Distribution map of the 555 field margins monitored at least one year between 2013 and 2021 in France. The black lines represent the limits of French departments. Orange: sites in Mediterranean zone (n = 57), blue: sites in Continental zone (n = 498). The contours of the Mediterranean zone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

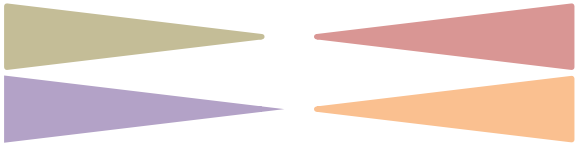
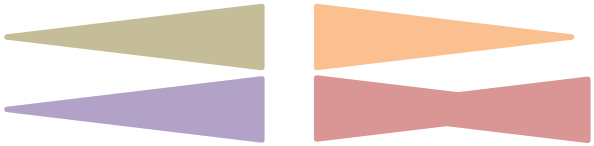
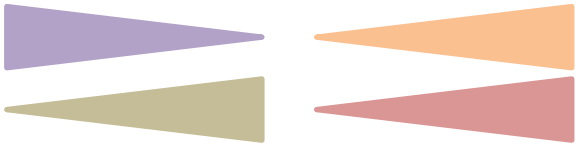
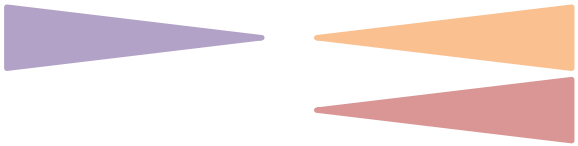
Climatic and agricultural variables

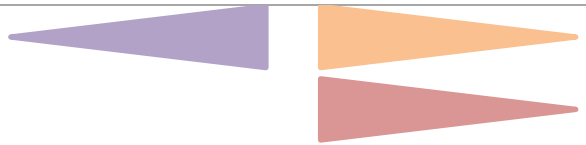
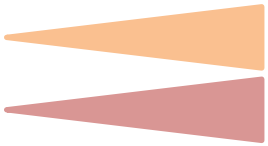
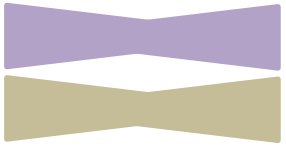
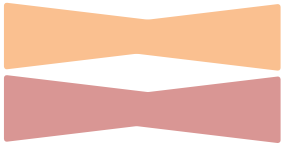
We gathered two types of explanatory variables: the first came directly from the 500-ENI network and reflects agricultural practices assessed directly on the monitoring sites; the second one included meteorological data from an external database (see below).

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. 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 noted the expected link of each factor and trait to the agricultural resource and disturbance gradient, and to climate change. A left-pointing triangle indicates an increase in relation to the corresponding factor of the same color. An hourglass symbol was used for relationships with 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		All types of management (mowing, grazing…). Number of 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		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

153

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 weight 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).

The species pool was defined by the biogeographic region in the spatial analyses, and by site in the temporal analyses (see below), to focus on the relevant axes of variation we were most interested in. We extracted biogeographic regions from the VégétalLocal map (Office français de la biodiversité, 2021). To quantify the difference between observed and null CWV, we computed effect sizes

178 (**Appendix D**). A positive effect size denotes a divergence in trait values within the community
179 (convergence for negative effect size). We performed a normed PCA on the CWM of traits (by site for
180 spatial analyses, by observation for temporal analyses) and we took the first two axes, representing
181 different combinations of traits.

182 *Temporal trends in climate, agricultural practices and plant communities*

183 To assess the main temporal trends in our dataset, we used Spearman correlation coefficients with the
184 year of observation (Martin et al., 2019; **Appendix E**) on our variables of interest (climate, agricultural
185 practices, plant diversity, CWM and CWV). For all analyses, we chose a p-value threshold of 0.01 to
186 focus on the effects for which our confidence level was highest. We also repeated this analysis on
187 subsets of data, including Mediterranean (MZ) vs Continental (CZ) zones, margins adjacent to annual
188 crops vs vineyards, and annual vs perennial plant species (**Fig. 1**).

189 *Spatial analyses of plant communities*

190 To analyze the effects of spatial variations in agricultural practices, explanatory factors and species
191 abundances were averaged across years within sites having at least five years of data and five floristic
192 observations, leaving a total of 349 sites. Using spatial simultaneous autoregressive models (SAR;
193 package SPDEP, function *errorsarlm*; Cressie, 2015), we examined the relationship between each
194 response variable and the explanatory factors. The Nagelkerke pseudo-R^2 was used to assess the
195 model's explanatory power, and we controlled for the observer bias by adding the number of
196 successive observers in a site as a fixed effect.

197

198 *Temporal analyses of plant communities*

199 To disentangle temporal effects on plant communities, we used generalized additive mixed models
200 (GAMM) to account for repeated measures at a site, with a Gaussian distribution in most cases (but
201 see **Appendix F**, **Table SF.2**). We included the site identity as a random effect, and a first-order

temporal autocorrelation structure within sites (Box et al., 2015). Observer bias was accounted for by including the observer identity as a random term nested within sites. 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 F**), resulting in varying observation numbers across models (see **Fig. 4**).

Results

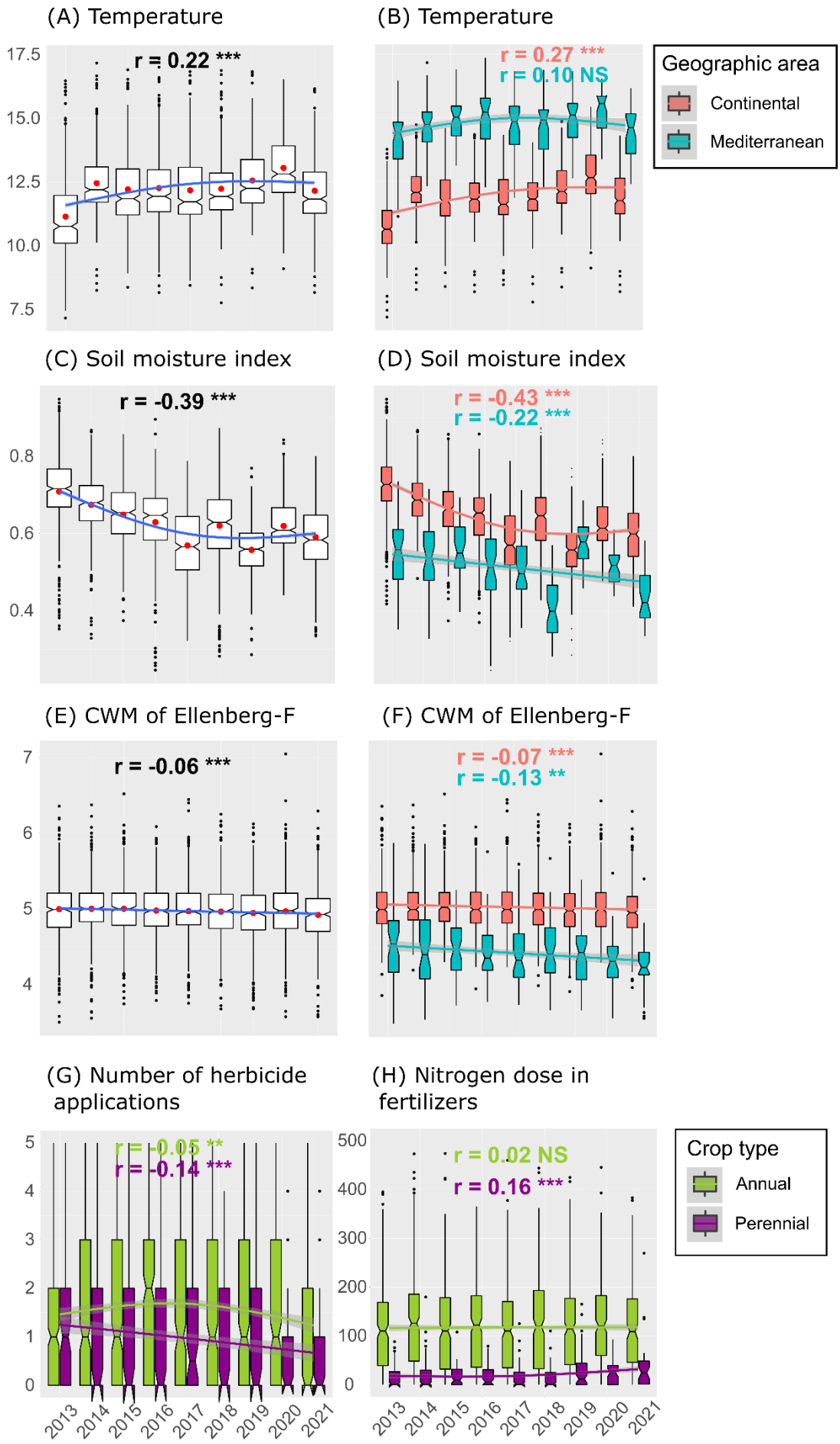
Temporal trends in climate, agricultural practices and plant communities

Temperatures have significantly increased ($r = 0.22$, $p < 0.001$) by an average of 1.13°C over a decade (0.45°C in the Mediterranean Zone), while soil moisture has steadily declined ($r = -0.39$, $p < 0.001$, -14% by decade) (**Fig. 2**, and **Appendix E**). These trends differed between the Mediterranean Zone (MZ) and the Continental Zone (CZ), with the MZ experiencing a slower decline in soil moisture of only -8.8% by decade due to a high cumulative precipitation in 2019 (**Fig. 2**). Regarding agricultural practices, herbicides slightly decreased over time in vineyards ($r = -0.14$, $p < 0.001$; **Fig. 2**), with an even weaker trend in annual crops ($r = -0.05$, $p = 0.008$). Fertilization showed no significant temporal trend, except in vineyards where the cumulative dose of nitrogen has slightly increased ($r = 0.16$, $p < 0.001$). The number of margin management events decreased in the MZ ($r = -0.17$, $p = 0.004$), where most vineyards are located, but this trend was not observed in vineyards across the entire country, nor in the CZ. Floristic surveys were conducted increasingly earlier in the season in the CZ ($r = -0.13$, $p < 0.001$, 10.48 days earlier by decade) (**Appendix E**). Overall, there is a clear warming and drying trend in climate, but agricultural trends remain elusive.

Plant species richness has slightly increased over time at the national scale ($r = 0.07$, $p < 0.001$, 1.3 species per decade), even more in the MZ ($r = 0.20$, $p < 0.001$, 4.2 species by decade) and vineyards ($r = 0.17$, $p < 0.001$, 3.3 species by decade). In France, we saw an increase in the CWM of maximal height ($r = 0.08$, $p < 0.001$), seed mass ($r = 0.10$, $p < 0.001$), flowering onset ($r = 0.07$, $p < 0.001$, 3.12 days by

227 decade) and a decrease of flowering duration ($r = -0.10$, $p < 0.001$, -7.83 days by decade) (**Appendix E**).
228 The Ellenberg-L, T and R values have increased ($r = 0.06$, 0.14 and 0.11 respectively, $p < 0.001$), while
229 the Ellenberg-F and N values have declined ($r = -0.06$ and -0.07 respectively, $p < 0.001$). CWV have
230 decreased for most of traits, and particularly for phenological traits such as flowering onset and
231 flowering duration ($r = -0.12$ and -0.09 respectively, $p < 0.001$), while they have increased for most of
232 Ellenberg values and particularly for the Ellenberg-T, R and K ($r = 0.16$, 0.11 and 0.09 respectively, $p <$
233 0.001). Changes in functional traits were more pronounced in the MZ, with an important reduction in
234 the range of flowering onset and duration (**Appendix E**). Conversely, changes in Ellenberg values were
235 only significant in the CZ and in annual crops. One exception was the temperature (Ellenberg-T) and
236 moisture (Ellenberg-F) requirements, which have significantly changed in both the MZ and CZ.
237 Interestingly, Ellenberg values showed a temporal trend mainly for perennial species, while only
238 functional traits shifted in annual communities, with e.g. a convergence towards shorter and later
239 flowering (**Appendix E**).

240


(A) Temperature
r = 0.22 ***
(B) Temperature
r = 0.27 ***
r = 0.10 NS
Geographic area
Continental
Mediterranean
(C) Soil moisture index
r = -0.39 ***
(D) Soil moisture index
r = -0.43 ***
r = -0.22 ***
(E) CWM of Ellenberg-F
r = -0.06 ***
(F) CWM of Ellenberg-F
r = -0.07 ***
r = -0.13 **
(G) Number of herbicide applications
r = -0.05 **
r = -0.14 ***
(H) Nitrogen dose in fertilizers
r = 0.02 NS
r = 0.16 ***
Crop type
Annual
Perennial
2013
2014
2015
2016
2017
2018
2019
2020
2021

241

242 **Fig. 2**. Temporal changes in temperature, soil moisture, CWM of Ellenberg-F, number of herbicide and
243 nitrogen dose in fertilizers. Red dots represent mean values. The curves are from a GAM, with a smooth
244 term on the year restricted to three effective degrees of freedom. (A, C, E) National trend. (B, D, F)
245 Trend by geographic area: CZ and MZ. (G, H) Trend by crop type: annual (wheat, maize, lettuce) and
246 perennial (vineyard). Spearman coefficients are reported and significance of correlation coefficients is
247 referred as following: NS $p \geq 0.01$; ** $p < 0.01$; *** $p < 0.001$.

248

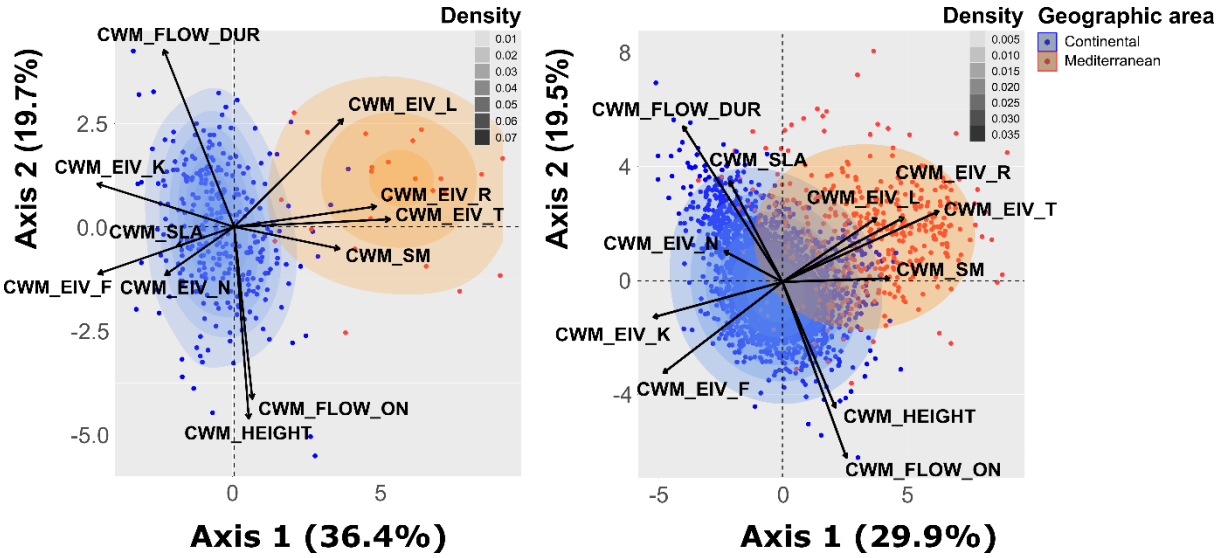
249 *Spatial analyses of plant communities*

250 The first PCA axis (named thereafter stress-tolerance axis) explained 36.4% of the variation and
251 revealed a gradient from continental hygrophilous, ruderal and competitive species associated with
252 resource-rich environments, to Mediterranean xero-thermophilous stress-tolerant species adapted to
253 resource-poor and arid environments (**Fig. 3, Appendix G, Fig. SG.2**). Communities with continental
254 species were more nitrophilous, had a higher SLA and flowering duration, while Mediterranean
255 communities had a higher seed mass. The second PCA axis (named thereafter ruderal axis) explained
256 19.7% of the variation and contrasted competitive/conservative species adapted to low disturbance
257 (high stature, late and short flowering) with ruderal/acquisitive species adapted to high disturbance
258 (short stature, early and long flowering).

259 Spatial models revealed that climate had a predominant impact on functional composition and
260 particularly on Ellenberg values, opposing in a consistent way Mediterranean species to nitrophilous
261 continental ones along the stress-tolerance axis (**Fig. 4**). Temperature increased the CWM of seed mass
262 and decreased the CWM and CWV of SLA (convergence). High temperatures lead to divergence in all
263 Ellenberg values except the Ellenberg-L, while soil moisture brought convergence in the Ellenberg-T
264 and K. Field margin management was the agricultural practice with the strongest effect, favoring
265 ruderal species with higher SLA and/or lower seed mass (PCA Axis 1), shorter stature and longer
266 flowering duration (PCA Axis 2). Herbicide applications had no significant effect, while the average

267 annual nitrogen dose in fertilizers decreased the species richness and Ellenberg-R, but increased
268 Ellenberg-N, SLA and divergence in flowering duration (**Fig. 4**). The number of observers surveying a
269 site over the 9-year period was positively correlated with species richness (average increase of 1.68
270 species by observer) and with the CWM and CWV of flowering duration.

271



272

273 **Fig. 3**. Normed PCA on CWM (first two axes). (A) Scores of CWM of functional traits computed by site.
274 (B) Scores of CWM of functional traits computed by observation. The color of the dots indicates the
275 region to which they belong and the density curve highlights the concentration of data points in a given
276 area. The correlations of traits to the PCA axes are in **Appendix G**, **Fig. SG.1** and the PCA for annual and
277 perennial species in **Fig. SG. 3**. Abbreviations for CWM: CWM_SLA, specific leaf area; CWM_HEIGHT,
278 maximum plant height; CWM_SM, seed mass; CWM_FLOW_ON, flowering onset; CWM_FLOW_DUR,
279 flowering duration; CWM_EIV_L/T/K/F/R/N, Ellenberg-L/T/K/F/R/N.

280

281 *Temporal analyses of plant communities*

282 PCA on CWM by observation closely mirrored PCA on CWM by site (**Fig. 3**). The first two axes
283 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.

Climatic factors were also the most influential in temporal models, with high R^2 for the CWM of Ellenberg-T (R^2 = 0.33) and stress-tolerance axis (R^2 = 0.27, **Fig. 4**). Regressions between Ellenberg values and climatic factors remained consistent across spatial and temporal models, with increasing temperature leading to an increase and divergence in Ellenberg-T values. However, new patterns emerged in temporal models, with increasing temperature and drought associated with shorter flowering duration, and later flowering onset only for increasing temperature (**Fig. 4**). Here again, margin management was the agricultural practice with the largest impact on community changes, with an increase in its frequency associated with more ruderal species. The date of observation also influenced community changes, with a later observation related to more conservative, competitive and continental species, and to a decrease in species richness.

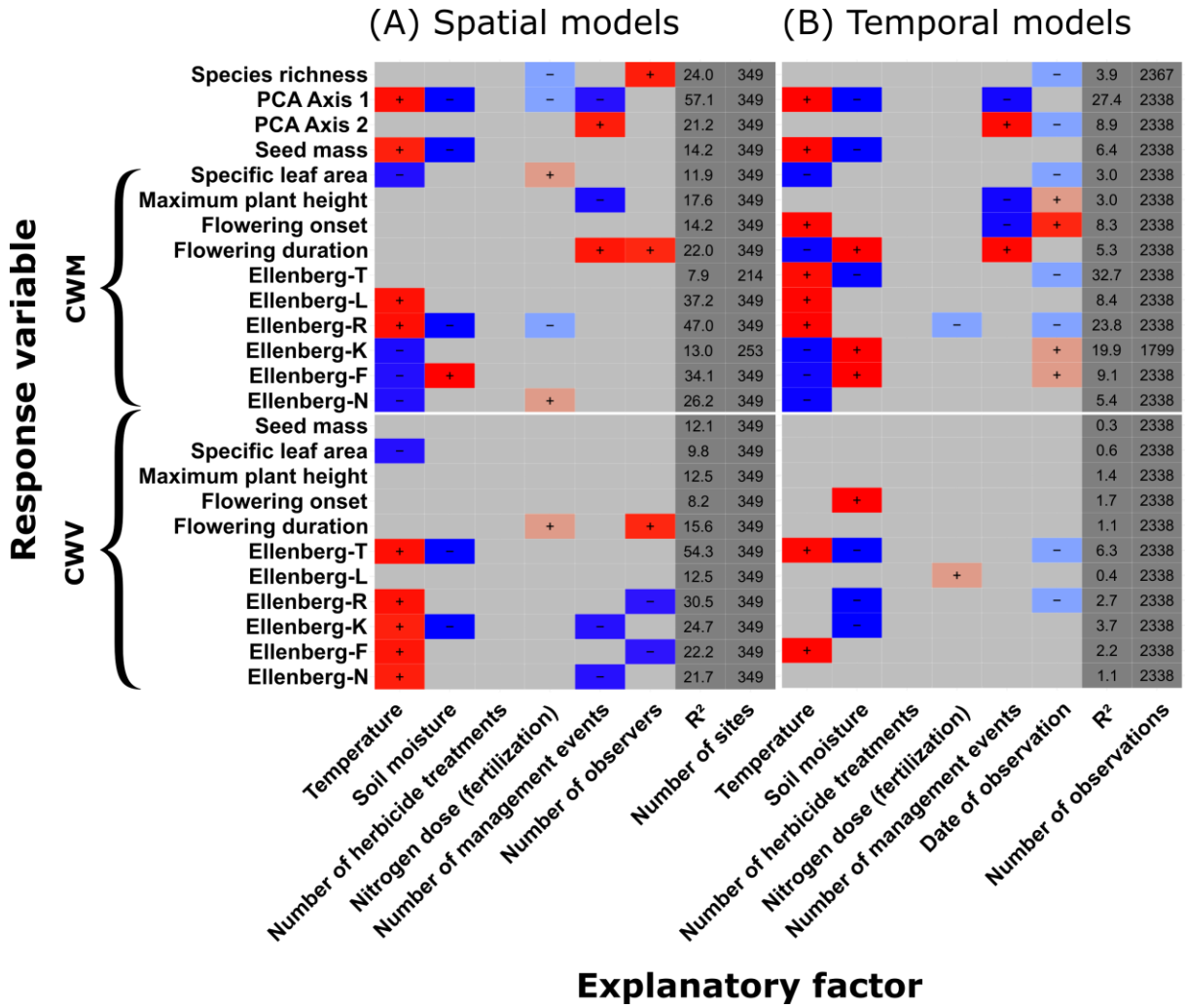


Fig. 4. Results of (A) spatial (SAR) and (B) temporal models (GAMM), with response variables in rows and explanatory factors in columns. The adjusted R^2, expressed as a percentage of variation, and the number of observations are reported. Significance is indicated by colored cells, with a p-value threshold of 0.01. Positive estimates are in red, negative estimates in blue, and the strength of the relationship (based on the estimates) is reflected by the lightness of the color (weaker when lighter). As response variables were standardized prior to the analysis, estimates can be compared (see **Appendix H** for raw values).

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 Ellenberg-T and decreased SLA in the MZ. In the MZ, Mediterranean species declined (decrease of Ellenberg-T and convergence towards higher values of Ellenberg-K) in frequently managed margins. 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. The effect of the observation date was opposite in the MZ compared to the national scale, with Ellenberg-L increasing and Ellenberg-R and N decreasing across the season. Annuals were more impacted by climatic variations and seasonal effects than perennials, with high R^2 for the Ellenberg-T (R^2 = 0.39) and F (R^2 = 0.32). Margin management affected perennials and annuals differently. For perennials, only the height was reduced with increasingly frequent management, while annuals flowered earlier and longer. Finally, fertilization had a negative effect on species richness and caused a shift towards more continental and late-flowering species in annuals.

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. 5**; 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. 5**). 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 species, primarily driven by climate (Díaz et al., 2016; Pakeman et al., 2009). 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 a functional convergence of Ellenberg values in wet and cold sites, while sites increasingly or already warmer and drier allowed for coexistence of a wider functional variety of species.

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 trends that align well with the existing literature, including a decrease in mean SLA and an increase in mean seed mass (Alarcón Víllora et al., 2019; Kühn et al., 2021). These trait values (low SLA, high seed mass) are also known to be linked to less intensive agriculture (Fried et al., 2020; Richner et al., 2015). 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.

Finally, temporal analyses showed additional phenological changes, suggesting that climate change could increase the abundance of late-emerging and late-flowering species, i.e. species that have high thermal requirements to complete their life cycle (Peters et al., 2014). Critically, such changes can reduce the ability of species to escape field margin management, which typically favors early and long flowering species, 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. Maximum height was the only trait of the ruderal axis that did not respond to climate, but only to the level of disturbance. Interestingly, this trait tended to increase more in the MZ, where a decrease in the frequency of margin management was observed. This potentially suggests a functional change in response to declining agricultural intensification in the MZ, that would warrant further investigations. It is worth noting that the ruderal axis partially partitions annual from perennial species (Lavorel & Garnier, 2002; also the PCA are not exactly similar on these two sets of species, see **Appendix G**), consistent with studies showing that agricultural disturbances benefit more annual species in field margins (Bassa et al., 2011; Hall et al., 2020).

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., under review). 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 have only slightly increased over time, primarily in vineyards. This aligns with the weak change in global nitrophily levels in plant communities over time, suggesting that eutrophication may no longer be the primary driver of changes in vegetation (Alignier, 2018; Duchenne et al., 2021).

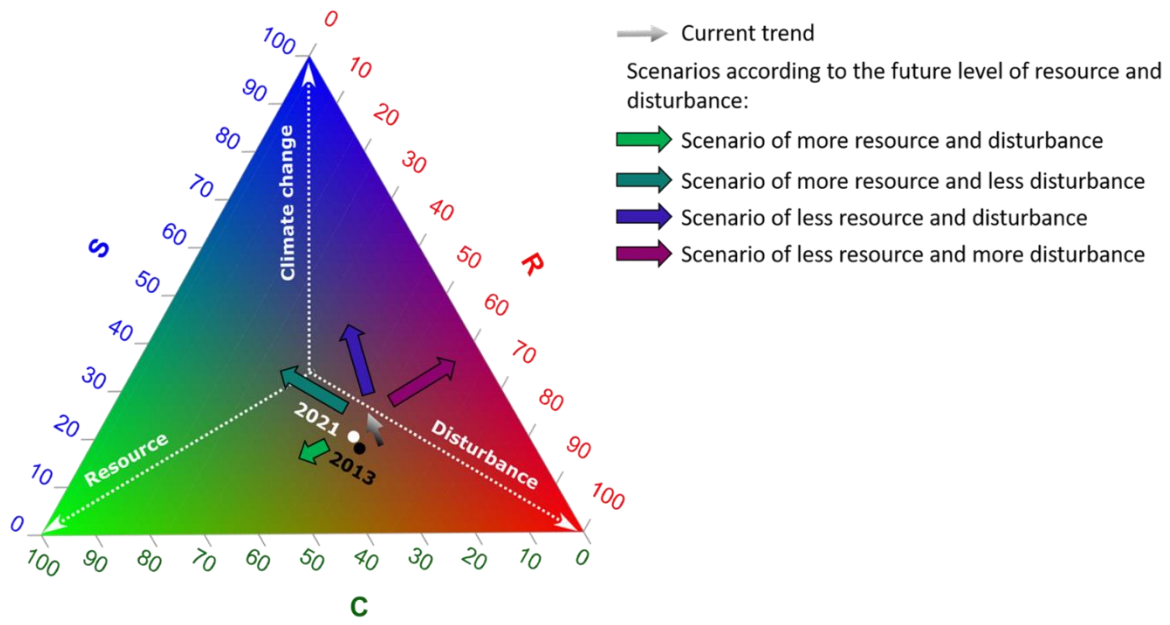


Fig. 5. Grime's CSR triangle depicting the temporal trajectory of community strategies between 2013 and 2021. The CSR scores for 119 out of 142 focal species were extracted from Pierce et al. (2017). We computed community-weighted means of CSR scores by observation, which were then averaged by year. 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). White arrows indicate expected impacts of climate change, disturbance, and resource levels. Colored arrows represent scenarios based on future agricultural intensification levels, assuming persistent or intensified climate change (thus ignoring the right corner scenario of declining stress-tolerant and increasing ruderal species). Increased resource and disturbance levels could lead to a collapse in functional diversity, represented by a shorter arrow.

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

Our findings revealed that resource level (driven by fertilization) and climate vary the position of communities along the stress-tolerance axis, while disturbance level (driven by field margin management) and climate varies the position of communities along the ruderal axis. This supports the view that functional trade-offs are not only evident on a global scale as found by Wright et al. (2004)

409 and Díaz et al. (2016), but can also occurred within a narrower functional range (such as plants
410 colonizing agricultural field margins). As a result, agricultural intensification and climate change act in
411 opposite ways on the functional composition of communities. Climate change favors species that are
412 adapted to high temperatures and drought, but not to intensive agriculture. On the contrary,
413 agricultural disturbances select species more sensitive to current climatic trends.

414 These trade-offs emphasize the need to consider the existing interactions between climate and
415 agricultural practices when predicting future community trajectories (Garnier et al., 2019; Pakeman et
416 al., 2009). Our results show little effect of agricultural practices, likely because of their limited temporal
417 trend and great range of spatial variability. Our findings allow us to distinguish main trends in
418 community trajectories according to four climatic and agricultural scenarios (**Fig. 5**). The most likely
419 scenario is accelerating climate change coupled with an agricultural abandonment and more extensive
420 practices in Europe (blue arrow in **Fig. 5**, Miller et al., 2022; Peeters et al., 2021), which will likely result
421 in an increase in xero-thermophilous and conservative species. However, a large part of these species
422 are specialized to their habitat (e.g. Mediterranean species as found in Munoz et al. (2017); Fried,
423 Chauvel, et al., 2009) and have a high affinity for calcareous soils, which will probably limit their
424 expansion towards the CZ. Areas where they are unable to colonize might suffer a decrease in species
425 richness, and this scenario could be worsen if current levels of agricultural intensification are
426 maintained or increased. Mediterranean species could face severe agricultural intensification in
427 northern France, that would likely limit their expansion, while at the same time ruderal species would
428 become less frequent mostly because of drought. This highlights the need to consider the conjunction
429 of climate change and intensive agriculture.

430

431 **Conclusion**

432 Our study highlights climate as the primary factor affecting field margin plant communities in France,
433 with increasing temperatures and decreasing soil moisture fostering Mediterranean, stress-tolerant

434 and conservative species, while negatively affecting ruderal species. In comparison, agricultural
435 practices had a limited effect on diversity and species assembly at the national level, with field margin
436 management having the greatest impact. It is clear from our findings that the persistence of intensive
437 agricultural practices and accelerating climate change would have critical consequences for the
438 conservation of floristic diversity in agroecosystems, as species selected by climate change are poorly
439 adapted to intensive farming. To preserve biodiversity, future agricultural practices should prioritize
440 the creation of a favorable microclimate for species persistence while reducing local intensification.
441 Our findings suggest a likely reduction in ruderality and an increase in stress-tolerance according to
442 Grime's strategies, raising concerns about potential loss of plant diversity in intensively managed areas.
443 Considering the synergies between climate change and agricultural practices, even at a regional level,
444 is thus crucial for addressing future agriculture challenges.

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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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