Functional trade-offs: exploring the temporal response of field margin plant communities to climate change and agricultural practices

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Abstract

Over the past decades, agricultural intensification and climate change have led to vegetation shifts. 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 temporal response of diversity and functional traits to variations in climate and intensity of agricultural practices. 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 agricultural practices (e.g. seed mass, specific leaf area), across 555 sites in France between 2013 and 2021. We found clear temporal climatic trends (temperature increased while soil moisture decreased), whereas trends in agricultural practices were weak over the past decade, with only slight decreases in herbicides and margin management intensity. During the same period, functional changes in plant communities were significant, showing an increase of thermophilic species (including some Mediterranean species) with a conservative resource acquisition strategy (high stature, late and short flowering), mainly explained by climate change. The reduction in field margin management intensity (mainly mowing), also resulted in a vegetation shift towards a more conservative strategy. In contrast, there was no impact of the slight temporal changes of practices conducted within cultivated fields (herbicides, fertilization) on vegetation changes. Our findings suggest that species adapted to climate change (including Mediterranean and conservative species) have temporally 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 temporal decline of competitive and ruderal species in favor of stress-tolerant species better adapted to climate change. Choosing less intensive management can broaden the functional spectrum of agricultural plant communities, by maintaining the ability of stress-tolerant species selected by climate change to colonize habitats largely dominated

47   by ruderals. Put together, these results suggest that climate change and agricultural intensification

48   could have synergistic negative impacts on plant diversity in field margins, highlighting the need to

49   study several biodiversity drivers at the same time in anthropized landscapes.

50

51   **Keywords:** functional trade-offs, climate change, temporal variation, field margin, plant diversity,

52   agricultural practices, CSR strategies, Mediterranean species, phenology

53   **Introduction**

54

55   Since the 1950s, agricultural intensification has led to declining biodiversity (Emmerson et al., 2016),

56   while climate change has caused notable changes in a wide range of taxa and habitats (Lovejoy, 2006).

57   However, teasing out the relative importance of these two drivers on community trajectories can be

58   quite challenging (Oliver & Morecroft, 2014). Since agricultural intensification took place in the 1950s

59   in Europe, the main changes linked to agricultural practices (notably in terms of intensity in pesticide

60   use and fertilization) in plant communities have likely already occurred (Lososová et al., 2004). For

61   example, a meta-analysis considering 32 studies across Europe and covering the time period from 1939

62   to 2011 showed that weed species richness declined up to the 1980s, but has stabilized or even

63   increased since then (Richner et al., 2015). Pesticide reduction plans have had so far little effect in

64   France (Guichard et al., 2017), hindering the detection of temporal changes in biodiversity linked to

65   changes in pesticide use. Conversely, short-term declines in species diversity due to climate change

66   have been observed (e.g. Fonty et al., 2009), and recent temperature increases in France may impact

67   plant communities similarly (Baude et al., 2022; Martin et al., 2019).

68   Temporal changes in plant communities cannot be discerned solely using taxonomic approaches due

69   to the differing traits affected by resource availability and disturbance levels (Garnier & Navas, 2012);

70   therefore, a functional approach provides an additional perspective to accurately understand these

71   changes. This is particularly important in agroecosystems, where both resource (fertilization) and

72   disturbance (herbicides, field margin management) gradients play crucial roles in shaping communities

73   (Gaba et al., 2014; MacLaren et al., 2020). For instance, weeds with a ruderal strategy (low height and

74   seed mass, long and early flowering, high SLA) are better adapted to agricultural disturbances, such as

75   tillage, herbicides or management by mowing (Grime, 2006; Fried et al., 2022). At the same time, traits

76   responding to agricultural practices can co-vary with other traits that are linked to resource acquisition,

77   competitive ability, or climate. For example, seed mass, which is often used as a proxy for competitive

78   ability, increases along soil fertility, temperature and solar radiation gradients (Fried et al., 2022;

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79   Murray et al., 2004). Furthermore, correlations among different traits may represent trade-offs that

80   impact community adaptation (Díaz et al., 2016; Wright et al., 2004). Because of these trade-offs,

81   selective pressures due to one driver (e.g. climate change) may impact community properties along

82   the other (e.g. agricultural intensification). In this context, Grime (1977) proposed a framework called

83   the CSR triangle, which defines three strategies (competitiveness, stress-tolerance, and ruderality)

84   along two axes of variation (resource and disturbance). These strategies are correlated to multiple

85   traits and have proven useful to understand plant community dynamics in agroecosystems (Fried et

86   al., 2022). As traits responding to climate and agricultural practices may co-vary (Garnier & Navas,

87   2012), it can be difficult to identify the main drivers behind community changes, making this

88   framework potentially useful to understand such trade-offs.

89   To understand the complex interactions between climate change and agricultural practices, it is thus

90   essential to examine temporal changes in species trait distribution. For example, in French wheat

91   fields, ruderal species increased their frequency between the 1970s and 2000s, potentially due to their

92   ability to escape recurrent disturbances, such as herbicide applications (Fried et al., 2012). Inter-annual

93   variations in specific leaf area, leaf dry matter content and plant height are related to nitrogen supply

94   (Borgy et al., 2017; Gaba et al., 2014), while increased precipitations push the foliar economic spectrum

95   towards more acquisitive species (i.e. with higher SLA; Wheeler et al., 2023). Additionally, mean

96   thermal preference of plant communities, as well as their phenology, can vary over time in response

97   to temperature changes, even over relatively short periods (Bellard et al., 2012; Martin et al., 2019).

98   These temporal variations in functional traits reveal patterns that cannot be assessed solely with

99   space-for-time substitution.

100   In this study, we aimed at deciphering how inter-annual temporal variations and temporal trends in

101   climate (temperature, soil moisture) and agricultural practices (frequency of herbicide use, margin

102   management and nitrogen dose in fertilizers) in France structure species richness, trait composition

103   and ecological strategies of field margin plant communities. We studied the herbaceous field margin,

104 which represents the uncultivated vegetated area located between the cultivated strip and the

105 adjacent habitat. Using a standardized national monitoring effort spanning 9 years (2013-2021) in 555

106 agricultural field margins covering continental France, our study stands as one of the first to investigate

107 the temporal trends in agricultural practices and climate, and explore the response of species richness,

108 trait composition and ecological strategies to these trends at such extensive scales. We hypothesized

109 that plant traits sensitive to temperature and soil moisture will co-vary with temporal warming trends

110 while agricultural practices would have a comparatively weaker temporal influence on plant

111 communities, as we did not expect clear temporal trends in these practices. We also expected a limited

112 impact of agricultural practices on margin plant communities, because field margins only receive a

113 small amount of nitrogen and herbicides drifting from neighboring plots. Furthermore, we explored

114 the connection between Grime's CSR strategies, climate and farming practices. Considering that these

115 strategies are linked to resource and disturbance levels, we hypothesized that they would respond to

116 climate factors (particularly reduced soil moisture) and agricultural practices (disturbance and

117 resource provision through fertilization). On top of the national analyses, and because this dataset

118 includes the Mediterranean flora, which has been shown to respond more strongly to some

119 agricultural filters (Poinas et al., 2023), we included analyses separating this region from the rest of

120 France. We also separated vineyards from annual crops, because vineyards include very different

121 management practices and no crop rotation (Metay et al., 2022). Finally, we also analyzed annual plant

122 species separately, as they may respond more rapidly to environmental changes (Martin et al., 2019;

123 Fitter & Fitter, 2002).

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6

125 **Materials and methods**

126 *Vegetation surveys*

127 We used vegetation data from the 500-ENI network, which is funded by the French Ministry of

128 Agriculture (see details in Andrade et al., 2021) and monitored 555 agricultural field margins across

129 continental France between 2013 and 2021 (with some site turnover) (**Fig. 1**). These survey sites

130 represented three main crop types **(Appendix A, Fig. SA. 1)**: annual crops (with winter wheat or maize

131 as the main crop production in the rotation), market gardening crops (mainly lettuce) and vineyards.

132 The proportion of sites under organic farming was roughly 20%, but agricultural practices covered a

133 wide range of pesticide application, fertilizers and soil management. Within each survey site, plant

134 species were identified in ten 1 m² quadrats along the field margin (**Appendix A**, **Fig. SA.2**). Presence-

135 absence of each species was recorded for each quadrat, which provided a frequency of occurrence

136 from 0 to 10 in each field margin, used here as an index of relative abundance. Surveys were performed

137 once per year at peak flowering (between the end of April and the beginning of August, depending on

138 the region). At the national scale, this represented 4172 observations (year x site), leading to the

139 identification of 852 taxa. Because observers changed among sites and over time (312 observers in

140 total, each observer following on average 5 distinct sites during 4 years) and did not have the same

141 level of expertise, we constrained our analyses to a subset of 142 focal species (Andrade et al., 2021)

142 which are expected to be known by all the observers (and thus removing 11% of the total abundances).
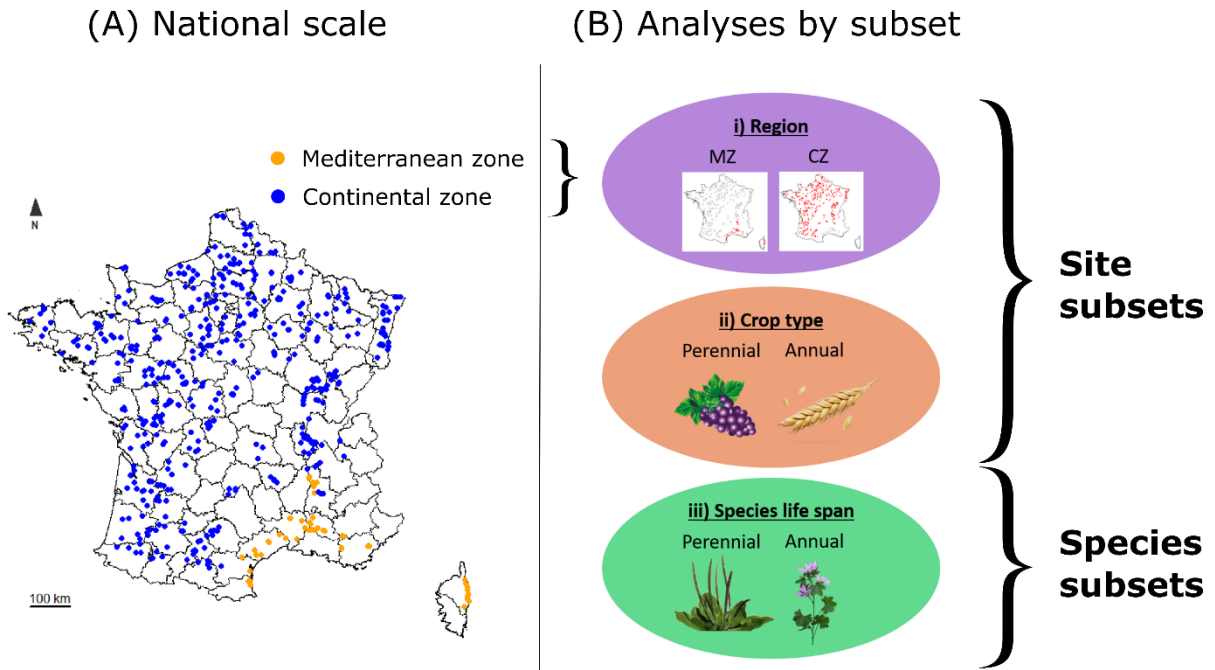
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Fig. 1. (A) Distribution map of the 555 field margins monitored at least one year between 2013 and 2021 in France. The black lines represent the limits of French departments. Orange: sites in Mediterranean zone (n = 57), blue: sites in Continental 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

160   factors, as a previous study on the same dataset demonstrated that landscape variables account for a

161   negligible proportion of variance at the national scale, in contrast to climate (Poinas et al., 2023).

162   Agricultural practices were reported yearly from interviews of farmers into a standardized online

163   database. Data collected relate to fertilization, herbicide use and field margin management (mainly

164   mowing of vegetation). Daily meteorological data were extracted from the SAFRAN climate model of

165   Météo France, with a resolution of 8 km (Le Moigne, 2002). Meteorological data were averaged over

166   a one-year window prior to each floristic observation, while agricultural data were summed over the

167   same period (**Table 1**). We selected variables that were weakly correlated (Spearman correlation <

168   0.65, **Appendix B**) and have been shown to influence plant communities in previous studies (**Table 1,**

169   see **Appendix C** for the choice of variables).

170 **Table 1.** List of explanatory factors (blue), functional traits and ecological requirements (green) and response variables (red) with their abbreviations, units

171 and calculation. We have illustrated by arrows the expected link of each factor and trait to the agricultural resource (fertilization) and disturbance gradient

172 (herbicides and margin management), and to the climatic gradient (drought and increasing temperature). We also used arrows to illustrate the expected

173 direction of variation of these gradients within a year (i.e. climatic and agricultural changes according to the date of observation). Horizontal arrows indicate

174 contradictory findings in the literature (see **Appendix C** for the references).

Factors Functional traits Response variables	Abbreviations	Units	Index used	Hypothesis of response to the temporal agricultural gradient: Disturbance (Di) and Resource (R)	Hypothesis of response to the temporal climatic gradient: Drought (Dr) and Temperature (T)
Temperature	TEMP	°C	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 field margin 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		↘ ↘	↗ ↗

Trait	Abbr.	Units	Description		
Specific leaf area	SLA	m² 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,	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),	EIV_N: ↗	EIV_F: ↘

moisture, pH and nutrients			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_T: ↗ ↗
Species richness	S		Number of species	→? →?	→? →?
Trait 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)		
Trait 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_C: ↘

CWM_S:

CWM_S:

CWM_R:

176   *Plant functional traits*

177   We extracted from external databases five functional traits and six species-level indices of ecological

178   requirements (i.e. Ellenberg values; Ellenberg, 1974), assumed to respond to agricultural or climatic

179   factors (**Table 1**, **Appendix B-C**). Functional traits were missing for four species, two of which could be

180   imputed from an average over other species of the same genus. The remaining two species were

181   removed from the analysis (representing 0.01% of the total abundances among the 142 species

182   considered).

183   To characterize plant communities, we calculated species richness, community-weighted means

184   (CWM) and community-weighted variances (CWV) of traits and ecological requirements for

185   observations with at least three species (59 out of 4172 observations were excluded). The computation

186   was performed using the R v.4.0.0 package ₍FD₎, function *dbFD* for CWM, with the following formulas:

187   $\text{CWM} = \sum_{i=0}^{n} p_i \times trait_i$ **(Eq. 1)**

188   $\text{CWV} = \sum_{i=0}^{n} p_i \times (trait_i - CWM)^2$ **(Eq. 2)**

189   Where p_i is the relative abundance, $trait_i$ is the value of trait for species *i,* and *n* is the total number

190   of species. To correct for correlation between CWV and species richness, we used a null model

191   approach, shuffling the abundances in the species matrix for species of the species pool, while keeping

192   the species x trait matrix unchanged (Bopp et al., 2022). The species pool was defined by the site,

193   allowing us to investigate temporal variations. This procedure keeps trait correlations, species richness

194   and total abundance in a site unchanged, while dissociating abundances from trait values (Bernard-

195   Verdier et al., 2012). To quantify the difference between observed and null CWV, we computed effect

196   sizes (**Appendix D**). A positive effect size denotes a divergence in trait values within the community

197   (convergence for negative effect size). These effect sizes (and not the raw CWV) were used in our

198   analyses and referred to as CWV in the subsequent sections. We performed a normed PCA on the

199   CWM of traits to classify each community based on its average trait combination or ecological strategy,

200   which is reflected by its position on the first two axes.

201

202   *Plant functional strategies*

203   According to Grime (1988), stress (i.e. a shortage of resources such as nutrients, water and light) and

204   disturbance (i.e. the partial or total destruction of plant biomass) determine three main plant

205   strategies representing combinations of traits that are viable under conditions of low disturbances and

206   high resources (competitor, C), low disturbances and low resources (stress-tolerant, S) or high

207   disturbances and high resources (ruderal, R). Originally developed to classify individual plant species

208   into strategies, Grime's theory can be useful to interpret functional changes in plant communities,

209   especially in the context of global changes where vegetation is subject to harsher climatic conditions

210   (more droughts) and various levels of agricultural disturbances.

211   To assess these strategies, we extracted the CSR scores for 119 out of 142 focal species from Pierce et

212   al. (2017). CWM of CSR scores were computed by observation and were added to the PCA on the CWM

213   of traits as supplementary variables. They were plotted on a CSR triangle to illustrate temporal trends

214   in strategies.

215

216   *Temporal analyses of plant communities*

217   The general framework of analyses is presented in **Fig. 2**. First, we checked if there was a temporal

218   trend on the raw variables, and then we used climate and agricultural practices as predictors for the

219   different response variables. In all cases, we used generalized additive mixed models (GAMM) to

220   account for repeated measures at a site, with a Gaussian distribution in most cases (but see **Appendix**

221   **E**, **Table SE.2**), and site identity as a random effect. Observer bias was accounted for by including the

222   observer identity as a random term nested within sites. For each response variable (species richness,

223   CWM, CWV and CSR strategies) and explanatory factor (temperature, soil moisture, nitrogen dose,

224   herbicides and margin management), we built a first model with the year as a linear fixed effect. Then,

15

225 a second model was built for each response variable, where climate, agricultural practices and

226 observation date were linear explanatory factors. A first-order temporal autocorrelation structure

227 within sites was included (Box et al., 2015). We removed observations with missing values in climatic

228 and agricultural factors (1805 out of 4172 observations), and a few observations that distorted trait

229 distributions (**Appendix E**), resulting in varying observation numbers across models (see **Fig. 5**). We

230 repeated this analysis on subsets of data, including Mediterranean (MZ) vs Continental zones (CZ),

231 margins adjacent to annual crops vs vineyards, and annual vs perennial plant species (**Fig. 1**). For all

232 analyses, we chose a p-value threshold of 0.01 to focus on the effects for which our confidence level

233 was highest.

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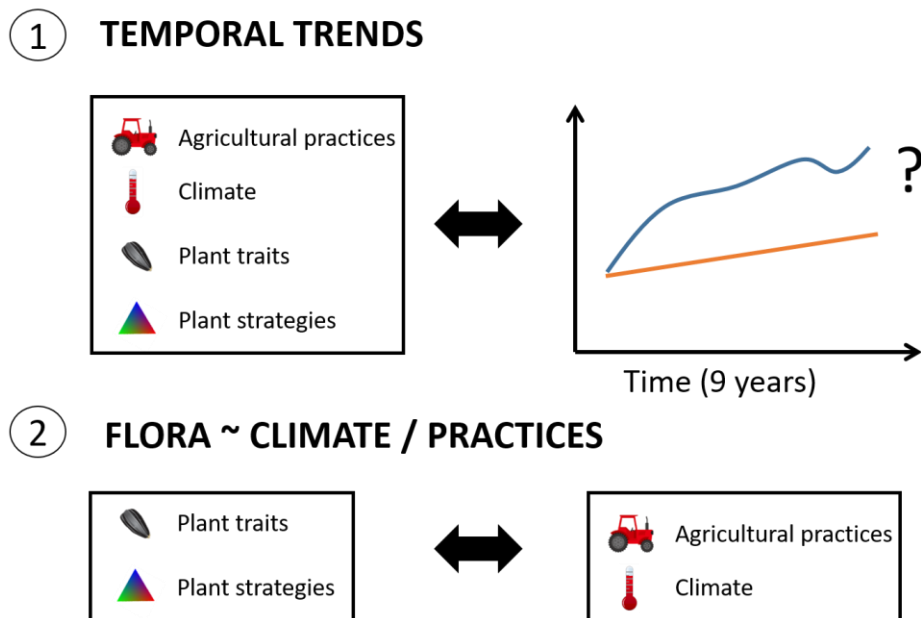
235 **Fig. 2.** General framework of our analyses involved two main steps. (1) Firstly, we investigated the

236 presence of any temporal trends in species richness, trait composition, ecological strategies, climatic

237 and agricultural factors, as this provides crucial insights for the subsequent analysis. Indeed, given that

238 we expected minimal temporal trends in agricultural practices, we did not expect significant temporal

239 changes in flora in response to practices. (2) Secondly, we explored how plant communities have

240 responded to the temporal changes in climate and agricultural practices.

241

242 **Results**

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

244 Temperatures have significantly increased by an average of 1.2°C over a decade (0.7°C in the

245 Mediterranean Zone), while soil moisture has steadily declined (-14.1% by decade) (**Fig. 3**, and

246 **Appendix F**). These trends differed between the Mediterranean zone (MZ) and the Continental zone

247 (CZ), with the MZ experiencing a slower decline in soil moisture due to a high cumulative precipitation

248 in 2019 (**Fig. 3**). Regarding agricultural practices, herbicides slightly decreased over time in vineyards

249 (-0.9 application by decade; **Fig. 3**), with an even weaker trend in annual crops (-0.2 application by

250 decade). Fertilization showed no significant temporal trend, except in vineyards where the cumulative

251 dose of nitrogen has recently slightly increased (**Fig. 3**). The number of margin management events

252 has decreased and particularly in the MZ (-0.5 by decade). Floristic surveys were conducted

253 increasingly earlier in the season in the CZ (10.4 days earlier by decade) (**Appendix F**). Overall, there

254 was a clear warming and drying trend in climate, but agricultural trends were weaker.

255 Plant species richness has slightly increased over time at the national scale (+0.1 species by decade,

256 **Fig. 5**), even more in the MZ (+0.4 species by decade) and vineyards (+0.3 species by decade) and only

257 for annual species (**Appendix H**). We saw an increase in the CWM of maximum height (+5.8 cm by

258 decade), seed mass (+0.2 g by decade), flowering onset (+3.1 days by decade) and a decrease in

259 flowering duration (-7.8 days by decade, **Fig. 5**). The requirements for light, temperature and pH have

260 increased, while those for moisture and nitrogen have declined. CWV (i.e. computed by comparison

261 with expected CWV in a community of same richness) have decreased for most traits indicating trait

262 convergence, and particularly for phenological traits such as flowering onset and flowering duration (-

263 3.6 and -2.6 days by decade respectively), while they have increased for the requirements for

264 temperature, pH and continentality, indicating trait divergence.

265 Changes in functional traits were more pronounced in the MZ, particularly for the flowering onset (+8.8

266 days by decade) and duration (-18.9 days by decade; **Appendix F**). Conversely, changes in Ellenberg

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267   values (environmental requirements) were only significant in the CZ and in annual crops. One

268   exception was the temperature (Ellenberg-T) and moisture (Ellenberg-F) requirements, which have

269   significantly changed in both the MZ and CZ. Interestingly, functional traits (and not environmental

270   requirements) showed a temporal trend mainly for annual species (**Appendix F**).

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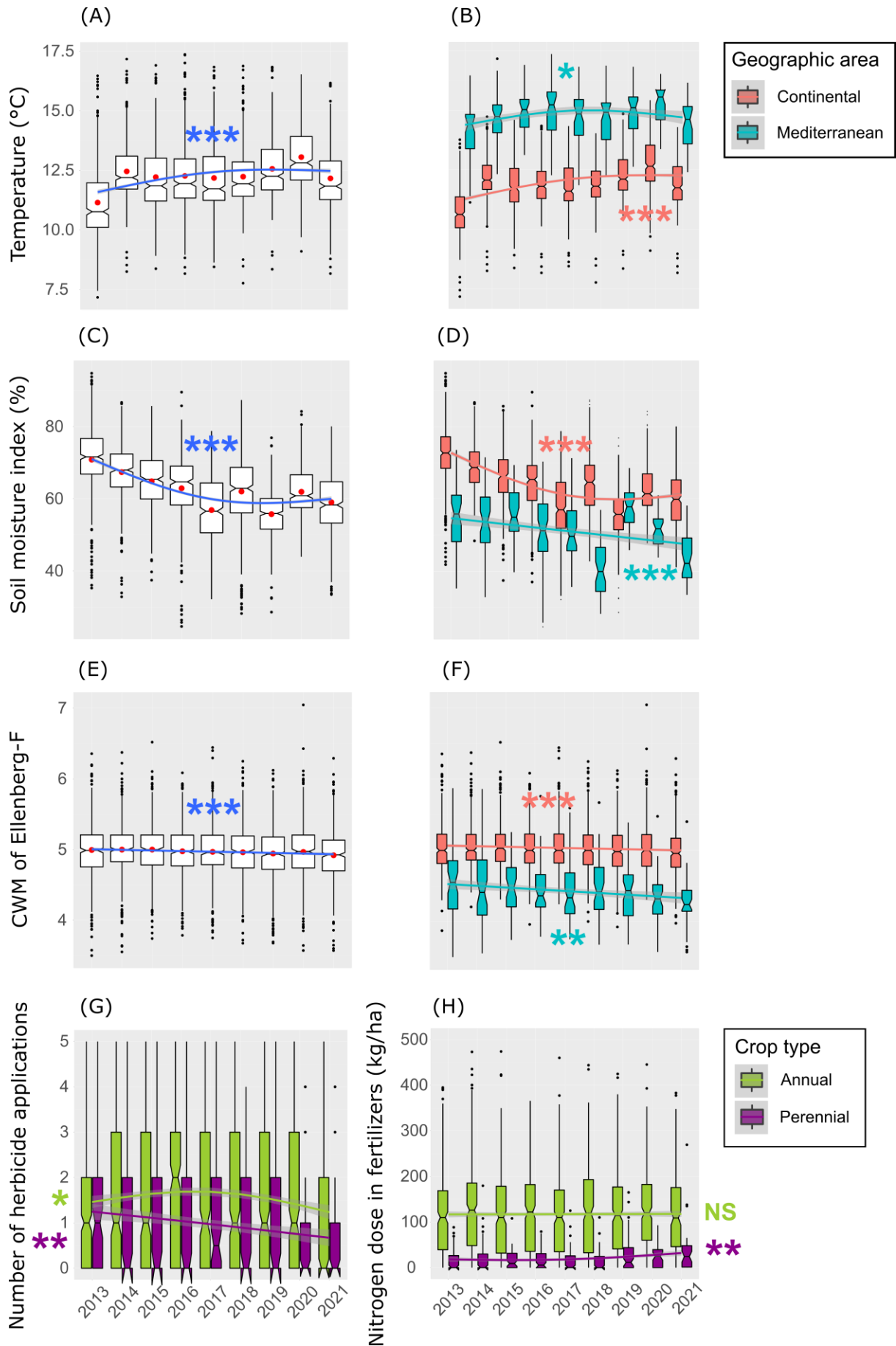
273 **Fig. 3**. Temporal changes in temperature, soil moisture, CWM of Ellenberg-F (moisture requirement),

274 number of herbicide applications and nitrogen dose in fertilizers. Red dots represent mean values. The

275 curves are from a GAM, with a smooth term on the year restricted to three effective degrees of

276 freedom. (A, C, E) National trend. (B, D, F) Trend by geographic area: CZ and MZ. (G, H) Trend by crop

277 type: annual (wheat, maize, lettuce) and perennial (vineyard). Significance of smooth terms is referred

278 as following: NS $p \geq 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

279

280 *Functional trade-offs*

281 The first PCA axis (named thereafter stress-tolerance axis, see **Appendix G, Fig. SG.1** for the correlation

282 of each CSR strategy with each axis) explained 29.9% of the variation in traits and revealed a gradient

283 from continental hygrophilous communities (high Ellenberg-K and F) associated with moist and

284 resource-rich environments (high Ellenberg-N), to Mediterranean xero-thermophilous stress-tolerant

285 communities (high Ellenberg-T and L, low Ellenberg-F) adapted to warm, arid and resource-poor

286 environments (**Fig. 4, Appendix G, Fig. SG.2**). Communities with continental species were more

287 nitrophilous (high Ellenberg-N), while Mediterranean communities had a higher seed mass. The second

288 PCA axis (named thereafter ruderal axis) explained 19.5% of the variation and contrasted stress-

289 tolerant/conservative communities adapted to low disturbance (low SLA, high stature, late and short

290 flowering) with ruderal/acquisitive communities adapted to high disturbance (high SLA, short stature,

291 early and long flowering).

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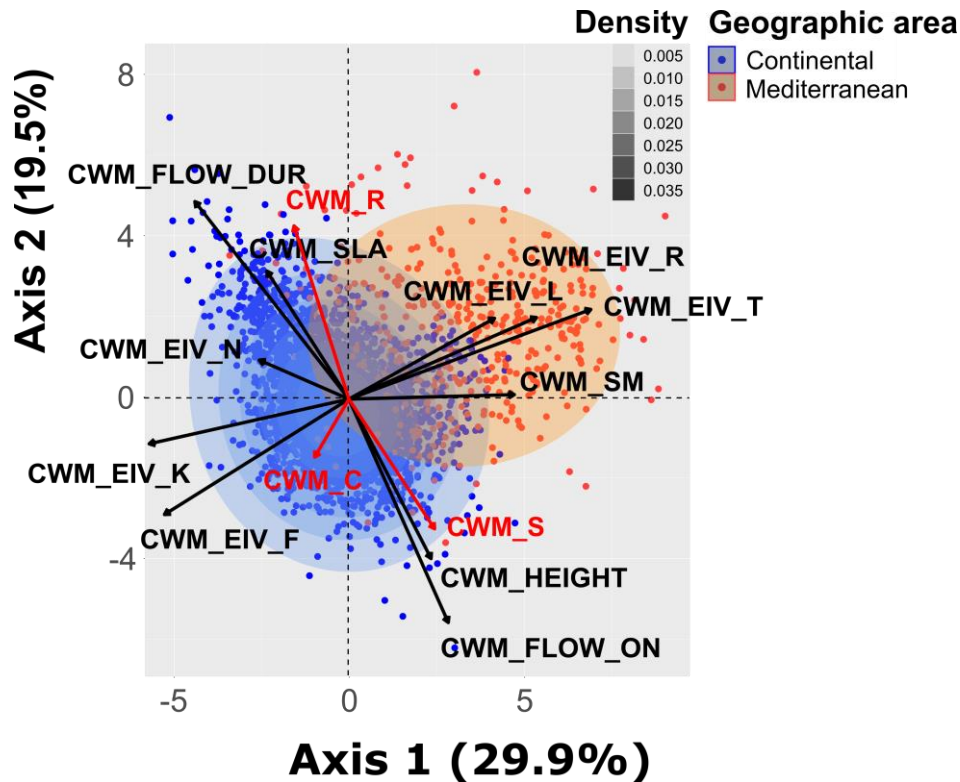
Fig. 4. Normed PCA on CWM (first two axes) of functional traits and ecological requirements computed by observation. The color of the dots indicates the region to which they belong and the density curve highlights the concentration of data points in a given area. The correlations of traits to the PCA 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

Climatic factors were the predominant drivers of changes in community trait composition, with high R^2 for the temperature requirement (R^2 = 0.33) and stress-tolerance axis (see previous section, R^2 = 0.27, **Fig. 5**). Associations between each Ellenberg value and climatic factors opposed in a consistent

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307   way Mediterranean communities to nitrophilous continental ones along the stress-tolerance axis (**Fig.**

308   **5**). Increasing temperature increased the CWM of seed mass and Ellenberg-T (requirement for

309   temperature) and decreased the CWM of SLA. Increasing temperature led to more divergence in the

310   requirement for temperature and moisture (compared to a community of same richness). Conversely,

311   increasing soil moisture brought convergence in the requirement for temperature, continentality and

312   soil pH. Increasing temperature and drought were also associated with shorter flowering duration (-

313   2.2 days by °C and +0.15 days by % of soil moisture), and later flowering onset only for increasing

314   temperature (+1.6 days by °C; **Fig. 5**).

315   Margin management was the agricultural practice with the largest impact on changes in community

316   trait composition, with an increase in its frequency associated with more ruderality (-1.2 cm in

317   maximum height, -0.8 days in flowering onset and +2.1 days in flowering duration by management

318   event). The date of observation also influenced changes in community trait composition, as a later

319   observation was related to more conservative, competitive and continental communities, and to a

320   decrease in species richness. Changes in the frequency of herbicide treatments had no significant

321   effect, while an increasing annual nitrogen dose in fertilizers only slightly decreased the pH

322   requirement (**Fig. 5**).

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Response variable (rows) × **Explanatory factor** (columns)

Response variable	Group	Temperature (°C)	Soil moisture (10%)	No. herbicide treatments	Nitrogen dose (kg/ha)	No. management events	Date of observation (day)	Decade (yearx10)	R²	Nb obs
Species richness							-2.6e-3	0.1	3.8	2367
PCA Axis 1 (stress-tolerance)		0.4	-0.2		-9.9e-2			0.9	27.4	2338
PCA Axis 2 (ruderality)							0.1	-1.4e-2	8.9	2338
SM (g)	CWM (mean)	5.5e-2	-5.3e-2					0.2	6.1	2338
SLA (m²/kg)	CWM (mean)	-0.3						-1.0e-2	3.0	2338
HEIGHT (cm)	CWM (mean)	1.3				-1.2	8.9e-2	5.8	2.9	2336
FLOW_ON (day)	CWM (mean)	1.6				-0.8	0.1	3.1	8.3	2338
FLOW_DUR (day)	CWM (mean)	-2.2	1.5			2.1		-7.7	5.3	2338
EIV_T	CWM (mean)	1.1e-2	-4.0e-3				-1.5e-2	2.1e-2	30.7	2338
EIV_L	CWM (mean)	4.3e-2						7.8e-2	8.4	2338
EIV_R	CWM (mean)	7.9e-2		-2.0e-4			-2.3e-3	0.1	23.8	2338
EIV_K	CWM (mean)	-2.9e-2	2.0e-2				1.0e-3		19.9	1799
EIV_F	CWM (mean)	-2.5e-2	3.0e-2				1.2e-3	-0.1	9.0	2338
EIV_N	CWM (mean)	-5.0e-2						-8.9e-2	5.3	2338
SM (g)	CWV (variance)							4.9e-2	0.8	2338
SLA (m²/kg)	CWV (variance)							-5.6e-2	0.6	2338
HEIGHT (cm)	CWV (variance)	1.7							1.0	2336
FLOW_ON (day)	CWV (variance)		0.9					-3.6	1.7	2338
FLOW_DUR (day)	CWV (variance)							-2.6	1.1	2338
EIV_T	CWV (variance)	2.8e-2	-3.0e-2				-8.1e-4	0.2	6.3	2338
EIV_L	CWV (variance)				1.7e-4			-5.1e-2	0.4	2338
EIV_R	CWV (variance)		-2.0e-2				-8.0e-4	0.1	2.7	2338
EIV_K	CWV (variance)		-4.0e-2					0.1	3.7	2338
EIV_F	CWV (variance)	3.6e-2							2.2	2338
EIV_N	CWV (variance)								1.1	2338

Legend

Column

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

Row

CWM/CWV of functional traits
- SM = Seed mass
- SLA = Specific leaf area
- HEIGHT = Maximum plant height
- FLOW_ON = Flowering onset
- FLOW_DUR = Flowering duration

CWM/CWV 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

327

328

Fig. 5. Results of temporal models (GAMM) on the whole dataset, with response variables in rows and explanatory factors in columns. The adjusted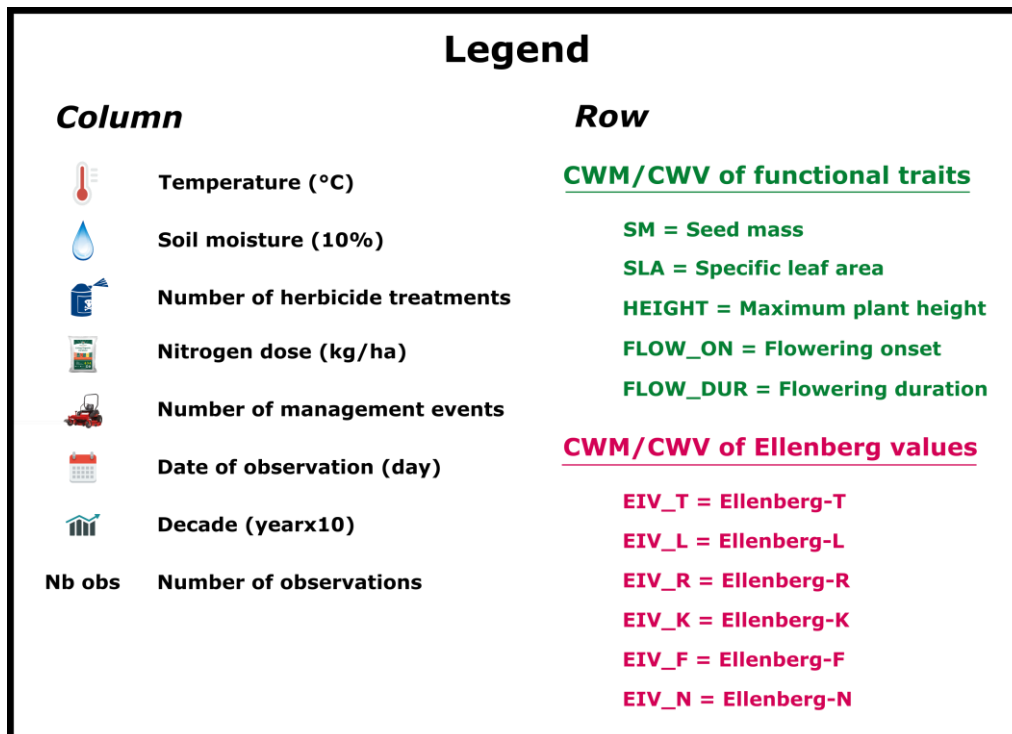 R², expressed as a percentage of variation, and the number of observations are reported. Significance is indicated by colored cells, with a p-value threshold of 0.01. Positive estimates are in red, negative estimates in blue, and the strength of the relationship (based on the standardized estimates) 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, changes in soil moisture did not have any influence on changes in species richness or community trait composition (**Appendix H**) and temperature only increased the requirement for temperature (Ellenberg-T) and decreased SLA. When margins were more frequently managed in the MZ, Mediterranean species declined (decrease of temperature requirement and convergence towards higher values of continentality, **Appendix H**). Increasing 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 at the national scale. Annuals were more impacted by climatic variations and seasonal effects (observation date) than perennials, with high R² for temperature (R² = 0.39) and moisture (R² = 0.32) requirements.

350 **Discussion**

351 Our study is one of the first to provide empirical evidence that climate change is already resulting in

352 detectable functional changes in plant communities over a relatively short time interval of 10 years

353 (see also Martin et al., 2019) (**Fig. 6**). Climate change tended to favor the stress-tolerance strategy at

354 the expense of ruderality. These contrasting strategies highlight the functional trade-offs that prevent

355 field margin plants from simultaneously adapting to climate change and intensive agricultural

356 practices. Interestingly, reducing the frequency of margin management mimicked the impact of

357 climate change on community trait composition, although the trend was less pronounced. Practices

358 applied in the adjacent agricultural fields, including herbicide use and fertilization, had almost no effect

359 on changes in community trait composition.

360

Explanatory factors and their temporal trend

Ecological strategies and their temporal trend		Temperature	Soil moisture	Number of herbicide treatments	Nitrogen dose	Number of management events
	Stress-tolerance ↑	*	*	ns	ns	*
	Ruderality ↓	*	*	ns	ns	*
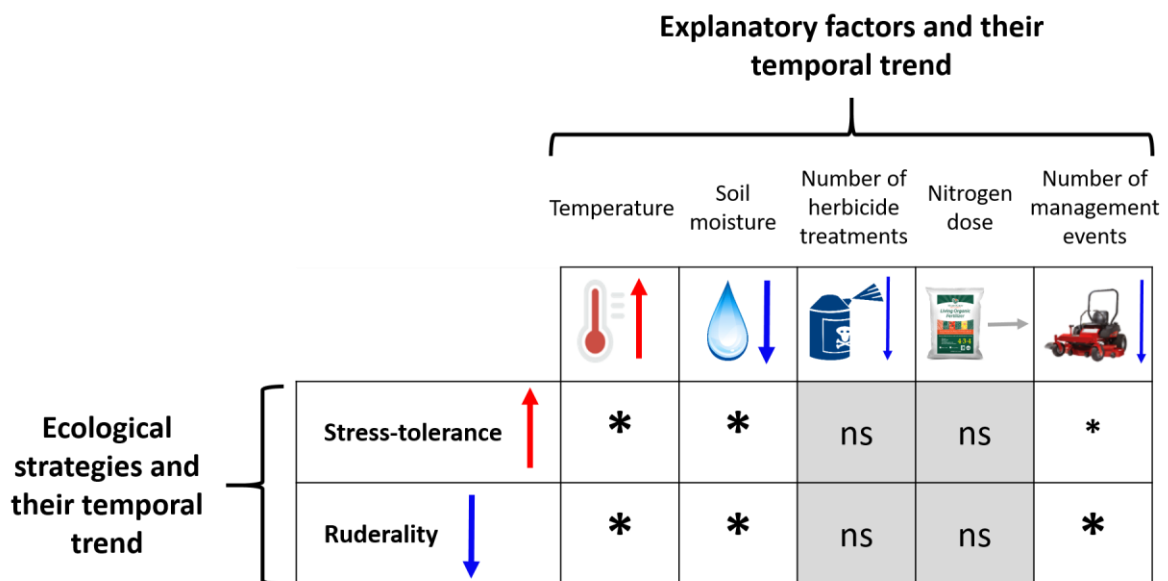
361

362 **Fig. 6.** Synthesis of results based on temporal trends and temporal analyses of community response to

363 changes in climate and practices. Ecological strategies are based on PCA axes (Axis 1 for stress-

364 tolerance and Axis 2 for ruderality) and their associated traits. Explanatory factors and ecological

365 strategies are depicted with their temporal trend over a decade (arrows). The asterisks illustrate the

366 links between temporal trends in climate and practices and the resulting trends in communities,

367 inferred from the coefficients in **Fig. 5** (ns = non-significant). The size of the asterisks represents the

368 strength of the relationship, estimated from the number of impacted traits and standardized estimates

369 in models.

370

371 *Climate as the main driver of temporal variations in field margin plant communities*

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

373 primarily driven by climate (Díaz et al., 2016; Pakeman et al., 2009). Since meteorological variables

374 were extracted at a 8 km resolution, changes in soil moisture can be confidently attributed to climate

375 change and not to the effect of soil compaction due to cultivation. Increasing temperature and drought

376 favored more xerophilous and thermophilous species, with higher seed mass and lower nitrogen

377 requirement, thus shifting the position of communities along the stress-tolerance axis. Our results also

378 indicated that sites increasingly warmer and drier allowed for coexistence of a wider functional set of

379 species, suggesting an increased abundance of thermophilous species without any loss of cold-adapted

380 species. The increase in species richness over time provided additional support for this hypothesis.

381 The increase in temperature requirement at the community-level with rising temperatures was already

382 documented, but mainly by studies covering entire floras (regional or local species pool) and time

383 scales of several decades to a century (Salinitro et al., 2019; Tamis et al., 2005). We found that this

384 trend is now detectable over a short-term period of only nine years (Martin et al., 2019). Interestingly,

385 as in other recent studies (Duchenne et al., 2021; Martin et al., 2019), this trend was more pronounced

386 in northern France, while Mediterranean communities responded less to climate change (**Appendix**

387 **H**). On top of the fact that climatic trends observed in the MZ were weaker than in the CZ,

388 Mediterranean species are already adapted to drought and heat stress, and might be more resilient to

389 extinction risks (Thuiller et al., 2005). Because of their geographic position north of the Mediterranean

390 Sea, they might also experience some competitive release due to the lack of immigrants coming from

391 the south, and the northward shift of more temperate species (Duchenne et al. 2021).

26

392   Beyond the increase in temperature requirement, our models revealed additional temporal changes

393   related to climate change that align well with the existing literature, including a decrease in mean SLA

394   and an increase in mean seed mass and maximum height (Alarcón Víllora et al., 2019; Kühn et al.,

395   2021). These trait values (low SLA, high seed mass and height) are also known to be linked to less

396   intensive agriculture (Fried et al., 2012; Richner et al., 2015). In our models, we observed a similar

397   pattern, with less frequent margin management associated with a decrease along the ruderality axis

398   and an increase along the stress-tolerance axis. All of this suggests that climate change and the

399   evolution towards more extensive agricultural practices will select the same trait values towards more

400   stress-tolerant and less ruderal strategies (MacLaren et al., 2020).

401   Finally, temporal analyses showed additional phenological changes, suggesting that climate change

402   could increase the occurrence or abundance of late-flowering species, i.e. species that have high

403   temperature requirement to complete their life cycle (Peters et al., 2014). These phenological shifts

404   coincided with a decrease in trait variance, leading to trait convergence within communities. Critically,

405   such changes can reduce the ability of species to escape field margin management, which typically

406   favors species able to flower all-year-round, as expected with a ruderal strategy. As species will not be

407   able to advance their phenology indefinitely, this can ultimately result in species losses in the long-

408   term. However, farmers are likely to adapt the temporality of their practices to climate change,

409   mitigating some of these impacts.

410

411   *Agricultural practices have a weaker impact on temporal community dynamics*

412   Temporal variations in agricultural practices over the short-term had a weaker influence on field

413   margin plant communities than climatic variations (Alarcón Víllora et al., 2019; Fried et al., 2019). Field

414   margin management was the most impactful practice, affecting traits related to the ruderal syndrome

415   in a consistent way. This supports the idea that field margin management, as the only practice applied

416   directly in the margin, has a greater impact than herbicides and fertilization applied in the adjacent

417   agricultural fields, which are likely to have only collateral effects.

418   The lack of herbicide effect on community trait composition could arise because the number of

419   herbicide applications has varied little in recent years or because we have omitted some traits that

420   reflect herbicide tolerance (e.g. leaf cuticle thickness, hairiness). Also, reducing the intensity of

421   agricultural practices may not necessarily influence the trait composition of communities, because

422   agricultural intensification has already greatly reduced functional diversity, and highly diverse

423   landscapes would be required for some species to recolonize field margins.

424   Fertilization had minimal influence on changes in community trait composition, but reduced species

425   richness (Kleijn & Verbeek, 2000), an effect detected in the MZ and leading to the loss of some annual

426   Mediterranean species (Poinas et al., 2023). Due to functional trade-offs, we saw that nitrophilous

427   plant species were less thermophilous and more acidiphilous, which explains why nitrogen dose was

428   related to affinity for acidic soils in our models. Nitrogen dose remained constant over time, which

429   aligns with the weak change in global nitrophily levels in plant communities, suggesting that

430   eutrophication may no longer be the primary driver of changes in arable vegetation (Alignier, 2018;

431   Duchenne et al., 2021).

432
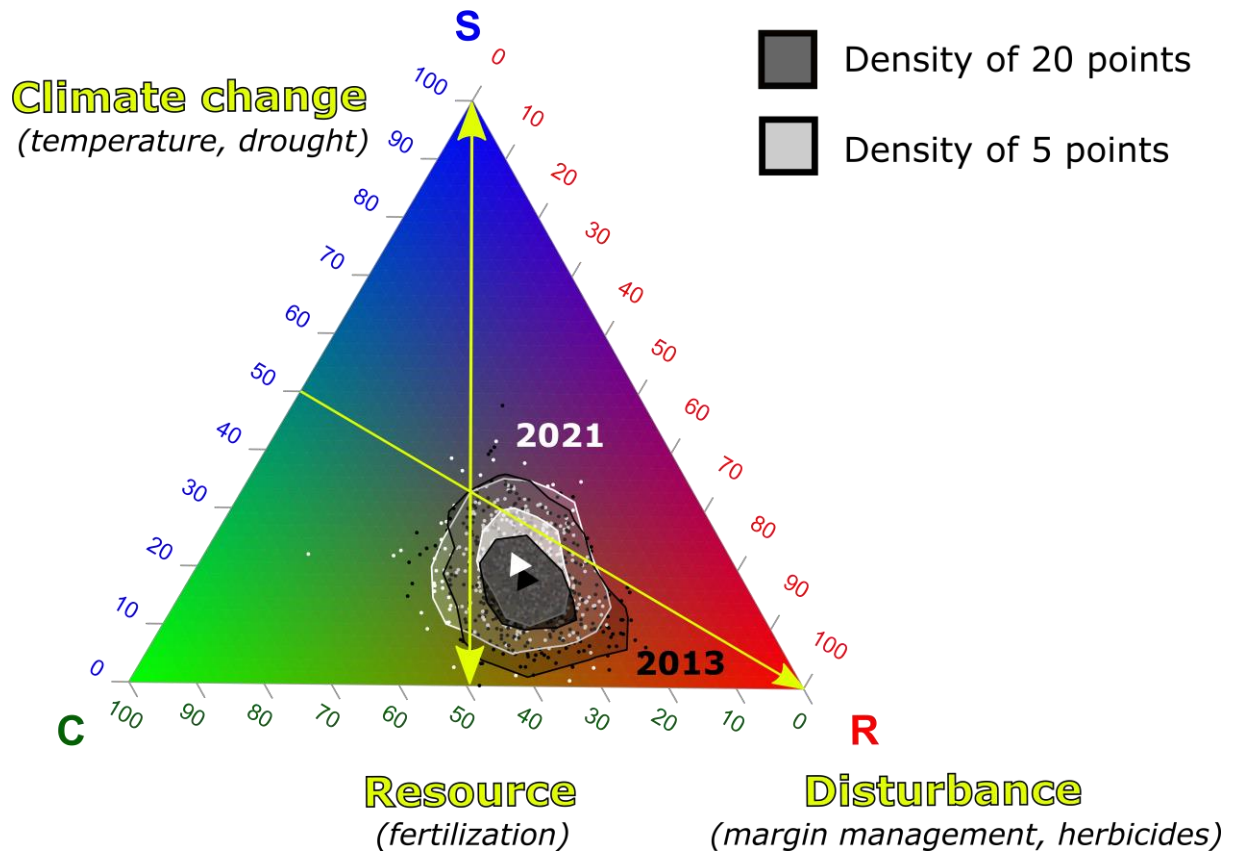
Fig. 7. Grime's CSR triangle depicting the temporal trajectory of community strategies between 2013 and 2021. To enhance clarity, we show only two levels of density curves, with each point representing a specific site. The relative percentages of each strategy are depicted through the use of green, blue and red colors (C = competitor, S = stress-tolerant and R = ruderal). Arrows indicate expected impacts of climate change, disturbance, and resource levels. Temporal models (GAMM) applied to the CWM of each strategy revealed significant decreases in ruderality (-1.14% by decade) and competitiveness (-0.81% by decade) scores of communities, and a significant increase in stress-tolerance scores (+1.80% by decade).

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

Our findings revealed that resource level (driven by fertilization) and climate vary the position of communities along the stress-tolerance axis (see **Appendix I** for more results on the effect of fertilization), while disturbance level (driven by field margin management) and climate vary the

29

447 position of communities along the ruderal axis (**Fig. 7**). This supports the view that functional trade-

448 offs are not only evident on a global scale as found by Wright et al. (2004) and Díaz et al. (2016), but

449 also occur within a narrower functional range (such as plants colonizing agricultural field margins). As

450 a result, agricultural intensification and climate change act in opposite ways on the trait composition

451 of field margin plant communities. Climate change favors species that are adapted to high

452 temperatures and drought, but not to intensive agriculture. It tends to expand the functional range for

453 traits related to stress-tolerance within communities (divergence), but reduces the functional range

454 for traits associated to ruderality (convergence). Conversely, agricultural disturbances select species

455 more sensitive to current climatic trends, without any particular trend in trait variance.

456 These trade-offs emphasize the need to consider the existing interactions between climate and

457 agricultural practices when predicting future community trajectories (Garnier et al., 2019; Pakeman et

458 al., 2009). Here, we acknowledge the difficulty in quantifying these interactions, particularly given the

459 limited changes observed in practices over time. However, the effects of practices were more

460 perceptible with analyses focused on spatial effects (**Appendix I** and see also Poinas et al., 2023),

461 allowing us to imagine main trends in community trajectories according to several scenarios (**Fig. 7**).

462 Accelerating climate change coupled with an agricultural abandonment and more extensive practices

463 in Europe (Miller et al., 2022; Peeters et al., 2021) will likely result in an increase in xero-thermophilous

464 and conservative species. However, a large part of these species are habitat specialists (e.g.

465 Mediterranean species as found in Munoz et al. (2017); Fried, Chauvel, et al., 2009) and have a high

466 affinity for calcareous soils, which will probably limit their expansion towards the CZ to restricted

467 calcareous areas, such as the Paris Basin. Areas where they are unable to colonize might suffer a

468 decrease in species richness, and this scenario could be worsen if current levels of agricultural

469 intensification are maintained or increased. Mediterranean species expanding in the northern half of

470 France could face severe agricultural intensification that would likely limit their expansion, while at the

471 same time ruderal species would become less frequent mostly because of drought. This highlights the

472   need to consider the conjunction of climate change and intensive agriculture when making future

473   predictions.

474

475   **Conclusion**

476   Our study highlights climate as the primary factor affecting field margin plant communities in France,

477   with increasing temperatures and decreasing soil moisture fostering Mediterranean, stress-tolerant

478   and conservative species, while negatively affecting ruderal species. In comparison, agricultural

479   practices had a limited effect on changes in species richness and trait composition, with field margin

480   management having the greatest impact. Our study suggests that the species selected by climate

481   change are poorly adapted to intensive farming, while the pool of species currently able to colonize

482   field margins is restricted to a limited functional range adapted to agricultural practices. The

483   persistence of intensive agricultural practices and accelerating climate change could thus have critical

484   consequences for the conservation of floristic diversity in agroecosystems. However, it is important to

485   consider the potential of adaptation of species, through intraspecific trait variability and phenotypic

486   plasticity (known to be particularly high in ruderal species, Baker, 1974), as it may enhance their

487   resilience to changing conditions. Our findings suggest a reduction in ruderality and an increase in

488   stress-tolerance according to Grime's strategies. Bopp (2023) highlighted a similar increase of stress-

489   tolerance in weeds in response to climate change, but did not observe a corresponding decrease in

490   ruderality. Further investigations are thus necessary to assess the generalizability of these results

491   across different habitats, including communities with broader or narrower functional niche, such as

492   weeds. Long-term monitoring programs are necessary to address other important research questions,

493   such as the potential time-lag in flora's response to environmental changes, the non-linearity in

494   temporal trends and the interactive effects between climate and agricultural changes. Finally, the

495   findings presented in this study call for rethinking our current agricultural model, urging us to prioritize

496   the development of agricultural practices that foster the creation of favorable microclimates while

31

497   minimizing local intensification. Promising approaches, such as agroforestry, hold the potential to align

498   agricultural production with biodiversity conservation goals by providing refuge habitats and

499   microclimate regulation.

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 https://doi.org/10.1101/2023.03.03.530956.

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