

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

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19

20 **Abstract**

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

45

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

47 agricultural practices, CSR strategies, Mediterranean species, phenology

48 **Introduction**

49

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

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

74 that are linked to resource acquisition, competitive ability, or climate. For example, seed mass, which
75 is often used as a proxy for competitive ability, increases along soil fertility, temperature and solar
76 radiation gradients (Fried et al., 2022; Murray et al., 2004). Furthermore, correlations among different
77 traits may represent trade-offs that impact community adaptation (Díaz et al., 2016; Wright et al.,
78 2004). In this context, Grime (1977) proposed a framework called the CSR triangle, which defines two
79 axes of variation - resource and disturbance - along which three strategies are distributed -
80 competitiveness, stress-tolerance, and ruderality - that are correlated to multiple traits and have
81 proven useful to understand plant community dynamics in agrosystems (Fried et al., 2022). As traits
82 responding to climate and agricultural practices may co-vary (Garnier & Navas, 2012), it can be difficult
83 to identify the main drivers behind community changes.

84 To understand the complex interactions between climate change and agricultural practices, it is thus
85 essential to examine the temporal dimension of functional inter-specific trait variations. For example,
86 in French wheat fields, small species with low seed mass and long germination and flowering periods
87 increased their frequency between the 1970s and 2000s, potentially due to their ability to escape
88 recurrent disturbances, such as herbicide applications (Fried et al., 2012). Inter-annual variations in
89 specific leaf area, leaf dry matter content and plant height are related to nitrogen supply, while
90 increased precipitations push the foliar economic spectrum towards more acquisitive species (Wheeler
91 et al., 2023). Additionally, mean thermal preference of plant communities, as well as their phenology,
92 can vary over time in response to temperature changes, even over relatively short periods (Bellard et
93 al., 2012; Martin et al., 2019). These temporal variations in functional traits reveal patterns that cannot
94 be assessed solely with a space-for-time approach.

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

99 uncultivated vegetated area located between the cultivated strip and the adjacent habitat. Using a
100 standardized national monitoring effort spanning 9 years (2013-2021) in 555 agricultural field margins
101 covering continental France, our study stands as one of the first to investigate the temporal trends in
102 agricultural practices and climate, and explore the spatial and temporal drivers of species richness and
103 functional traits at such extensive scales. We hypothesized that plant traits sensitive to temperature
104 and soil moisture will co-vary with both spatial climatic gradients and temporal warming trends while
105 agricultural practices would have a greater spatial than temporal influence on plant communities, as
106 we did not expect clear temporal trends in these practices. We also assumed that the impact of
107 agricultural practices on margin plant communities would likely be limited, as field margins only
108 receive a small amount of nitrogen and herbicides drifting from neighboring plots. Furthermore, we
109 explored the connection between Grime's CSR strategies, climate and farming practices. Considering
110 that these strategies are linked to resource and disturbance levels, we hypothesized that they would
111 respond to climate factors (particularly reduced water resource) and agricultural practices
112 (disturbance and resource provision through fertilization). On top of the national analyses, and
113 because this dataset includes the Mediterranean flora, which has been shown to respond more
114 strongly to some agricultural filters (Poinas et al., 2023), we included analyses separating this region
115 from the rest of France. We also separated vineyards from annual crops, because vineyards include
116 very different management practices and no crop rotation (Metay et al., 2022). Finally, we also
117 analyzed annual plant species separately, as they may respond more rapidly to environmental changes
118 (Martin et al., 2019; Fitter & Fitter, 2002).

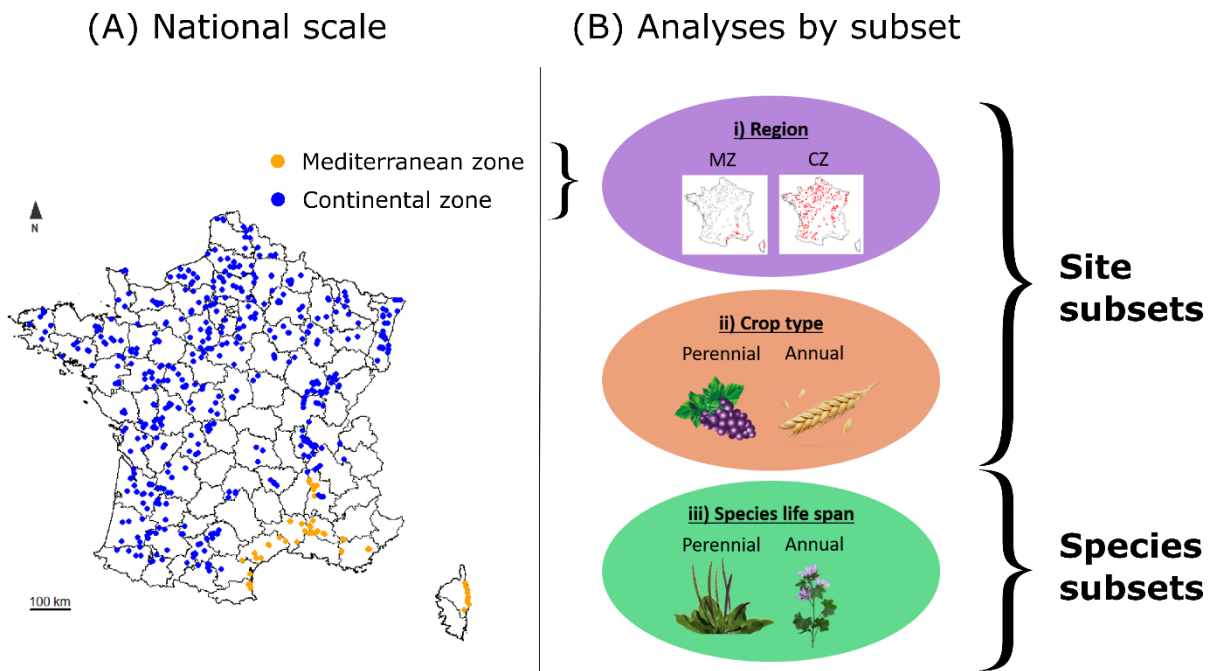
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120 **Materials and methods**

121 *Vegetation surveys*

122 We used vegetation data from the 500-ENI network, which is funded by the French Ministry of
123 Agriculture (see details in Andrade et al., 2021) and monitored 555 agricultural field margins across
124 continental France between 2013 and 2021 (with some site turnover) (**Fig. 1**). These survey sites
125 represented three main crop types (**Appendix A, Fig. SA. 1**): annual crops (with winter wheat or maize
126 as the main crop production in the rotation), market gardening crops (mainly lettuce) and vineyards.
127 The proportion of sites under organic farming was roughly 20%, but agricultural practices covered a
128 wide range of pesticide application, fertilizers and soil management. Within each survey site, plant
129 species were identified in ten 1 m² quadrats along the field margin (**Appendix A, Fig. SA.2**). Presence-
130 absence of each species was recorded for each quadrat, which provided a frequency of occurrence
131 from 0 to 10 in each field margin, used here as an index of relative abundance. Surveys were performed
132 once per year at peak flowering (between the end of April and the beginning of August, depending on
133 the region). At the national scale, this represented 4172 observations (year x site), leading to the
134 identification of 852 taxa. Because observers changed among sites and over time (312 observers in
135 total, each observer following on average 5 distinct sites during 4 years) and did not have the same
136 level of expertise, we constrained our analyses to a subset of 142 focal species (Andrade et al., 2021)
137 which are expected to be known by all the observers (and thus removing 11% of the total abundances).

138



139

140

141 **Fig. 1.** (A) Distribution map of the 555 field margins monitored at least one year between 2013 and
 142 2021 in France. The black lines represent the limits of French departments. Orange: sites in
 143 Mediterranean zone (n = 57), blue: sites in Continental zone (n = 498). The contours of the
 144 Mediterranean zone (MZ) were derived from the Mediterranean zone and Corsica as defined in the
 145 VégétalLocal map (Office français de la biodiversité, 2021); the rest of France will be referred to here
 146 as Continental zone (CZ). (B) Subsets of data used in additional analyses: i) the regional scale splits the
 147 MZ from the CZ; ii) annual crops included rotations based on wheat, maize and market gardening crops
 148 (n = 450); perennial crops only included vineyards (n = 105); iii) annual plants (n = 61) opposed to
 149 perennials (n = 79).

150










151 *Climatic and agricultural variables*

152 We gathered two types of explanatory variables: the first came directly from the 500-ENI network and
 153 reflects agricultural practices assessed directly on the monitoring sites; the second one included
 154 meteorological data from an external database (see below). Here, we chose not to include landscape









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









157 Agricultural practices were reported yearly from interviews of farmers into a standardized online
158 database. Data collected relate to fertilization, herbicide use and field margin management (mainly
159 mowing of vegetation). Daily meteorological data were extracted from the SAFRAN climate model of
160 Météo France, with a resolution of 8 km (Le Moigne, 2002). Meteorological data were averaged over
161 a one-year window prior to each floristic observation, while agricultural data were summed over the
162 same period (**Table 1**). We selected variables that were weakly correlated (Spearman correlation <
163 0.65, **Appendix B**) and have been shown to influence plant communities in previous studies (**Table 1**,
164 see **Appendix C** for the choice of variables).

165 **Table 1.** List of explanatory factors (blue), functional traits (green) and response variables (red) with their abbreviations, units and calculation. The variables
 166 only used in temporal models are underlined, while those only used in spatial ones are in italic. We have illustrated by arrows the expected link of each factor
 167 and trait to the agricultural resource and disturbance gradient, and to climate change. Horizontal arrows indicate contradictory findings in the literature (see
 168 **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: $Dose = \frac{Quantity \times N \text{ of the formulation}}{100}$ Doses were summed one year before observation |  | |
| Number of herbicide treatments | HERB | | Treatments were summed one year before observation |  | |
| Number of management events | MAN | | An event corresponds to the occurrence of vegetation management at a given time, most often by mowing or grinding. Management events were summed one year before observation. |  | |
| Date of observation | DATE | Julian days | |  |  |
| | | | |  |  |

| | | | | |
|----------------------------|----------|---------------------------------|---|----|
| <i>Number of observers</i> | OBS | | | |
| Specific leaf area | SLA | m ² kg ⁻¹ | ↗ | ↘ |
| | | | ↗ | →? |
| Maximum plant height | HEIGHT | m | ↘ | →? |
| | | | ↗ | →? |
| Seed mass | SM | g | ↘ | ↗ |
| | | | ↗ | ↗ |
| Flowering onset | FLOW_ON | months | ↘ | ↗ |
| | | | | ↗ |
| Flowering duration | FLOW_DUR | Months | ↗ | ↘ |
| | | | | ↘ |

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

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

170 *Plant functional traits*

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

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

$$182 \quad CWM = \sum_{i=0}^n p_i \times trait_i \quad \text{(Eq. 1)}$$

$$183 \quad CWV = \sum_{i=0}^n p_i \times (trait_i - CWM)^2 \quad \text{(Eq. 2)}$$

184 Where p_i is the relative abundance, $trait_i$ is the value of trait for species i , and n is the total number
185 of species. To correct for correlation between CWV and species richness, we used a null model
186 approach, shuffling the abundances in the species matrix for species of the species pool, while keeping
187 the species x trait matrix unchanged (Bopp et al., 2022). This procedure keeps trait correlations, species
188 richness and total abundance in a site unchanged, while dissociating abundances from trait values
189 (Bernard-Verdier et al., 2012).

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

194 observed and null CWV, we computed effect sizes (**Appendix D**). A positive effect size denotes a
195 divergence in trait values within the community (convergence for negative effect size). These effect
196 sizes (and not the raw CWV) were used in our analyses and referred to as CWV in the subsequent
197 sections. We performed a normed PCA on the CWM of traits (by site for spatial analyses, by
198 observation for temporal analyses) to classify each community based on its average trait combination
199 or ecological strategy, which is reflected by its position on the first two axes.

200

201 *Plant functional strategies*

202 We extracted the CSR scores for 119 out of 142 focal species from Pierce et al. (2017). CWM of CSR
203 scores were computed by observation and by site and were added to the PCA on the CWM of traits as
204 supplementary variables. The CWM of CSR scores computed by observation were plotted on a CSR
205 triangle to illustrate temporal trends in strategies.

206

207 *Spatial analyses of plant communities*

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

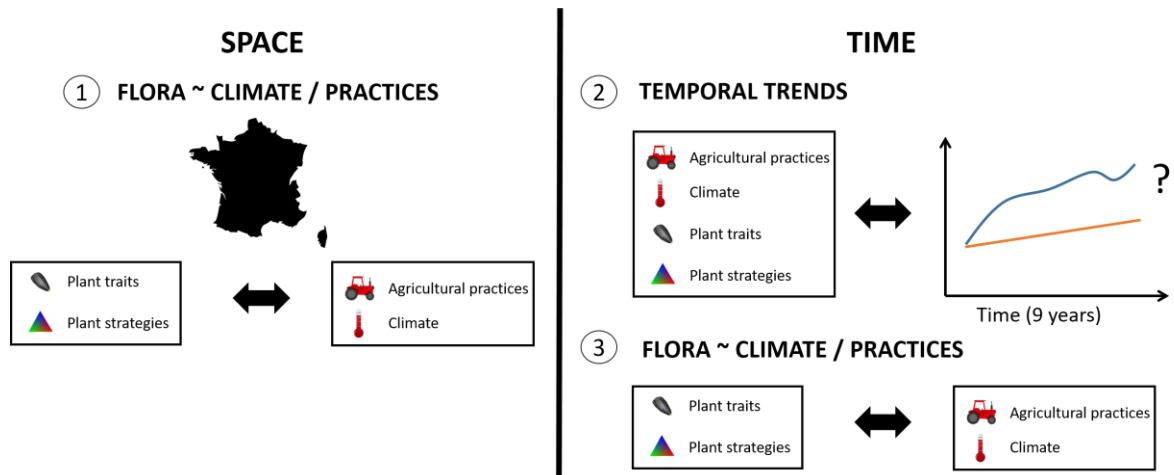
218 we controlled for the observer bias by adding the number of successive observers in a site as a fixed
219 effect. For all analyses, we chose a p-value threshold of 0.01 to focus on the effects for which our
220 confidence level was highest.

221

222 *Temporal analyses of plant communities*

223 In a second stage, we wanted to assess the extent to which spatial patterns on climate and agricultural
224 practices were also reflected on temporal trends. We checked first if there was a temporal trend on
225 the raw variables, and then we used climate and agricultural practices as predictors for the different
226 response variables. In all cases, we used generalized additive mixed models (GAMM) to account for
227 repeated measures at a site, with a Gaussian distribution in most cases (but see **Appendix E, Table**
228 **SE.2**), and site identity as a random effect. Observer bias was accounted for by including the observer
229 identity as a random term nested within sites. For each response variable (species richness, functional
230 composition, divergence and CSR strategies) and explanatory factor (temperature, soil moisture,
231 nitrogen dose, herbicides and margin management), we built a first model with the year as a linear
232 fixed effect. Then, a second model was built for each response variable, where climate, agricultural
233 practices and observation date were linear explanatory factors. A first-order temporal autocorrelation
234 structure within sites was included (Box et al., 2015). We removed observations with missing values in
235 climatic and agricultural factors (1805 out of 4172 observations), and a few observations that distorted
236 trait distributions (**Appendix E**), resulting in varying observation numbers across models (see **Fig. 5**).
237 We repeated this analysis on subsets of data, including Mediterranean (MZ) vs Continental (CZ) zones,
238 margins adjacent to annual crops vs vineyards, and annual vs perennial plant species (**Fig. 1**).

239



240

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

249

250 Results

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

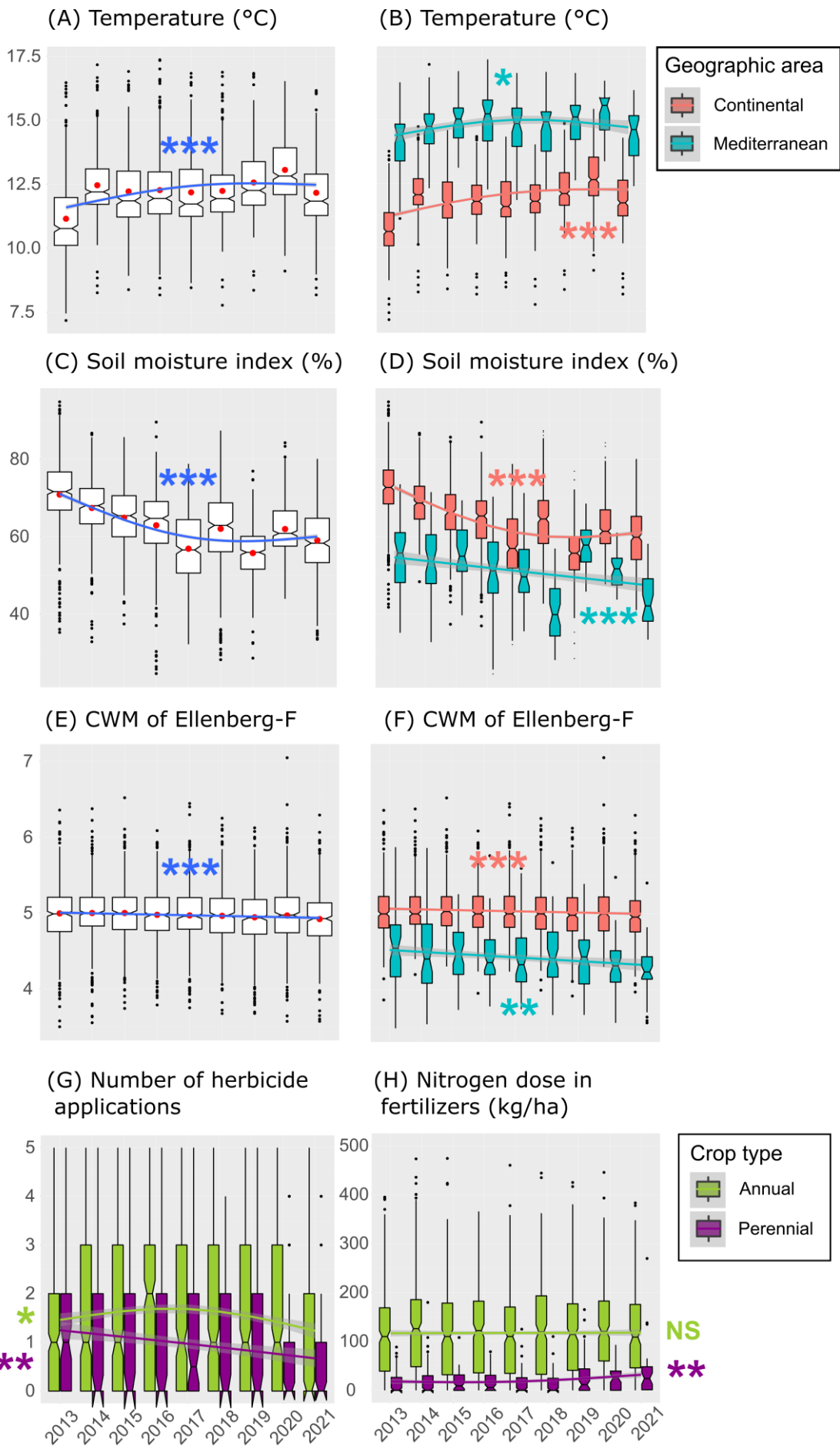
252 Temperatures have significantly increased by an average of 1.2°C over a decade (0.7°C in the
 253 Mediterranean Zone), while soil moisture has steadily declined (-14.1% by decade) (**Fig. 3**, and
 254 **Appendix F**). These trends differed between the Mediterranean Zone (MZ) and the Continental Zone
 255 (CZ), with the MZ experiencing a slower decline in soil moisture due to a high cumulative precipitation
 256 in 2019 (**Fig. 3**). Regarding agricultural practices, herbicides slightly decreased over time in vineyards
 257 (-0.9 application by decade; **Fig. 3**), with an even weaker trend in annual crops (-0.2 application by

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

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

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

279



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

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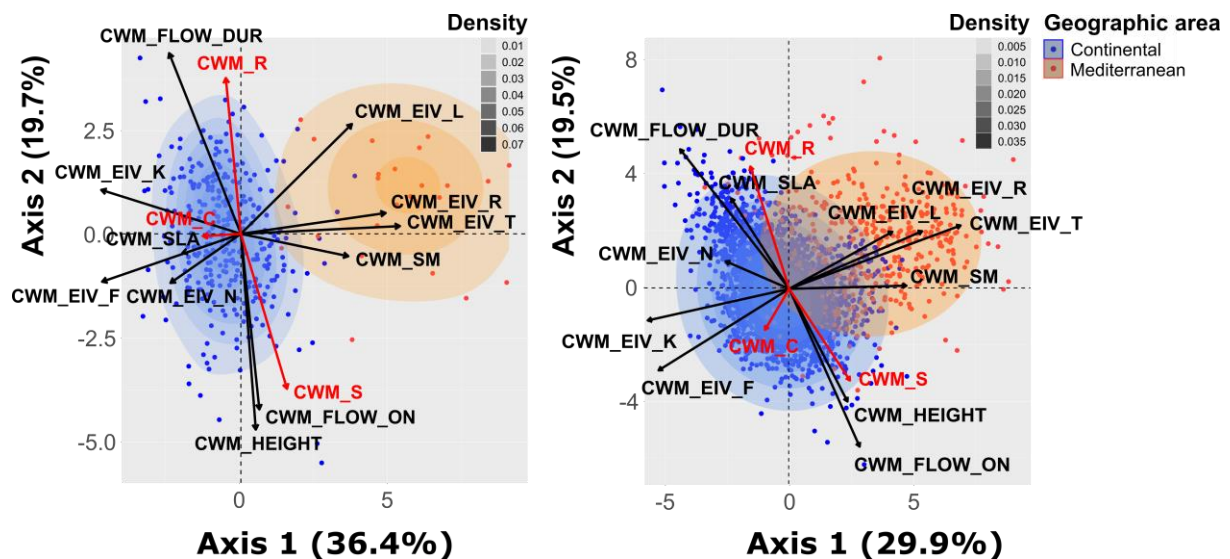
288 *Spatial analyses of plant communities*

289 The first PCA axis (named thereafter stress-tolerance axis, see **Appendix G, Fig. SG.1** for the correlation
290 of each strategy with each axis) explained 36.4% of the variation and revealed a gradient from
291 continental hygrophilous, ruderal and competitive communities associated with resource-rich
292 environments, to Mediterranean xero-thermophilous stress-tolerant communities adapted to
293 resource-poor and arid environments (**Fig. 4, Appendix G, Fig. SG.2**). Communities with continental
294 species were more nitrophilous, had a higher SLA and flowering duration, while Mediterranean
295 communities had a higher seed mass. The second PCA axis (named thereafter ruderal axis) explained
296 19.7% of the variation and contrasted stress-tolerant/conservative communities adapted to low
297 disturbance (high stature, late and short flowering) with ruderal/acquisitive communities adapted to
298 high disturbance (short stature, early and long flowering).

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

306 management favored ruderal communities with higher SLA and/or lower seed mass (PCA Axis 1),
 307 shorter stature (-7.1 cm by management event) and longer flowering duration (+3.7 days by
 308 management event; PCA Axis 2). Herbicide applications had no significant effect, while the average
 309 annual nitrogen dose in fertilizers slightly decreased the species richness (-3.2×10^{-2} species by kg/ha)
 310 and pH requirement, and increased the nitrogen requirement, SLA and divergence in flowering
 311 duration (**Fig. 5**). The number of observers surveying a site over the 9-year period was positively
 312 correlated with species richness (average increase of 1.7 species by observer) and with the CWM and
 313 CWV of flowering duration (divergence).

314



315

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

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

325

326 *Temporal analyses of plant communities*

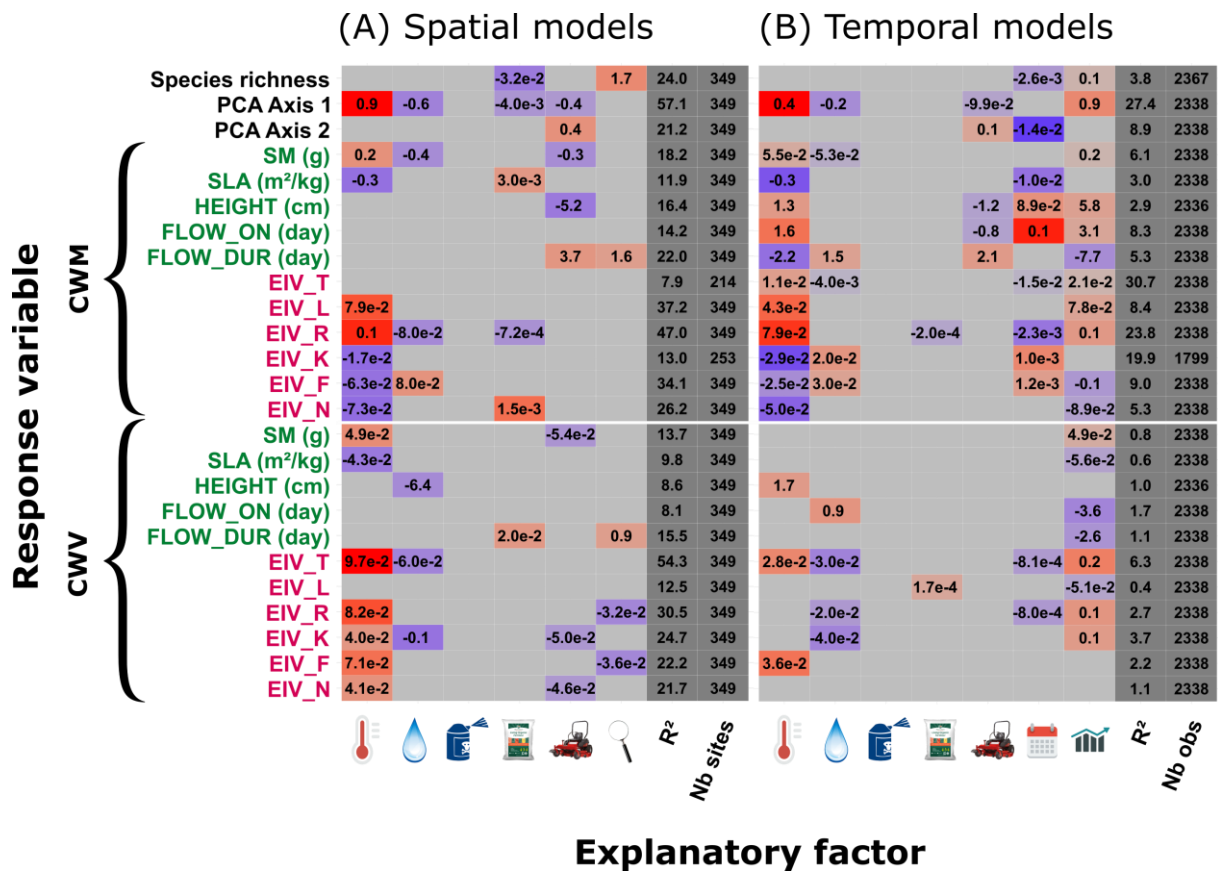
327 PCA on CWM by observation closely mirrored PCA on CWM by site (**Fig. 4**). The first two axes
328 represented the same ecological strategies, explaining 29.9% and 19.5% of the variation, respectively.
329 However, one difference was that SLA was more correlated to the ruderal rather than the stress-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

332 Climatic factors were also the most influential in temporal models, with high R^2 for the temperature
333 requirement ($R^2 = 0.33$) and stress-tolerance axis ($R^2 = 0.27$, **Fig. 5**). Regressions between each
334 Ellenberg value and climatic factors remained consistent across spatial and temporal models, with
335 increasing temperature leading to an increase and divergence in Ellenberg-T values (requirement for
336 temperature). However, new patterns emerged in temporal models, with increasing temperature and
337 drought associated with shorter flowering duration (-2.2 days by $^{\circ}\text{C}$ and +0.15 days by % of soil
338 moisture), and later flowering onset only for increasing temperature (+1.6 days by $^{\circ}\text{C}$; **Fig. 5**). Margin
339 management was the agricultural practice with the largest impact on community changes, with an
340 increase in its frequency associated with more ruderality (-1.2 cm in maximum height, -0.8 days in
341 flowering onset and +2.1 days in flowering duration by management event). The date of observation
342 also influenced community changes, as a later observation was related to more conservative,
343 competitive and continental communities, and to a decrease in species richness.

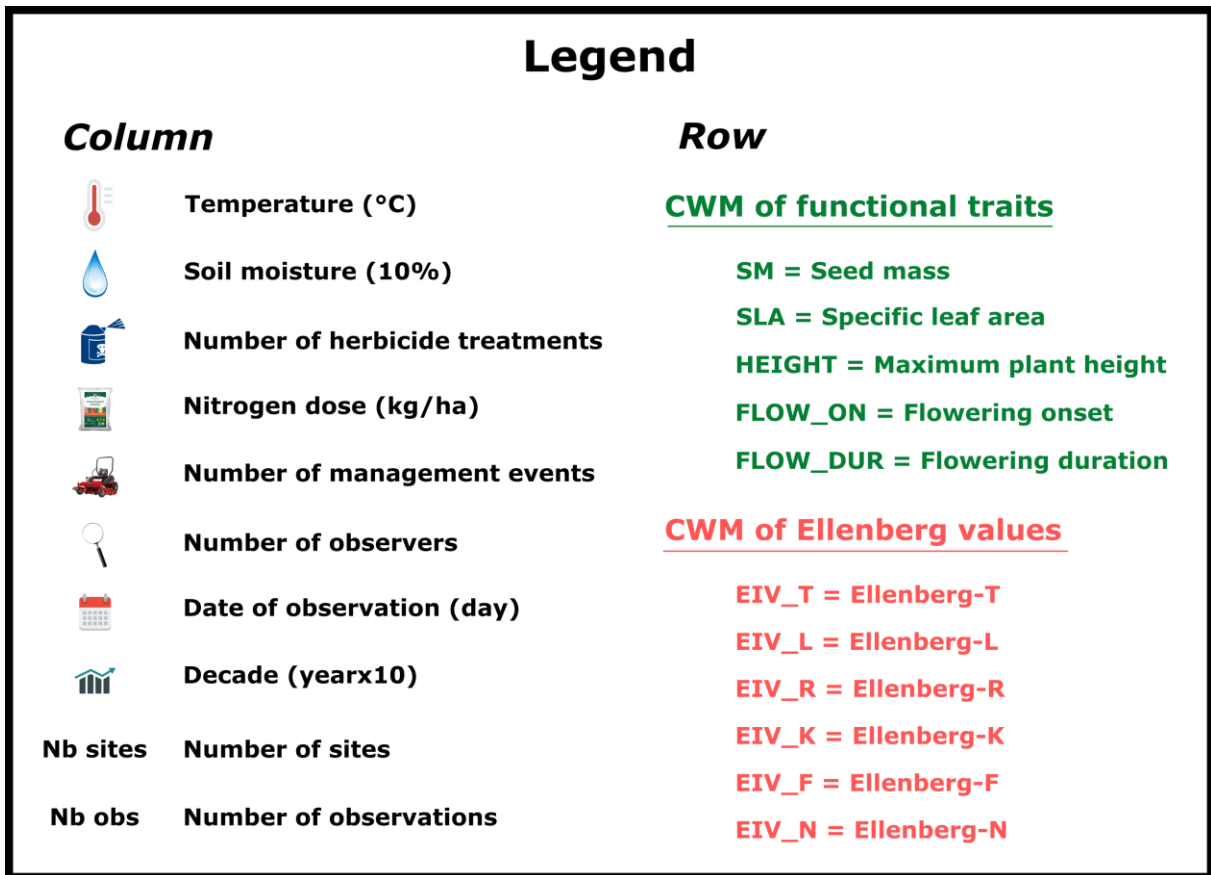
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348

349 **Fig. 5.** Results of (A) spatial (SAR) and (B) temporal models (GAMM) on the whole dataset, with
350 response variables in rows and explanatory factors in columns. The adjusted R^2 , expressed as a
351 percentage of variation, and the number of observations are reported. Significance is indicated by
352 colored cells, with a p-value threshold of 0.01. Positive estimates are in red, negative estimates in blue,
353 and the strength of the relationship (based on the standardized estimates) is reflected by the lightness
354 of the color (weaker when lighter). It is important to note that the strength of the relationship can only
355 be compared among explanatory factors for a same response variable. Reported values are the raw
356 estimates and can be interpreted in the units of response and explanatory variables (e.g. an increase
357 of 1°C in temperature leads to an increase in 1.6 days in the CWM of flowering onset). Models with
358 the year as explanatory factor were run separately.

359

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

368

369 **Discussion**

370

371 The changes observed in both spatial and temporal analyses can be interpreted through the lens of
372 Grime's competitor, stress-tolerant, ruderal (CSR) framework (**Fig. 6**; Grime, 1988). According to
373 Grime, stress (i.e. a shortage of resources such as nutrients, water and light) and disturbance (i.e. the
374 partial or total destruction of plant biomass) determine three main plant strategies representing
375 combinations of traits that are viable under conditions of low disturbances and high resources
376 (competitor, C), low disturbances and low resources (stress-tolerant, S) or high disturbances and high
377 resources (ruderal, R). Originally developed to classify individual plant species into strategies, Grime's
378 theory can be useful to interpret functional changes in plant communities, especially in the context of
379 global changes where vegetation is subject to harsher climatic conditions (more droughts) and various
380 levels of agricultural disturbances (**Fig. 6**). Below, we use this framework to contextualize our results.

381

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

383 Our analyses revealed a shift towards more stress-tolerant and less ruderal communities, primarily
384 driven by climate (Díaz et al., 2016; Pakeman et al., 2009). Since meteorological variables were
385 extracted at a 8 km resolution, changes in soil moisture can be confidently attributed to climate change
386 and not to the effect of soil compaction due to cultivation. Increasing temperature and drought
387 favored more xerophilous (Ellenberg-F) and thermophilous (Ellenberg-T) species, with higher seed
388 mass and lower nitrogen requirement, thus shifting the position of communities along the stress-
389 tolerance axis. Our results also indicated that sites increasingly or already warmer and drier allowed
390 for coexistence of a wider functional variety of species, suggesting a potential dominance of generalist
391 species with a wider temperature tolerance range, or an increased abundance of thermophilic species
392 without any loss of cold-adapted species. The increase in species richness over time provided
393 additional support for this latter hypothesis.

394 Our study is one of the first to provide empirical evidence that climate change is already resulting in
395 detectable functional changes in plant communities over a relatively short time interval of 10 years
396 (see also Martin et al., 2019). The increase in mean thermal preference at the community-level with
397 rising temperatures was already documented, but mainly by studies covering entire floras (regional or
398 local species pool) and time scales of several decades to a century (Salinitro et al., 2019; Tamis et al.,
399 2005). We found that this trend is now detectable over a short-term period of only nine years (Martin
400 et al., 2019). Interestingly, as in other recent studies (Duchenne et al., 2021; Martin et al., 2019), this
401 trend was more pronounced in northern France, while Mediterranean communities responded less to
402 climate change (**Appendix H**). On top of the fact that climatic trends observed in the MZ were weaker
403 than in the CZ, Mediterranean species are already adapted to dry and heat stress, and might be more
404 resilient to extinction risks (Thuiller et al., 2005). Because of their geographic position north of the
405 Mediterranean Sea, they might also experience some competitive release due to the lack of
406 immigrants coming from the south, and the northward shift of more temperate species (Duchenne et
407 al. 2021).

408 Beyond the increase in mean thermal preference, our temporal models revealed additional temporal
409 changes related to climate change that align well with the existing literature, including a decrease in
410 mean SLA and an increase in mean seed mass and maximum height (Alarcón VÍllora et al., 2019; Kühn
411 et al., 2021). These trait values (low SLA, high seed mass and height) are also known to be linked to
412 less intensive agriculture (Fried et al., 2012; Richner et al., 2015). In our models, we observed a similar
413 pattern, with less intensive margin management associated with a decrease along the ruderality axis
414 and an increase along the stress-tolerance axis. All of this suggests that climate change and the
415 evolution towards more extensive agricultural practices will select the same trait values towards more
416 stress-tolerant and less ruderal strategies. However, we cannot entirely rule out the possibility that
417 plant communities are also responding to past landscape diversification, which could have generated
418 a functional response similar to the one observed for climate change, leading to a decrease in ruderal
419 species as arable lands decrease.

420 Finally, temporal analyses showed additional phenological changes, suggesting that climate change
421 could increase the occurrence or abundance of late-flowering species, i.e. species that have high
422 thermal requirements to complete their life cycle (Peters et al., 2014). These phenological shifts
423 coincided with a decrease in trait variance, leading to a reduction in functional diversity. Critically, such
424 changes can reduce the ability of species to escape field margin management, which typically favors
425 species able to flower all-year-round, as expected with a ruderal strategy. As species will not be able
426 to advance their phenology indefinitely, this can ultimately result in species losses in the long-term,
427 unless farmers may also adapt the temporality of their practices to climate change.

428

429 *Agricultural practices have a weaker impact on diversity and species assembly*

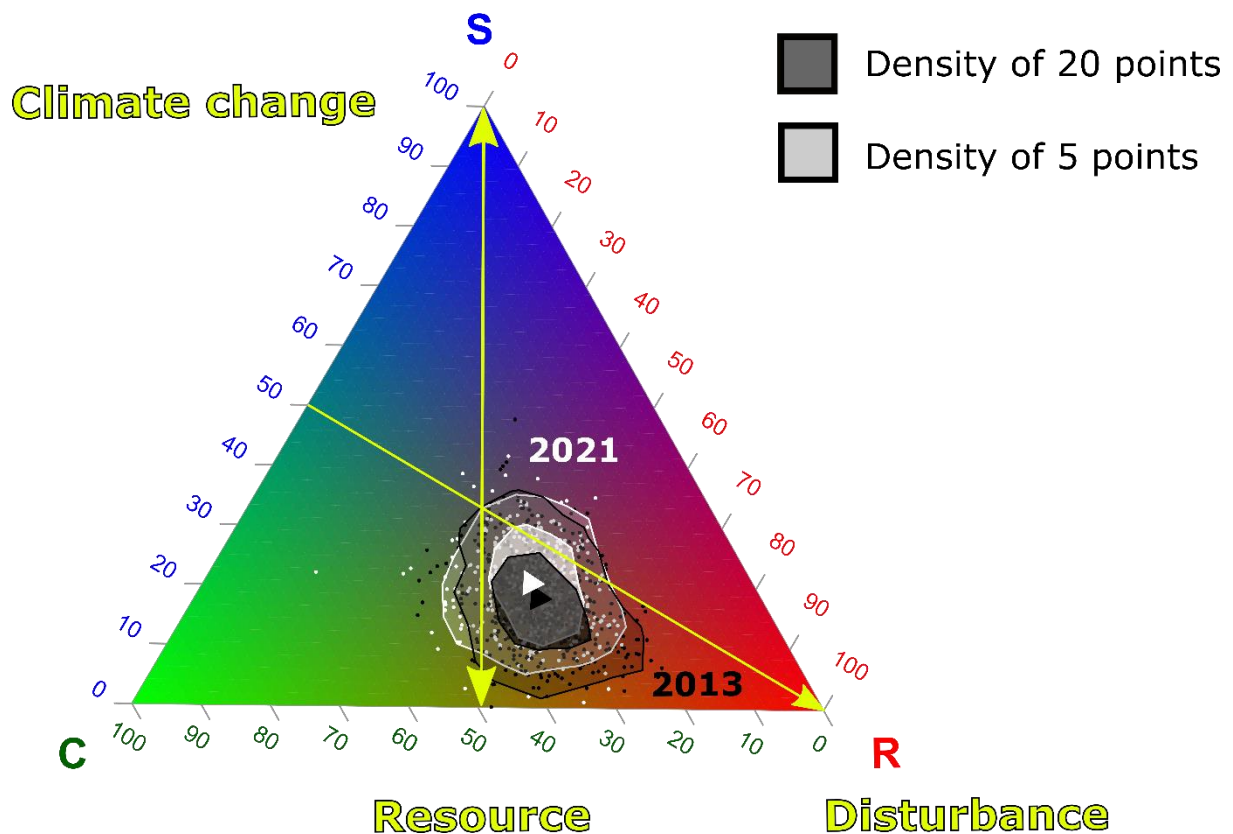
430 Temporal variations in agricultural practices over the short-term had a weaker influence on diversity
431 and species assembly than climatic variations (Alarcón Villora et al., 2019; Fried et al., 2019). Field
432 margin management was the most impactful practice, affecting traits related to the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

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

445 Verbeek, 2000), an effect detected in the MZ and leading to the loss of some annual Mediterranean
 446 species (Poinas et al., 2023). Due to functional trade-offs, high nitrogen levels can favor nitrophilous
 447 plant species, which are often less thermophilous and more acidiphilous, explaining that nitrogen dose
 448 was related to affinity for acidic soils in our models. Nitrogen application levels remained constant over
 449 time, which aligns with the weak change in global nitrophily levels in plant communities, suggesting
 450 that eutrophication may no longer be the primary driver of changes in vegetation (Alignier, 2018;
 451 Duchenne et al., 2021).

452

453



454

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

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

462

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

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

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

484 Munoz et al. (2017); Fried, Chauvel, et al., 2009) and have a high affinity for calcareous soils, which will
485 probably limit their expansion towards the CZ to restricted areas. Areas where they are unable to
486 colonize might suffer a decrease in species richness, and this scenario could be worsen if current levels
487 of agricultural intensification are maintained or increased. Mediterranean species expanding in the
488 northern half of France could face severe agricultural intensification that would likely limit their
489 expansion, while at the same time ruderal species would become less frequent mostly because of
490 drought. This highlights the need to consider the conjunction of climate change and intensive
491 agriculture.

492

493 **Conclusion**

494 Our study highlights climate as the primary factor affecting field margin plant communities in France,
495 with increasing temperatures and decreasing soil moisture fostering Mediterranean, stress-tolerant
496 and conservative species, while negatively affecting ruderal species. In comparison, agricultural
497 practices had a limited effect on species richness and assembly at the national level, with field margin
498 management having the greatest impact. The species selected by climate change are poorly adapted
499 to intensive farming, while the pool of species currently able to colonize field margins is restricted to
500 a limited functional range adapted to agricultural practices. The persistence of intensive agricultural
501 practices and accelerating climate change could thus have critical consequences for the conservation
502 of floristic diversity in agroecosystems. However, it is important to consider the potential of adaptation
503 of species, through intraspecific trait variability and phenotypic plasticity (known to be particularly high
504 in ruderal species, Baker, 1974), as it may enhance their resilience to changing conditions. Our findings
505 suggest a likely reduction in ruderality and an increase in stress-tolerance according to Grime's
506 strategies. Bopp (2023) highlighted a similar increase of stress-tolerance in weeds in response to
507 climate change, but did not observe a corresponding decrease in ruderality. Further investigations are
508 thus necessary to assess the generalizability of these results across different habitats, including

509 communities with broader or narrower functional niche, such as weeds. Long-term monitoring
510 programs are necessary to address some perspectives, such as the potential time-lag in flora's
511 response to environmental changes, the non-linearity in temporal trends and the interactive effects
512 between climate and agricultural changes. Finally, the findings presented in this study call for a rethink
513 of our current agricultural model, urging us to prioritize the development of agricultural practices that
514 foster the creation of favorable microclimates while minimizing local intensification. Promising
515 approaches, such as agroforestry, hold the potential to align agricultural production with biodiversity
516 conservation goals by providing habitat diversity, microclimate regulation, and maintenance of
517 ecosystem services.

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525

526 **Conflict of interest disclosure**

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

529

530 **Appendix A-H. Supplementary data**

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

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