Dear Isis Poinas and co-authors,

Many thanks for submitting your manuscript "Functional trade-offs: exploring the effects of climate change and agricultural practices as drivers of field margin plant communities". I found your work timely and relevant for current discussions on the role of agricultural practices in the face of the food and biodiversity crisis.

After receiving the review of three colleagues (Dr. Clelia Sirami, Dr. Ignasi Bartomeus and Dr. Diego Gurvich) and my own review, I decided to ask you for a major revision of your manuscript. You will see that all reviewers found your article very interesting and highlight the impressive dataset that you analysed as well as the importance of sharing your results to discuss the effects of climate change and intensive agriculture on biodiversity of field margins. I agree with such positive conclusion on your work. However, Dr. Sirami, Dr. Bartomeus and I made several major comments, observations and suggestions that I expect you will consider or provide specific arguments in case you decide to not include them. I hope you will find our contributions valuable and that they will improve your manuscript.

In general, we all had concerns on methodological, design and analytical decisions that lacked a clear explanation or arguments. These decisions may affect your results so need to be clarified (e.g. decisions on data collection, selection of common species, information on landscape heterogeneity, crop type, history of production of farms). There is also general agreement on a lack of centrality of Grime's strategies background in your introduction, which should be changed as it became the core of your discussion. Figures 4 and 5, which ar central to your

contribution, were not clear ofr Dr. Bartomeous and I, and we made suggestions that I hope will improve them. In that vein, I suggest you try to simplify your results keeping in mind your interest in sharing your work with stakeholders. Dr. Sirami and I also made several suggestions to your discussion section, in order to include discussions on other results beyond Grime's strategies (e.g., trait variance at community scale), the interaction among climate and agricultural practices, implications/perspectives on landscapes management and perspectives/feedback on the public program that guides data collection.

You will find more specific comments on the reviews of Dr. Sirami, Dr. Bartomeus and Dr. Gurvich. I Attach a pdf with my review.

Thank you for your positive feedback, we hope this new version addresses your concerns appropriately. We have addressed your comments directly in the PDF.

I will wait for a new version of your manuscript and your specific responses to reviewers to make a decision about recommending your article for PCI Ecology.

Thank you very much again for sending your contribution to PCI Ecology.

Best wishes

Julia

Review by [Ignasi Bartomeus](#), 30 Mar 2023 22:14

The manuscript presents an impressive dataset to ask how ruderal plants have changed in the last decade across space in France. The challenge is to explain such complex patterns effectively. While the manuscript is overall sound, my main concern is that some details or decisions are unclear or not justified. Most of my comments are in this direction.

First, given the several analysis conducted, I would recommend focusing the discussion on the effect sizes of the different models and avoiding using p-values. The authors are aware of that and already report p-values at alpha 0.01, and highlight the R2 of the models, but I miss a clear interpretation of the models in terms of the effect observed. How many e.g. species on average were lost over years? If the authors can translate the results into clear units, the paper will be much easier to follow. A clear example is Fig 4, which is a nice summary of "important" variables, but it tells nothing about how big were each of the effects.

We have followed your recommendation, both in the text and in Fig.4: we translated all observed effects into clear units when possible, we removed p-values from this figure, and we repeated all models by standardizing the predictors, which gives an idea of the relative strength of each effect size (lightness of the color in Fig 4).

Second, while I like the distinction between temporal and spatial patterns, I am not sure if using a single modeling technique would help explain better the story. First, temporal correlations are shown, but those treat all site-year combinations as independent. I would expect "site" to be modeled e.g. through a random structure as done for other analyses. Second, spatial trends are done by pooling across years, but I am not sure if this pooling can mask some interesting effects. Finally, a more detailed temporal analysis is done, this time considering "site" as random (this is in part redundant with the first analysis?). Moreover, all these models are run for different subsets of data. Would it be possible to tackle all questions within a single analytical framework? For example, by modeling the interaction between time and environment e.g. CWM ~ Time * Region would avoid doing a test for each region. I am not suggesting that all analyses need to be re-done, but if you can simplify the number of tests done, without losing insights the paper would gain clarity and robustness.

Regarding your first comment, we agree that adding a mixed effect to consider the repeated measures linked to the plots that were visited multiple times was a good idea when analyzing temporal trends, so we implemented this by replacing the Spearman rank correlations with GAMMs that incorporate site as random effect and year as predictor in the estimate of the temporal trends. This also allowed simplifying somewhat the materials and methods, and did not change the results in terms of which variables present or not a temporal trend.
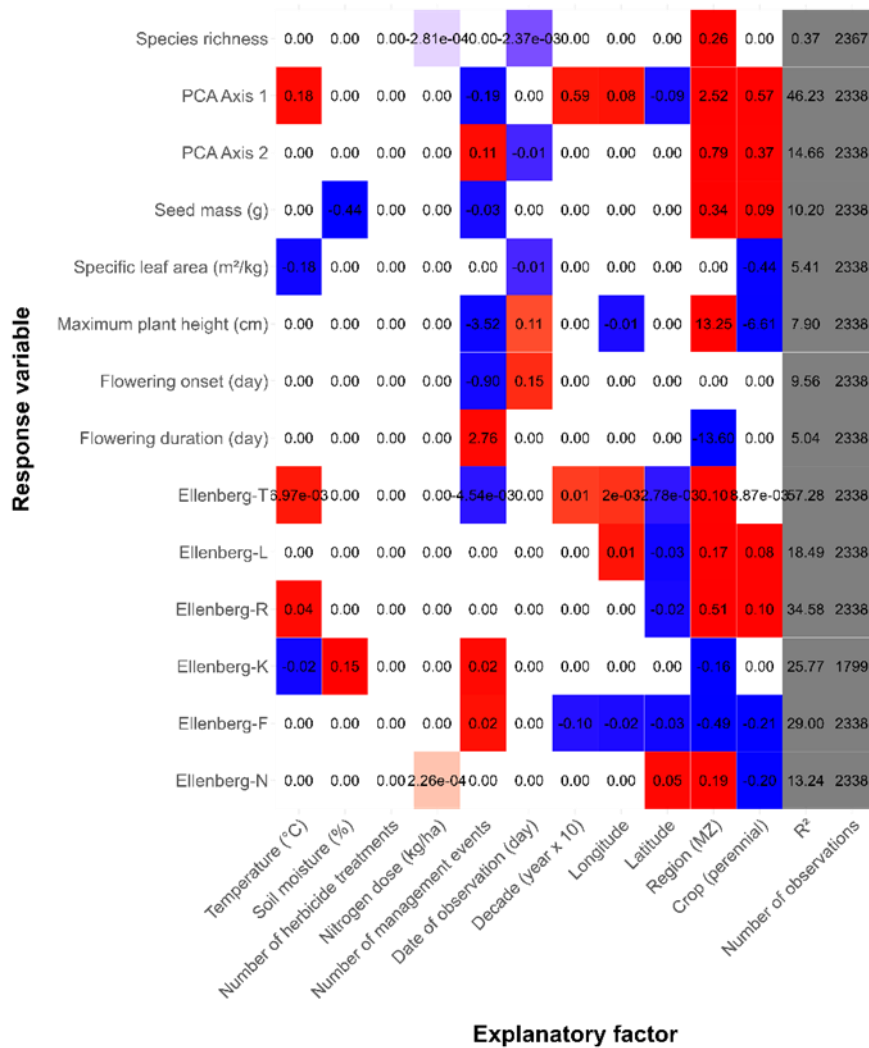
Regarding your second comment, pooling across years allows focusing on the spatial trends, and ignoring to a certain degree the observation bias, since we are only taking sites that have been surveyed over several (>5 years) times. This ensures that estimates of richness and

functional composition is as complete as possible (see our reply to reviewer 2 with the accumulation curve), and also ensures that temporal patterns are not masking spatial patterns.

Regarding your third comment, when considering space and time in the last model, we need to include site as a random effect because sites were visited several times (and are therefore repeated measures, which is usually modeled with these random effects). It would therefore be incorrect to consider that each visit to the same site is an independent measure. Notice that in this model we also included observer as a random effect and, since a single observer can visit several sites, observer is nested within site as a random effect. This is as close as a full model as we can get.

Unfortunately, analyzing temporal and spatial trends, and including a random effect for sites as you suggested becomes difficult very quickly because there are no statistical models to our knowledge that can properly incorporate all such structures at once (repeated measures + temporal autocorrelation + spatial autocorrelation), and once you consider one, the effects of the other become tangled in the interpretations. A GAMM with repeated measures and spatial autocorrelation for example is not feasible, as the algorithm will return an error when geographic distances are equal to 0. A feasible alternative that is often used is a GAMM with site as random effect, year as a predictor (to consider time) and latitude / longitude as spatial predictors (which will consider large-scale spatial trends, not necessarily spatial autocorrelation). Although we considered this model (see below), there are at least two issues that we would like to avoid because they render this model's interpretation more difficult: (1) including these variables as predictors will likely eliminate real causal variables from the set of significant ones because geographic coordinates and time present strong correlations with those proximal predictors and (2) including too many of these factors, in particular the interactions, will increase exponentially the degrees of freedom required in the analysis, which would not be appropriate for our sampling size (even though having 500 plots over several years is still a fairly unique dataset in ecology).

Taking into account this comment, along with one of reviewer 2 (who suggested we also added region and crop type as predictors), we re-run all models as specified above (observer as random effect, year, latitude and longitude as predictors, plus crop type and region as additional factors). As expected, adding these predictors often eliminates significance for the predictors we are most interested in. Consistent with our previous concerns, the variables that were identified in the first stage as presenting a temporal trend become non-significant because year and geographical coordinates become significant predictors. This makes the results difficult to interpret and we are also adding several more degrees of freedom required for the analyses, making the results even more uncertain (especially those that become non-significant). Notice, however, that the relationships that are still significant are consistent with those shown in our original analysis:

Response variable	Temperature (°C)	Soil moisture (%)	Number of herbicide treatments	Nitrogen dose (kg/ha)	Number of management events	Date of observation (day)	Decade (year x 10)	Longitude	Latitude	Region (MZ)	Crop (perennial)	R^2	Number of observations
Species richness	0.00	0.00	0.00	-2.81e-04	0.00	-2.37e-03	0.00	0.00	0.00	0.26	0.00	0.37	2367
PCA Axis 1	0.18	0.00	0.00	0.00	-0.19	0.00	0.59	0.08	-0.09	2.52	0.57	46.23	2338
PCA Axis 2	0.00	0.00	0.00	0.00	0.11	-0.01	0.00	0.00	0.00	0.79	0.37	14.66	2338
Seed mass (g)	0.00	-0.44	0.00	0.00	-0.03	0.00	0.00	0.00	0.00	0.34	0.09	10.20	2338
Specific leaf area (m²/kg)	-0.18	0.00	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	-0.44	5.41	2338
Maximum plant height (cm)	0.00	0.00	0.00	0.00	-3.52	0.11	0.00	-0.01	0.00	13.25	-8.61	7.90	2338
Flowering onset (day)	0.00	0.00	0.00	0.00	-0.90	0.15	0.00	0.00	0.00	0.00	0.00	9.56	2338
Flowering duration (day)	0.00	0.00	0.00	0.00	2.76	0.00	0.00	0.00	0.00	-13.60	0.00	5.04	2338
Ellenberg-T	6.97e-03	0.00	0.00	0.00	-4.54e-03	0.00	0.01	2e-03	2.78e-03	0.10	8.87e-03	57.28	2338
Ellenberg-L	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	-0.03	0.17	0.08	18.49	2338
Ellenberg-R	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.02	0.51	0.10	34.58	2338
Ellenberg-K	-0.02	0.15	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.16	0.00	25.77	1799
Ellenberg-F	0.00	0.00	0.00	0.00	0.02	0.00	-0.10	-0.02	-0.03	-0.49	-0.21	29.00	2338
Ellenberg-N	0.00	0.00	0.00	2.26e-04	0.00	0.00	0.00	0.00	0.05	0.19	0.20	13.24	2338

Explanatory factor

Instead, our two-stage approach allows concentrating on one factor at a time (space, then time) and consider time effects after having analyzed which predictors are potentially causing such patterns (since those that do not present a temporal trend could not possibly be responsible for temporal trends on the response variable). We think this is still the simplest way to approach the problem without overextending on the trade-off between sampling size and degrees of freedom and without using non-causal predictors in the model. Moreover, the residuals of the models presented in the manuscript were further analyzed to look for spatial or temporal autocorrelation, which they did not show, suggesting that the predictors included in the models already take into account such spatial and temporal patterns. However, we also realize that we did not explain enough of this logic in our previous version of the manuscript, and therefore added some clarifications.

Regarding simplification of our modelling framework, in this version we tried to homogenize, for example by including the same GAMM framework with site as random effect for temporal trends and other analyses wherever possible (it was not possible for spatial models, as the spatial correlation term in GAMM is less appropriate than the one in SAR, i.e. there was still residual spatial autocorrelation). Regarding the repetition of the same analytical framework on different subsets of data, we considered adding an effect of interaction with the region but found out that

it would not be the right choice as the estimate of this interaction term would only inform on the difference of slope between the two regions. Adding a fixed effect of the region or crop would only inform on functional differences across regions and crops, thus providing redundant information with the regional effect depicted in the PCA on CWM. We thus kept most models, but greatly simplified the presentation of the text and appendix by only including relevant information, and provided a better justification of the two-stage space vs time modelling process (Fig. 2).

Finally, while I appreciate the context of Grime's triangle, this appears only in the discussion, and for me was very hard to relate the analysis performed to this framework. For example line 333 says your analysis shows changes in stress-tolerant species, but you did not previously relate your analyzed variables with the CSR strategies. This can be easily fixed by introducing this earlier on, or alternatively, this comparison can be deleted, as the manuscript is already quite complex. I have to say I did not fully understand Fig 5. Calculating CWM on CSR scores, and averaging across space is oversimplifying the story, and the two data points (a mean of means) are very close to each other precisely because this averaging masks more subtle trends, but the variation across species might explain a better story. In any case, this should be integrated into methods and in your modeling framework. Otherwise, sentences such as 417-418 are not convincing.

The CSR triangle was already mentioned in the Introduction (Lines 76-79), but we now expand a bit to make it more central to the introduction and added it into the Material & Methods section.

We added this paragraph at the end of the introduction:

"Furthermore, we explored the connection between Grime's CSR strategies, climate and farming practices. Considering that these strategies are linked to resource and disturbance levels, we hypothesized that they would respond to climate factors (particularly water resource) and agricultural practices (disturbance and resource provision through fertilization)." (Lines 106-110)

To link the CSR strategies with the previously analyzed traits, we included them as supplementary variables in the PCA, as explained in a new paragraph in the MM section:

 "Plant functional strategies

We extracted the CSR scores for 119 out of 142 focal species from Pierce et al. (2017). CWM of CSR scores were computed by observation and by site and were added to the PCA on the CWM of traits as supplementary variables. The CWM of CSR scores computed by observation were plotted on a CSR triangle to illustrate temporal trends in strategies." (Lines 200-203)

We agree with the statement that averaging across space per year is an oversimplification. However, notice that we calculated mean trait values (CWM) in the previous analysis. This simplification is therefore a further step in a chain of analyses that goes in the direction of understanding a temporal pattern in trait changes at the community level, and not the variability per se. To consider this comment and show a more complete picture in the CSR triangle, we now depict not only the means for 2013 and 2021, but also the inter-site variations (see Fig. 5).

In-line comments:

Line 21-22: This justification is poor, and mixes a technique (meta-analysis), with an index (taxonomic diversity). I think it can be safely deleted. The abstract can be enhanced for clarity.

Done

Line 79: I think there is an extra s in traits.

Done

Line 111: You mention 4 crop types, but mention only three.

We corrected by "three". We noted "four" because we distinguished crop rotations with maize or wheat as the main crop production, but it seems more logical to group them together.

Line 123: By removing rare species your analysis focuses on changes in common species. This is fine but should be discussed and interpreted as such.

Agreed. Following the suggestion of another reviewer, we performed the same models using all the species in the dataset. We found that the effects were essentially the same as those obtained using only the focal species, with the exception of a slight increase in SLA that was not detected when focusing on the focal species. We have thus kept our previous analysis on the set of focal species.

Note also that the dominant species, which constitute the highest percentage of total abundance, are considered as focal species in our study. As our research focused on the CWM approach, where species traits are weighted by their abundance, we anticipated only minor variations in the outcomes between the two sets of species.

Table 1. The underlines, italics etc... are really hard to keep in mind, especially as afterward you refer to e.g. "explanatory variables" without mentioning them explicitly again. I am not sure which is the best solution, but maybe adding a column to indicate predictors, explanatory variables, etc... and mentioning them again when you specify the models might help.

Done. We mentioned again each response and explanatory variables when specifying the models.

Line 177: It's unclear if you always use this "richness detrended" CWM index, or if you also use the raw index in your models. I think both are valuable and tell you different things. In fact, the species richness detrended CWM is hard to interpret, and if this is the one you report in the analysis, this should be made very explicit and help the reader interpret it with phrases such as "smaller CWM than expected given a community of this richness".

We used "richness detrended" CWV in all analyses to avoid any bias in the CWV comparisons. We have made this more explicit in the text and provided guidance to the reader on how to interpret the results.

"These effect sizes (and not the raw CWV) were used in our analyses and referred to as CWV in the subsequent sections."

Line 179: Why perform the PCA on CWM values, and not in the pool of species values first, and then calculate metrics by communities (e.g. as done by Villager, Laliberte et al. in the FD package you use to calculate the metrics)? My concern is that CWM is losing information by focusing on the mean (you lose the variance), but maybe there is a rationale to do this. Explaining it would help the reader.

Notice that we calculated both the mean (CWM) and the variance (CWV). This method allows us to understand both facets separately. If we had directly plotted the PCA on species traits and then computed diversity indices as suggested by Villeger et al., the resulting metrics would have incorporated both the mean and variance per community in the same index, making interpretations more difficult. Additionally, we were interested in categorizing communities based on their average ecological strategy, which is not feasible with FD diversity indices as they only provide information on the functional volume occupied.

We added a sentence to explain this: "We performed a normed PCA on the CWM of traits (by site for spatial analyses, by observation for temporal analyses) to classify each community based on its average trait combination or ecological strategy, which is reflected by its position on the first two axes."

Line 195: Adding the number of observers does not fix observer bias (differences among observers). You do this later on by using observe id as random, but I don't think here is accomplished. Maybe I am losing something.

The effect of observer identity can only be incorporated into models that analyze individual observations. For spatial models, however, the data were aggregated by site, and multiple observers can succeed within a given site. As a result, it is not possible to summarize observer identity by site.

However, it is important to consider the effect of the number of observers in this context. While it does not account for all observer related biases, some metrics may vary depending on the number of observers involved. For example, we anticipated a correlation between the total number of species detected in a site and the number of observers in this site. This assumption was made under the premise that each observer would know different species, and our findings corroborated this expectation.

Line 263: Here is an example of the complexity for the reader to follow up on all the details. By using Ellemberg T, the reader needs to track what this variable meant. I would prefer to be redundant and explain what variables should be interpreted every now and then.

Agreed. At each mention of the Ellenberg values, we have specified in the text the meaning of the variable, in order to make the interpretations more explicit.

Best,

Ignasi Bartomeus

Review by Clelia Sirami, 04 Apr 2023 14:20

General comment

The manuscript entitled "Functional trade-offs: exploring the effects of climate change and agricultural practices as drivers of field margin plant communities" presents a very interesting study of the interactive effects of climate changes and land-use changes on plant diversity in agricultural landscapes. It develops a spatial and temporal analysis of a large national dataset, based on a functional approach (species traits and the conceptual framework of Grime's CSR triangle), to assess potential trade-offs in the response of plant species to climate changes and land-use changes. The results of this study may contribute to better predictive models and improved conservation strategies for plant species in agricultural landscapes.

The manuscript is well written. The introduction convincingly argues for the need to use a functional approach to understand the interactive effects of climate changes and land-use changes on biodiversity and develops sound hypotheses based on the literature. The material and method section presents the complex dataset collected within the 500 ENI monitoring program and the set of statistical analyses used to test hypotheses. Results are explained clearly. The discussion is structured around three straightforward messages: the effect of climate, the effect of agricultural practices and their interactive effects on field margin plant communities.

I believe there is still a margin for improvement in terms of clarity of the study design and in terms of interpretation of the results. I therefore provide two sets of comments that will hopefully help the authors to improve their manuscript, as well as a third set of comments on other specific points.

Study design

This study is based on a national dataset collected within the 500 ENI monitoring program. Such programs tend to produce large but complex datasets. It seems to me like some key variables (based on the literature) were not considered in the study and some methodological choices were presented only briefly. Since these variables and methods have the potential to influence the outcomes of this study, it seems important to clarify their consequences (or lack therefore). Below, I develop four main comments regarding the study design.

1)   The herbaceous field margin represents the uncultivated vegetated area located between the cultivated strip and the adjacent habitat. The manuscript mentions that crop type varied within the ENI dataset, with a clear latitudinal gradient (wheat in the north, vineyard in the south; see Appendix A). Similarly, the type of adjacent habitat is likely to vary within the ENI dataset (e.g. crop, grassland, woodland, road, hedgerow…). Yet, these two variables were not considered. What is the likely influence of the type of crop and adjacent habitat on plant communities in the field margin? Could the authors explain why these effects do not create a bias in the study?

Regarding the influence of crop type, our analysis shows that there are significant differences across crops. Vineyards generally require less herbicides than cereal crops, and vineyards in the South of France use even less herbicides than those in the North. A model incorporating crop type as factor shows significant differences (in terms of traits and strategies), but does not allow understanding the nature of these differences (see model presented above in response 2 to reviewer 1). Knowing that the main differences between field margin communities are between vineyards and annual crops and between the Mediterranean region and the rest of France, our strategy was rather to analyze field margin communities variations within these homogeneous entities. By doing so, i.e. analyzing crop type (or region) separately, we can get a more detailed picture of changes related to climate and/or practices.

Regarding adjacent habitat type, our dataset only allows us to explore spatial variations, not temporal ones (because we only have a single snapshot of habitat type characterization). We observed that species richness did not differ according to the type of adjacent habitat. The functional composition was not affected by adjacent habitat, except for wetlands and ditches, which tended to favor species with a conservative strategy (i.e. tall species with a late flowering). To investigate this further, we conducted additional temporal models on sites with wetlands or ditches as adjacent habitats. We found that the observed trends remained largely consistent, but there were fewer climatic effects, particularly those related to soil moisture. This would deserve further analysis, but our dataset is not optimally suited for this purpose since the margins were intentionally selected to avoid habitats of this type.

2)   Landscape structure is a major determinant of biodiversity. Andrade et al. (2021) actually explains that landscape variables were measured around each field within the ENI programme. Moreover, the effects of landscape variables on biodiversity have been shown to interact with the effects of agricultural practices (e.g. Ricci et al. 2019). Yet, landscape variables were not considered in the present study (unlike in another manuscript from the same authors on the same dataset, which is currently under review). There may be some valuable reasons for this omission, but I believe these reasons need to be provided and, here again, the absence of bias needs to be justified.

We did not include landscape in the spatial models since our previous manuscript (the one you mentioned above) explored the influence of spatial scale on landscape effects and demonstrated that landscape is an important explanatory factor at large resolution and regional extent but not at the site resolution and national extent (at this scale, the climate accounts for a very large portion of the compositional differences). Consequently, we made the assumption that excluding landscape from these analyses would introduce minimal bias.

Lines 152-154: "Here, we chose not to include landscape factors, as a previous study on the same dataset demonstrated that landscape variables account for a negligible proportion of variance at the national scale, in contrast to climate (Poinas et al., 2023)."

For temporal models, we saw (with OSO landscape data from 2013 to 2021) that landscape has changed little since 2013 and that these changes did not explain the temporal trends observed on communities. However, we discussed this possible bias in the paper, but noted that previous studies have shown there is a time lag in the response of flora to landscape effects and that landscape trends remained very weak in comparison to climatic trends.

L. 414-417: "However, we cannot entirely rule out the possibility that plant communities are also responding to past landscape diversification, which could have generated a functional response similar to the one observed for climate change, leading to a decrease in ruderal species as arable lands decrease."

3)   The manuscript develops both a spatial and a temporal approach. However, it does not provide a clear description of the data available for these two approaches. It states L190 "To analyze the effects of spatial variations in agricultural practices, explanatory factors and abundances were averaged across years within sites having at least five years of data and five floristic observations, leaving a total of 349 sites". This sentence suggests that some sites were not surveyed every year. Could the authors provide some statistics about the data available and explain why the absence of data for some years does not influence the results of the temporal analysis? Moreover, it is not clear how using the average value across years may influence the spatial analysis. It would certainly be useful to know more about the temporal variability of vegetation and practices at the field level.

The vast majority of sites were monitored every year. However, some observers may not have been able to provide data in a given year, either for biodiversity observations or for data on certain practices or all practices. In these various cases, we cannot use the data from these plots in the years affected by one or more of these missing data. In some cases, farmers no longer wish to take part in the 500 ENI monitoring program, in which case their plot is replaced by another. We present a table below showing the number of sites with available flora data, grouped by the number of years of data. In our spatial analyses, we only considered sites with at least five years of data, which for flora represents 485 sites. However, due to missing data in the explanatory factors (mainly agricultural practices) and as we also ensured a minimum of five years of data for the explanatory variables (agricultural and climatic), the number of sites used in the spatial models was only 349.

Number of years of flora data	1	2	3	4	5	6	7	8	9
Number of sites	20	20	14	16	21	29	47	94	294

The goal of excluding sites with less than 5 years of surveys in the spatial analysis was to maximize the chance of including an exhaustive diversity estimate per site. This approach helps mitigate observer bias that we had to consider as a random effect in the temporal models (see below).

With the graph below, depicting the cumulative species richness (for focal species), it appears that 5 years is a suitable balance between capturing an adequate number of species and having a sufficient number of sites for our analyses. It is worth noting that the number of species continues to marginally increase after 5 years (around 9 additional species per site when extending the sampling period to 9 years), but this could potentially be attributed to the flora's response to environmental changes rather than a non-exhaustive sampling.
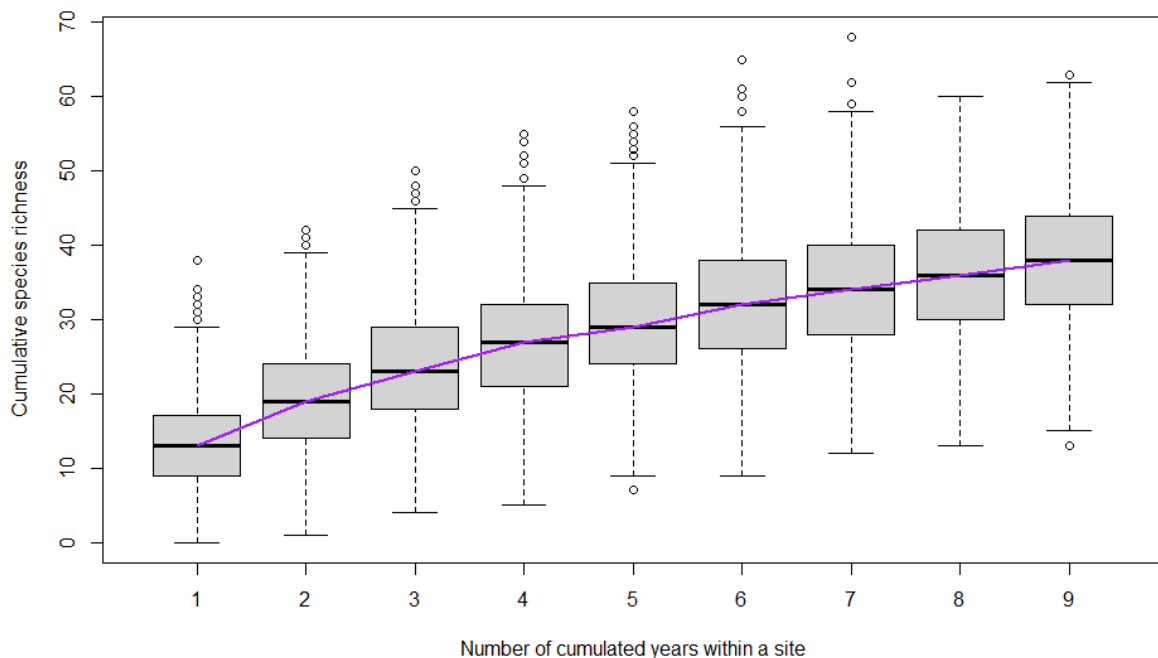
For our temporal models, we included all observations for all sites, regardless of the number of years of data. For the purposes of this review, we check if this bias may have had an influence on our results, by performing a random resampling of three observations per site. Models run with this new dataset yield similar results to the original analyses. Although a few effects became non-significant (e.g. temporal trends in species richness, Ellenberg-L, and N), this was likely the consequence of a reduced statistical power (fewer observations).

In response to your comment about the temporal variability of vegetation and practices at the field level, we found that agricultural practices exhibit greater variation between sites than within a specific site over time. Indeed, there have been very few conversions to organic farming, and the main crop has remained constant over time. Similarly, when examining vegetation, we observed a similar pattern where there was more turnover among different sites than within a single site across years.

4)   A subset of well-known species (142 species over 855 taxa) was used for this study. I fully understand that this selection was necessary to avoid observer biases. However, it is not clear whether this choice may have triggered other biases. For instance, this may have resulted in a stronger underestimation of species richness in species-rich field margins. It may also have resulted in the selection of a subset of species with specific traits. Could the authors present the traits of selected species compared to the whole species pool? Could the authors explain why using this subset have not influenced the results, on either species richness or traits?

First, we want to point out that all traits analyzed were weighted by the species relative abundances, and that despite the apparent large number of species eliminated, they represent less than 12% of the total abundances and less than 15% of total occurrences. Therefore, their influence on all trait-related analyses is relatively small. On top of this, observers received special training regarding the focal species considered here, another reason why this subset is likely to reduce overall observer biases on the analyses.

That been said, we carried out some complementary analysis here to address this comment. The species' PCA now presented in Appendix G (Fig. G.2) was performed on all 601 taxa with available traits. The scores on Axis 1 and 2 were significantly different between focal and non-focal species. Focal species tended to be more continental and ruderal than other species. However, it is important to note that these differences were relatively small, and there was a considerable overlap between the two sets of species. Indeed, the focal species were initially selected by botanists to maximize the functional range of this subset for several traits (life cycle, nutrient requirements (Ellenberg-N), pollination mode, etc…, see Box 2 in Andrade et al., 2021).

We also had carried out the same temporal models using all species and the results remained consistent with our previous findings, including the temporal trend in species richness. Additionally, we detected one effect that was not previously identified: a decrease in SLA over time. This finding aligns with the trends already highlighted in our study (e.g. a trend toward more stress-tolerant communities). Overall, these results further support the robustness and generalizability of our findings to the broader species dataset. However, we do not present these supplementary results in the main manuscript, as we think they will render the methods more complex, by adding another layer of analysis. We now simply mention in the Appendix that "However, the results of temporal models, on the entire species dataset did not differ from those obtained with the focal species (not shown here)."

Discussion of results and perspectives

This study focuses on field margin plant communities but also aims to discuss its broader implications regarding the interactive effects of climate changes and land-use changes on plant communities in agricultural landscapes. The authors discuss their results in a very straightforward way but I believe they could further discuss some unexpected results, the implications for other plant communities within agricultural landscapes and possible avenues to further explore the ENI dataset. Below, I develop four main comments regarding the discussion and perspectives.

1)   The authors state L416 "Our results show little effect of agricultural practices, likely because of their limited temporal trend and great range of spatial variability". It is however hard for the reader to grasp this spatial variability. Could the authors provide more detailed information on the spatial variability of agricultural practices? and further discuss why this great range of spatial variability did not result in a stronger effect of agricultural practices in spatial analyses? The reader may also wonder to which extent this lack of effect of agricultural practices may result in underestimating the interactive effects of climate changes and land-use changes. This may be harder to assess but it may warrant a comment in the discussion.

Regarding the spatial variability of agricultural practices, we have already addressed this topic in our paper currently under review (Poinas et al., 2023; https://doi.org/10.1101/2023.03.02.530797). In the Appendix F of this paper, we can see how practices and crops greatly varied among regions. Broadly, the use of herbicides differs based on the production mode (less in organic than in conventional plots), on the crop type (less in vineyards than in annual crops) and on the region (less in the South than in the North), while fertilization varies according to the crop type (less in vineyards than in annual crops) and the region (less in the South than in the North).

Despite this significant spatial variability, our results suggest that agricultural effects are relatively weak compared to climatic effects. We attribute this to two factors: one is that at the scale of the whole country, pedoclimatic variables dominate the agricultural effects on plant communities (see paper under review); once these are considered within more climatically homogeneous regions, some agricultural practices become more important, but they vary depending on the region (see paper under review). Second, as shown in the first part of our analysis, agricultural practices have not varied consistently over time; therefore, it would be difficult to find any temporal effects of agricultural practices on our different response variables over time. We also have to remember that here we are looking at field margin communities: these are not the targets of fertilizers or herbicides in the adjacent agricultural fields and only receive minimal amounts of inputs.

We have included a paragraph in the discussion section to address these particular points:

"Here, we acknowledge the difficulty in quantifying these interactions between climate and agricultural practices, particularly given the limited changes observed in these practices over time. However, the effects of practices were more perceptible in space, allowing us to identify main trends in community trajectories according to several scenarios (Fig. 5)."

2) The authors conclude that agricultural practices have a weak effect, yet they claim that "the persistence of intensive agricultural practices and accelerating climate change would have critical consequences for the conservation of floristic diversity in agroecosystems". If I play devil's advocate, based on the lack of effect of in-field practices, I could argue that increasing fertilization and the number of herbicide treatments is likely to have a limited effect (or even no effect) on field margin plant communities, as long as the number of management actions in field margins remains low. This would correspond to a land sparing strategy. I certainly don't have the full picture but it feels like these results could actually be discussed in a more nuanced way than the usual conclusion "intensive agriculture is a threat for biodiversity".

While our study reveals limited effects of agricultural practices, it is important to note that this does not invalidate the risks associated with intensive agriculture. Indeed, an important aspect to consider is the functional niche occupied by species colonizing field margins. This niche is highly constrained within the CSR triangle, as field margin species are adapted to agricultural practices, i.e. predominantly ruderal, relatively less competitive, and stress-tolerant. Observed communities are already the outcome of species filtering resulting from disturbances and resource availability. This filtering is not apparent in our study, since we did not contrast field margins with less disturbed habitats, such as permanent grasslands. Currently, climate change tends to favor stress-tolerant species without causing any noticeable loss of species or functional convergence. However, as climate change intensifies, it could potentially lead to a contraction of the functional niche occupied by these species.

We have revised our conclusion to provide more nuanced insights, particularly regarding the fact that we have not studied the adaptive potential of species:

"The species selected by climate change are poorly adapted to intensive farming, while the pool of species currently able to colonize field margins is restricted to a limited functional range adapted to agricultural practices. The persistence of intensive agricultural practices and accelerating climate change could thus have critical consequences for the conservation of floristic diversity in agroecosystems. However, it is important to consider the potential of adaptation of species, through intraspecific trait variability and phenotypic plasticity (known to be particularly high in ruderal species, Baker, 1974), as it may enhance their resilience to changing conditions."

3) The authors provide a very valuable analysis of spatial and temporal variations based on a functional approach, which may allow more generic discussions based on Grime's CSR triangle. Are the functional trade-offs observed in this study likely to apply to other plant

communities within agricultural landscapes, in particular weeds? Are the conclusions on the interactive effects of climate changes and land-use changes likely to apply to them too? At present, the authors tend to draw broad conclusions about plant communities in agricultural landscapes without discussing to which extend their results can be generalized. I believe adding such discussion would strengthen the overall conclusion of the manuscript.

We agree with this comment, and added some discussion to this effect. We found supporting evidence from Fried et al., (2022) that weed communities also exhibit seasonal responses, with increased height and flowering onset during the summer, mirroring the patterns observed in our study. Furthermore, it has been documented that climate change favors the emergence of late-emerging thermophilic weeds (Peters et al., 2014). Another study encompassing a wider range of habitats (farmland, grassland, forest…) concluded that thermophilia increased in response to climate change from 2009 to 2017 (Martin et al., 2019). Climate change also led to an increase in stress-tolerant weeds in vineyards between 1980 and 2020 (Bopp, 2023). In this latter study, it was also observed that the decrease in competitor species could be attributed to a shift from chemical weed control to mowing in vineyards in the South of France. Consistent with our findings, weed richness has increased by 24% over 40 years. Although a PCA on species traits revealed slightly different covariations compared to our findings, it was clear that some functional trade-offs align well with our results: species adapted to climate change are less adapted to agricultural practices. However, some traits in this study exhibited contradictory trends compared to what we observed in field margins (e.g. an inverse trend for seed mass, flowering onset and duration, no increase in Ellenberg-T and L, an increase in SLA). It is worth noting that Bopp (2023) directly measured traits in situ, which could explain some of the observed differences with our study based on functional traits from species-level databases.

In conclusion, further studies are necessary to fully generalize these results. To address this point, we have included a statement in the discussion section:

"Our findings suggest a likely reduction in ruderality and an increase in stress-tolerance according to Grime's strategies, raising concerns about potential loss of plant diversity in intensively managed areas. Bopp (2023) highlighted a similar increase of stress-tolerance in weeds in response to climate change, but did not observe a corresponding decrease in ruderality. Further investigations are thus necessary to assess the generalizability of these results across different habitats, including communities with broader or narrower functional niche, such as weeds."

Bopp, M. (2023). *Dynamique spatio-temporelle des communautés d'espèces adventices en réponse aux pratiques de gestion des sols dans les vignobles: Une approche fonctionnelle* [Doctoral thesis, Montpellier, SupAgro]. https://www.theses.fr/s225831

Fried, G., Blanchet, C., Cazenave, L., Bopp, M.-C., Kazakou, E., Metay, A., Christen, M., Alard, D., & Cordeau, S. (2022). Consistent response of weeds according to Grime's

CSR strategies along disturbance and resource gradients in Bordeaux vineyards. *Weed Research*, *62*(5), 347–359. https://doi.org/10.1111/wre.12549

Martin, G., Devictor, V., Motard, E., Machon, N., & Porcher, E. (2019). Short-term climate-induced change in French plant communities. *Biology Letters*, *15*(7), 20190280. https://doi.org/10.1098/rsbl.2019.0280

Peters, K., Breitsameter, L., & Gerowitt, B. (2014). Impact of climate change on weeds in agriculture: A review. *Agronomy for Sustainable Development*, *34*(4), 707–721. https://doi.org/10.1007/s13593-014-0245-2

Poinas, I., Fried, G., Henckel, L., & Meynard, C. N. (2023). *Scale dependence in agricultural drivers of field margin plant communities: Influence of spatial resolution and extent*. bioRxiv. https://doi.org/10.1101/2023.03.02.530797

4)   The 500 ENI monitoring program has produced (and keeps producing) a huge dataset on plant communities as well as other taxonomic groups. The present study is among the first ones to analyse part of this dataset. I believe this study opens the way for very exciting research questions and it would be a shame not to discuss these perspectives (non linearity, time-lag, trophic networks, etc..). It may also be useful to provide a feedback on this program (are all relevant data on agricultural practices available, e.g. dosage, toxicity, type of adjacent habitat? Is the distribution of fields and years sampled adequate? Etc…)

Some of this feedback on the 500 ENI program has already been addressed in the datapaper of Andrade et al. (2021) and it would be difficult to cover in this paper all the perspectives that this network could potentially open up.

However, we added some perspectives in our manuscript:

"Long-term monitoring programs are necessary to address some perspectives, such as the potential time-lag in flora's response to environmental changes, the non-linearity in temporal trends and the interactive effects between climate and agricultural changes."

Other specific comments

L21 "However, these impacts are often studied using meta-analyses at large scales, or using taxonomic diversity" Why is the fact that they are studied "using meta-analyses at large scales" is a problem? It seems to me like the knowledge gap primarily comes from not considering

functional traits in order to understand the interactive effects of land use changes and climate changes.

Agree. We removed this sentence and replaced it:

"However, functional trade-offs linking traits responding to climate and farming practices are rarely analyzed, especially on large-scale empirical studies."

L30 "Changes in plant communities were noticeable, especially as they relate to climate change" This phrasing sounds ambiguous to me. It would be clearer to state whether changes are significant and what the key drivers of these changes are.

"Functional changes in plant communities were significant, showing an increase of thermophilic species with a conservative resource acquisition strategy mainly explained by climate change."

L58 The amount of pesticide use is not the only dimension of agricultural practices that influences biodiversity. The toxicity of pesticides has been shown to be a key aspect, as well as crop diversification, field margin/boundary management and landscape structure.

Exact. We modified the sentence accordingly:

"Given this clear trend in climate, contrasted with a lack of recent temporal trend in pesticides, combining spatial and temporal analyses seems necessary to study the effects of these two drivers on plant communities around agricultural fields. "

L98 It would be useful to clarify somewhere in your hypotheses (and not only in the discussion L374) that the impacts of in-field farming practices on vegetation in field margins are likely to be limited (more limited than for weeds).

Done:

"We also assumed that the impact of agricultural practices on plant communities would likely be limited, as field margins only receive a small amount of nitrogen and herbicides drifting from neighboring plots."

L101 I believe there are only two zones considered: Mediterranean and Continental.

Yes: "On top of the national analyses, and because this dataset includes the Mediterranean flora, which has been shown to respond more strongly to some agricultural filters (Poinas et al., under review), we included analyses separating this region from the rest of France."

L108 How were fields selected within the ENI programme? Are they representative of practices in France or are practices less intensive on average because farmers are volunteering? This might also contribute to the lack of temporal trend in agricultural practices.

The fields have been selected to represent the main landscapes and pedoclimatic contexts of the country. As explained in Andrade et al., (2021), the sampling was stratified, such that each region had a number of fields consistent with the importance of the focus crops at the regional scale. 20% of fields were under organic farming in each region, while it only represents 8% of the utilized agricultural area in France. Among both conventional and organic fields, there was very little conversion from one mode of production to another.

The plots in the ENI network were often selected from the farmers that were already part of the network of agricultural advisors of chambers of agriculture. This makes them more likely to have already reduced their inputs. However, when examining the data from the ENI network, we found that the average herbicide TFI (treatment frequency index) for the 499 field x year in common wheat was 1.7 (± 1.3). This is very consistent with the French agricultural statistics service (Agreste, N° 2019-3 - Juin 2019 "Pratiques culturales en grandes cultures 2017 IFT et nombre de traitements") who reported an average of 1.8 for the same crop in 2017. Therefore, we can assume that the plots in the 500 ENI network are relatively representative.

L149 It would be useful to make a clear link between Ellenberg codes and their meaning, probably both in Table 1 and in the text the first times they appear in a section, because it is not trivial for non-botanist.

Done

L155 I may have missed it but I couldn't find any information on where chorology data comes from.

Chorology data were extracted from Baseflor. We added this information in Appendix G (Fig. G.2).

L174-177 I find these two sentences hard to understand. It may be easier to follow if these sentences were moved to the relevant sub-section on temporal and spatial analyses.

As these sentences are precisely about the computation of CWV and their effect size, we think it is more relevant to keep them in this section. However, we revised the sentences to ensure they are understandable without having to read the sections on spatial and temporal models.

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

L191 What is the difference between a "year of data" and a "floristic observation"?

We used the term "years of data" to refer specifically to explanatory data. However, in this particular sentence, there was no need to differentiate between years of explanatory data and years of floristic data. Therefore, we combined both into a single expression.

"To analyze the effects of spatial variations in climate and agricultural practices, explanatory factors and species abundances were averaged across years within sites having at least five years of data, leaving a total of 349 sites."

L222 The term "elusive" does not seem appropriate here since you did observe some significant trends.

Exact. We replaced it by "more uncertain".

"Overall, there was a clear warming and drying trend in climate, but agricultural trends remained more uncertain."

L242 It may also be useful to specify the meaning of Ellenberg-F in the legend

Done

"Temporal changes in temperature, soil moisture, CWM of Ellenberg-F (moisture requirement), number of herbicide and nitrogen dose in fertilizers."

L251 The two PCA represent either sites or observations and not species. Please rephrase all sentences accordingly.

Done. We replaced "species" by "communities" in the text.

L288 "Regressions between Ellenberg values and climatic factors". This sentence gives the impression that you conducted several regressions rather than a single one with all explanatory variables. Please reword to avoid any confusion.

Done. "Regressions between each Ellenberg value and climatic factors remained consistent across spatial and temporal models"

L356 "These trait values (low SLA, high seed mass) are also known to be linked to less intensive agriculture" It is not clear whether the ENI dataset is consistent with this relationship?

Although our models did not reveal significant effects on these specific traits, we observed that the impact of margin management on PCA axis 1 and 2 aligned with the direction of lower SLA and higher seed mass for the more extensive plots. We have incorporated a sentence about it.

"In our models, we observed a similar pattern, with less intensive margin management associated with a decrease along the ruderality axis and an increase along the stress-tolerance axis."

L407 Change "varies" to "vary"

Done

L419 Is a trend towards more intensive practices not as likely, if not more likely, than a trend towards more extensive practices? This hypothesis also contrasts with the following sentences focusing on agriculture intensification.

We made this assumption based on the current European policy efforts, which aimed at agricultural extensification, primarily for ecological reasons but also likely in the future for economic reasons. This scenario thus appeared to be the most likely. However, examining historical trends, we have to acknowledge that plans to reduce the use of phytochemicals do not always translate into concrete changes. In light of this, we have revised the text to treat all scenarios as equally likely.

L426 "Mediterranean species could face severe agricultural intensification in northern France". Did you really mean "northern France"?

We meant "in the northern half of France".

In the data provided, the first row has shifted in files flora_temp and flora_spat

We corrected it.

Review by Diego Gurvich, 28 Mar 2023 12:06

Poinas et al. present a very interesting study where they analyse the trajectories of communities in relation to their functional characteristics. The study is very well planned and carried out. Their main conclusions are of great relevance in understanding how global changes (mainly climate change, but also changes in management) affect these aspects of communities.

I have some minor suggestions that could improve the manuscript.

Line 63. I do not consider functional analysis to be something that is required. It is simply another view of analysis.

Agree. We modified accordingly:

"therefore, a functional dimension provides an additional perspective to accurately understand these changes."

Line 73. Grimer proposed the triangle much earlier, in the 1970s. On the other hand I would start the paragraph with Grime's ideas, as they then become a central focus of the article.

We have updated the associated reference accordingly. However, we prefer to first introduce the gradients of resources and disturbances, discuss the covariations between traits, and then conclude with the strategies, reserving the mention of the CSR triangle for the end. As the CSR triangle is not the primary focus of this paper and as ecological strategies are directly derived from traits, this ordering allows for a clearer presentation of the concepts.

Line 83, intraspecific or interspecific? Seeing that the article concentrates on interspecific changes, I would clarify that point, so as not to raise doubts.

We added the mention of "interspecific" at the beginning of the paragraph:

"To understand the complex interactions between climate change and agricultural practices, it is thus essential to examine the temporal dimension of functional interspecific trait variations."

Line 95, If it is mentioned later, perhaps it would be good to mention what types of cells will be analysed.

Do you mean functional traits? We have already mentioned these traits in the previous paragraph, so we prefer to keep as it is.

Line 338. This could be due to higher dominance under these conditions?

Indeed, these results could potentially indicate a higher dominance of generalist species having a wider temperature tolerance range. However, it is important to note that this is not the unique possible explanation. Another possibility is that thermophilic species have increased in abundance without causing the loss of cold-adapted species, leading to an increase in the functional range of plant communities.

"Our results also indicated that sites increasingly or already warmer and drier allowed for coexistence of a wider functional variety of species, suggesting a potential dominance of generalist species with a wider temperature tolerance range, or an increased abundance of thermophilic species without any loss of cold-adapted species. The increase in species richness over time provided additional support for this latter hypothesis."

Line 342. This point would be better mentioned in the introduction, where it should be clearer that this is the most novel aspect of the article.

We added it in introduction:

"We studied the herbaceous field margin, which represents the uncultivated vegetated area located between the cultivated strip and the adjacent habitat. Using a standardized national monitoring effort spanning 9 years (2013-2021) in 555 agricultural field margins covering continental France, our study stands as one of the first to investigate the temporal trends in agricultural practices and climate, and explore the spatial and temporal drivers of species diversity and functional traits at such extensive scales."

Line 441. This is a no-brainer, but it should be clear that the position of the species in the triangle depends on what we are comparing. For example, all the species analysed here would be ruderal, if other forms of vide, such as woody, for example, are incorporated.

Absolutely. This can be seen on the new version of the Grime triangle, where the variability of sites is depicted. All the sites occupy a relatively small area within the triangle, indicating a limited functional range and an overall ruderal strategy. We have included a sentence in the conclusion to clarify this point.

"The species selected by climate change are poorly adapted to intensive farming, while the pool of species currently able to colonize field margins is restricted to a limited functional range adapted to agricultural practices."

Nevertheless, it is important to keep in mind that many non-ruderal species can persist in field margins, although it is not apparent in Grime's triangle depicting the CWM of CSR strategies. This is due to the dominance of ruderal species, which constitute a significant proportion of the total abundance, while the presence of other species is comparatively limited. We can see below, the position of each focal species in the CSR triangle.
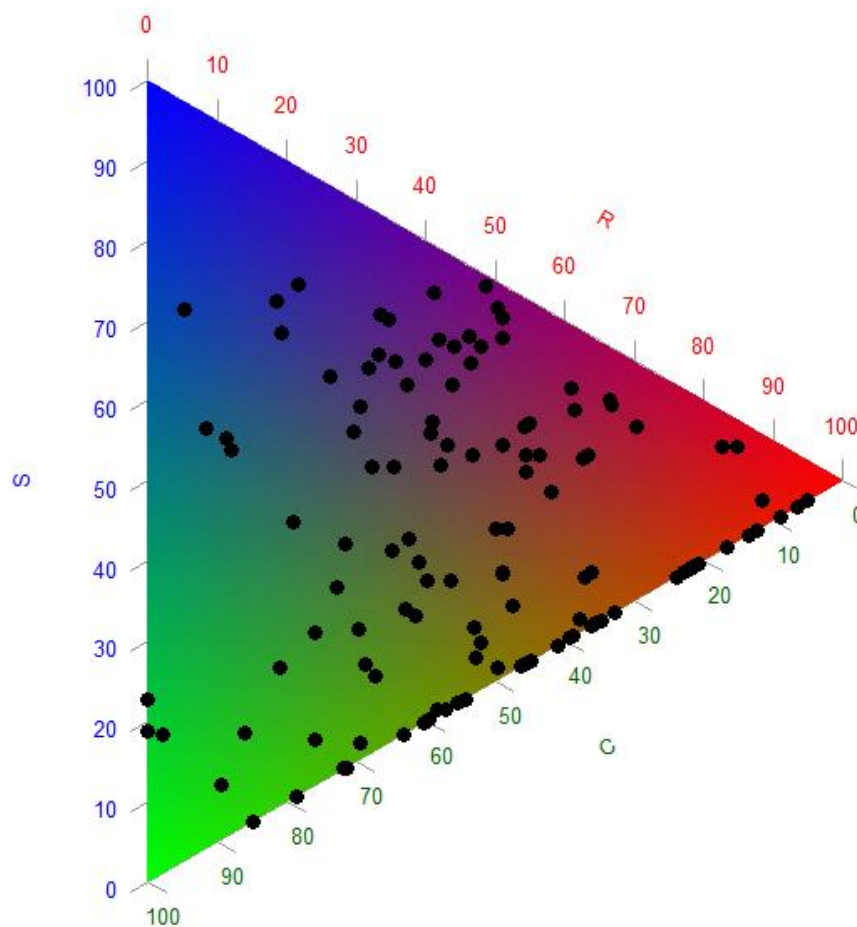
1 **Functional trade-offs: exploring the effects of climate change and agricultural**

2 **practices as drivers of field margin plant communities**

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8

13 **Number of words in abstract:** 269

14 **Number of words in main text (Introduction to Conclusion):** 4646

15 **Number of cited references:** 55

16 **Number of tables:** 1

17 **Number of figures:** 5

18

19 **Abstract**

20 Over the past decades, agricultural intensification and climate change have led to vegetation shifts in

21 Europe. However, these impacts are often studied using meta-analyses at large scales, or using

22 taxonomic diversity. Functional trade-offs linking traits responding to climate and farming practices

23 are 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, agricultural practices, plant species richness, and trait community-

27 weighted means and variances across 555 sites in France between 2013 and 2021. We found that

28 temperatures have increased while soil moisture has decreased, reflecting current climate change,

29 whereas the intensity of agricultural practices did not show clear temporal trends over the past

30 decade. Changes in plant communities were noticeable, especially as they relate to climate change,

31 while the impact of agricultural practices was limited and mainly exerted through field margin

32 management and to a lesser extent, fertilization. Mediterranean sites, vineyards and perennial species

33 demonstrated reduced response to climatic variations. Our findings suggest that species adapted to

34 climate change (including Mediterranean species) have increased in proportion and are spreading

35 northward. Importantly, we identified functional trade-offs suggesting that these species are also the

36 most vulnerable to intensive agricultural practices. We put these results into the conceptual

37 framework of Grime's CSR triangle and suggest that the convergence of climate change and the

38 maintenance of a highly intensive agriculture could carry a risk of abrupt declines in floristic diversity

39 of field margins, a concern that merits further attention.

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2

Introduction

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

Changes in plant communities cannot be discerned solely by taxonomic diversity due to the differing traits affected by resource availability and disturbance levels (Garnier & Navas, 2012); therefore, a functional dimension is required to accurately understand these changes. This is particularly important in an agroecological context, where both resource (fertilization) and disturbance (herbicides, field management) gradients play crucial roles (Gaba et al., 2014; MacLaren et al., 2020). For instance, weeds with a ruderal strategy are better adapted to agricultural disturbances, such as tillage, herbicides or frequent margin management (Grime, 2006; Fried et al., 2022). At the same time, traits responding to agricultural practices can co-vary with other traits that are linked to resources, competitive ability, or climate. For example, seed mass, which is often used as a proxy for competitive

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

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

72   impact community adaptation (Díaz et al., 2016; Wright et al., 2004). In this context, Grime (1988)

73   proposed a framework called the CSR triangle, which defines three axes of variation - competitive,

74   stress-tolerance, and ruderal adaptations - that are correlated to multiple traits and have proven useful

75   to understand plant community dynamics (Fried et al., 2022). As traits responding to climate and

76   agricultural practices may co-vary (Garnier & Navas, 2012), it can be difficult to identify the main

77   drivers behind community changes.

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

79   essential to examine the temporal dimension of functional traits variations. For example, in French

80   wheat fields, species with small height, low seed mass and long germination and flowering periods

81   increased their frequency between the 1970s and 2000s, potentially due to their ability to escape

82   recurrent disturbances, such as herbicide applications (Fried et al., 2012). Inter-annual variations in

83   specific leaf area, leaf dry matter content and plant height are related to nitrogen supply, while

84   increased precipitations push the foliar economic spectrum towards more acquisitive species (Wheeler

85   et al., 2023). Additionally, mean thermal preference of plant communities , as well as their phenology,

86   can vary over time in response to temperature changes, even over relatively short periods (Bellard et

87   al., 2012; Martin et al., 2019). These temporal variations in functional traits reveal patterns that cannot

88   be assessed solely with a space-for-time approach.

89   In this study, we aimed at deciphering how spatio-temporal variations of climate and agricultural

90   practices in France structure the diversity and trait composition of field margin plant communities. We

91   studied the herbaceous field margin, which represents the uncultivated vegetated area located

92   between the cultivated strip and the adjacent habitat. Using a standardized national monitoring effort

93   spanning 9 years (2013-2021) in 555 agricultural field margins covering continental France, we aimed

94   to determine temporal trends in agricultural practices and climate, and explore the spatial and

4

95   temporal drivers of species diversity and functional traits. We hypothesized that plant traits sensitive

96   to temperature and soil moisture will co-vary with both spatial climatic gradients and temporal

97   warming trends while agricultural practices would have a greater spatial than temporal influence on

98   plant communities, as we did not expect clear temporal trends in these practices . On top of the

99   national analyses, and because this dataset includes the Mediterranean flora, which has been shown

100   to respond more strongly to some agricultural filters (Poinas et al., under review), we included analyses

101   separating this region from the others. We also separated vineyards from annual crops, because

102   vineyards include very different management practices and no crop rotation (Metay et al., 2022).

103   Finally, we also analyzed annual plant species separately, as they may respond more rapidly to

104   environmental changes (Martin et al., 2019; Fitter & Fitter, 2002).

105

Materials and methods

Vegetation survey

We used vegetation data from the 500-ENI network, which is funded by the French Ministry of Agriculture (see details in Andrade et al., 2021) and yearly monitored 555 agricultural field margins across continental France between 2013 and 2021 (with some site turnover) (**Fig. 1**). These survey sites represented four main crop types **(Appendix A, Fig. SA. 1)**: annual crops (with winter wheat or maize as the main crop production in the rotation), market gardening crops (mainly lettuce) and vineyards. The proportion of sites under organic farming was roughly 20%, but agricultural practices covered a wide range of pesticide application, fertilizers and soil management. Within each survey site, plant species were identified in ten 1 m² quadrats along the field margin (**Appendix A**, **Fig. SA.2**). Presence-absence of each species was recorded for each quadrat, which provided a frequency of occurrence from 0 to 10 in each field margin, used here as an index of relative abundance. Surveys were performed at peak flowering (between the end of April and the beginning of August, depending on the region). At the national scale, this represented 4172 observations (year x site), leading to the identification of 855 taxa. As observers changed among sites and over time (312 observers in total, each observer following on average 5 distinct sites during 4 years) and did not have the same level of expertise, we constrained our analyses to a subset of 142 focal species (Andrade et al., 2021) which are expected to be known by all the observers (and thus removing 11% of the total abundances).
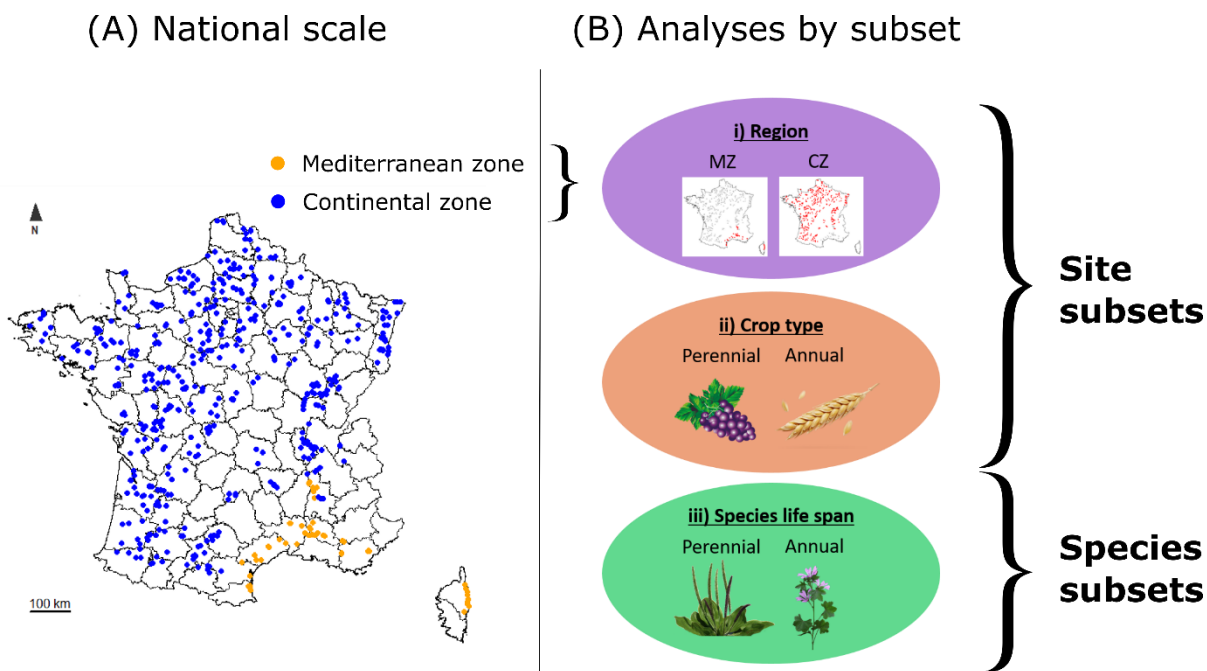
Fig. 1. (A) Distribution map of the 555 field margins monitored at least one year between 2013 and 2021 in France. The black lines represent the limits of French departments. Orange: sites in Mediterranean zone (n = 57), blue: sites in Continental zone (n = 498). The contours of the Mediterranean zone (MZ) were derived from the Mediterranean zone and Corsica as defined in the VégétalLocal map (Office français de la biodiversité, 2021); the rest of France will be referred to here as Continental zone (CZ). (B) Subsets of data used in additional analyses: i) the regional scale splits the MZ from the CZ; ii) annual crops included rotations based on wheat, maize and market gardening crops (n = 450); perennial crops only included vineyards (n = 105); iii) annual plants (n = 61) opposed to perennials (n = 79).

Climatic and agricultural variables

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

7

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

142   database. Data collected relate to fertilization, herbicide use and field margin management. Daily

143   meteorological data were extracted from the SAFRAN climate model of Météo France, with a

144   resolution of 8 km (Le Moigne, 2002). Meteorological data were averaged over a one-year window

145   prior to each floristic observation, while agricultural data were summed over the same period (**Table**

146   **1**). We selected variables that were weakly correlated (Spearman correlation < 0.65, **Appendix B**) and

147   have been shown to influence plant communities in previous studies (**Table 1,** see **Appendix C** for the

148   choice of variables).

Table 1. List of explanatory factors (blue), functional traits (green) and response variables (red) with their abbreviations, units and calculation. The variables only used in temporal models are underlined, while those only used in spatial ones are in italic. We noted the expected link of each factor and trait to the agricultural resource and disturbance gradient, and to climate change. A left-pointing triangle indicates an increase in relation to the corresponding factor of the same color. An hourglass symbol was used for relationships with contradictory findings in the literature (see **Appendix C** for the references).

Factors	Abbreviations	Units	Index used	Hypothesis of response to the Agricultural gradient: Disturbance (Di) and Resource (R)	Hypothesis of response to the Climatic gradient: Drought (Dr) and Increasing temperature (T)
Temperature	TEMP	°C	Annual mean of daily values		◀
Soil moisture	MOI	%	Annual mean of daily values		▶
Dose of nitrogen (fertilization)	N_DOSE	kg/ha	For each application: $$Dose = \frac{Quantity \times N\ of\ the\ formulation}{100}$$ Doses were summed one year before observation	◀	
Number of herbicide treatments	HERB		Treatments were summed one year before observation	◀	
Number of management events	MAN		All types of management (mowing, grazing…). Number of management events were summed one year before observation.	◀	

Date of observation	DATE	Julian days	
Number of observers	OBS		
Specific leaf area	SLA	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, moisture, pH and nutrients	EIV_L, EIV_T, EIV_K, EIV_F, EIV_R, EIV_N		EIV_N:	EIV_F: EIV_T:
Species richness	S	Number of species		
Functional composition	See abbreviations above for each trait preceded by "CWM_"	Community weighted means (CWM) : community trait values weighted by species abundance (Lavorel et al., 2008)		
Functional divergence	See abbreviations above for each trait preceded by "CWV_"	Community weighted variances (CWV) : community trait variability around the average value (Sonnier et al., 2010)		

| **PCA traits - axis 1** | PCA_1 | Scores of sites or observations on the 1st axis of the PCA including CWM of all traits |
| **PCA traits - axis 2** | PCA_2 | Scores of sites or observations on the 2nd axis of the PCA including CWM of all traits |

153

154   *Plant functional traits*

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

156   requirements, assumed to respond to agricultural or climatic factors (**Table 1**, **Appendix B-C**).

157   Functional traits were missing for four species, two of which could be imputed from an average over

158   other species of the same genus. The remaining two species were removed from the analysis

159   (representing 0.01% of the total abundances among the 142 species considered). In the following

160   analyses, maximal height and seed mass were log-transformed to ensure normality and reduce the

161   weight of extreme values.

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

163   (CWM) and community-weighted variances (CWV) of traits for sites and observations with at least

164   three species (59 out of 4172 observations were excluded). The computation was performed using the

165   R v.4.0.0 package $_{FD}$, function *dbFD* for CWM, with the following formulas:

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

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

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

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

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

171   the species x trait matrix unchanged (Bopp et al., 2022). This procedure keeps trait correlations, species

172   richness and total abundance in a site unchanged, while dissociating abundances from trait values

173   (Bernard-Verdier et al., 2012).

174   The species pool was defined by the biogeographic region in the spatial analyses, and by site in the

175   temporal analyses (see below), to focus on the relevant axes of variation we were most interested in.

176   We extracted biogeographic regions from the VégétalLocal map (Office français de la biodiversité,

177   2021). To quantify the difference between observed and null CWV, we computed effect sizes

13

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

179   (convergence for negative effect size). We performed a normed PCA on the CWM of traits (by site for

180   spatial analyses, by observation for temporal analyses) and we took the first two axes, representing

181   different combinations of traits.

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

183   To assess the main temporal trends in our dataset, we used Spearman correlation coefficients with the

184   year of observation (Martin et al., 2019; **Appendix E**) on our variables of interest (climate, agricultural

185   practices, plant diversity, CWM and CWV). For all analyses, we chose a p-value threshold of 0.01 to

186   focus on the effects for which our confidence level was highest. We also repeated this analysis on

187   subsets of data, including Mediterranean (MZ) vs Continental (CZ) zones, margins adjacent to annual

188   crops vs vineyards, and annual vs perennial plant species (**Fig. 1**).

189   *Spatial analyses of plant communities*

190   To analyze the effects of spatial variations in agricultural practices, explanatory factors and species

191   abundances were averaged across years within sites having at least five years of data and five floristic

192   observations, leaving a total of 349 sites. Using spatial simultaneous autoregressive models (SAR;

193   package ₛₚDₑₚ, function *errorsarlm*; Cressie, 2015), we examined the relationship between each

194   response variable and the explanatory factors. The Nagelkerke pseudo-R^2 was used to assess the

195   model's explanatory power, and we controlled for the observer bias by adding the number of

196   successive observers in a site as a fixed effect.

197

198   *Temporal analyses of plant communities*

199   To disentangle temporal effects on plant communities, we used generalized additive mixed models

200   (GAMM) to account for repeated measures at a site, with a Gaussian distribution in most cases (but

201   see **Appendix F**, **Table SF.2**). We included the site identity as a random effect, and a first-order

202 temporal autocorrelation structure within sites (Box et al., 2015). Observer bias was accounted for by

203 including the observer identity as a random term nested within sites. We removed observations with

204 missing values in climatic and agricultural factors (1805 out of 4172 observations), and a few

205 observations that distorted trait distributions (**Appendix F**), resulting in varying observation numbers

206 across models (see **Fig. 4**).

207

208 **Results**

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

210 Temperatures have significantly increased (r = 0.22, p < 0.001) by an average of 1.13°C over a decade

211 (0.45°C in the Mediterranean Zone), while soil moisture has steadily declined (r = -0.39, p < 0.001, -

212 14% by decade) (**Fig. 2**, and **Appendix E**). These trends differed between the Mediterranean Zone (MZ)

213 and the Continental Zone (CZ), with the MZ experiencing a slower decline in soil moisture of only -8.8%

214 by decade due to a high cumulative precipitation in 2019 (**Fig. 2**). Regarding agricultural practices,

215 herbicides slightly decreased over time in vineyards (r = -0.14, p < 0.001; **Fig. 2**), with an even weaker

216 trend in annual crops (r = -0.05, p = 0.008). Fertilization showed no significant temporal trend, except

217 in vineyards where the cumulative dose of nitrogen has slightly increased (r = 0.16, p < 0.001). The

218 number of margin management events decreased in the MZ (r = -0.17, p = 0.004), where most

219 vineyards are located, but this trend was not observed in vineyards across the entire country, nor in

220 the CZ. Floristic surveys were conducted increasingly earlier in the season in the CZ (r = -0.13, p < 0.001,

221 10.48 days earlier by decade) (**Appendix E**). Overall, there is a clear warming and drying trend in

222 climate, but agricultural trends remain elusive.

223 Plant species richness has slightly increased over time at the national scale (r = 0.07, p < 0.001, 1.3

224 species per decade), even more in the MZ (r = 0.20, p < 0.001, 4.2 species by decade) and vineyards (r

225 = 0.17, p < 0.001, 3.3 species by decade). In France, we saw an increase in the CWM of maximal height

226 (r = 0.08, p < 0.001), seed mass (r = 0.10, p < 0.001), flowering onset (r = 0.07, p < 0.001, 3.12 days by

15

227   decade) and a decrease of flowering duration (r = -0.10, p < 0.001, -7.83 days by decade) (**Appendix E**).

228   The Ellenberg-L, T and R values have increased (r = 0.06, 0.14 and 0.11 respectively, p < 0.001), while

229   the Ellenberg-F and N values have declined (r = -0.06 and -0.07 respectively, p < 0.001). CWV have

230   decreased for most of traits, and particularly for phenological traits such as flowering onset and

231   flowering duration (r = -0.12 and -0.09 respectively, p < 0.001), while they have increased for most of

232   Ellenberg values and particularly for the Ellenberg-T, R and K (r = 0.16, 0.11 and 0.09 respectively, p <

233   0.001). Changes in functional traits were more pronounced in the MZ, with an important reduction in

234   the range of flowering onset and duration (**Appendix E**). Conversely, changes in Ellenberg values were

235   only significant in the CZ and in annual crops. One exception was the temperature (Ellenberg-T) and

236   moisture (Ellenberg-F) requirements, which have significantly changed in both the MZ and CZ.

237   Interestingly, Ellenberg values showed a temporal trend mainly for perennial species, while only

238   functional traits shifted in annual communities, with e.g. a convergence towards shorter and later

239   flowering (**Appendix E**).

240
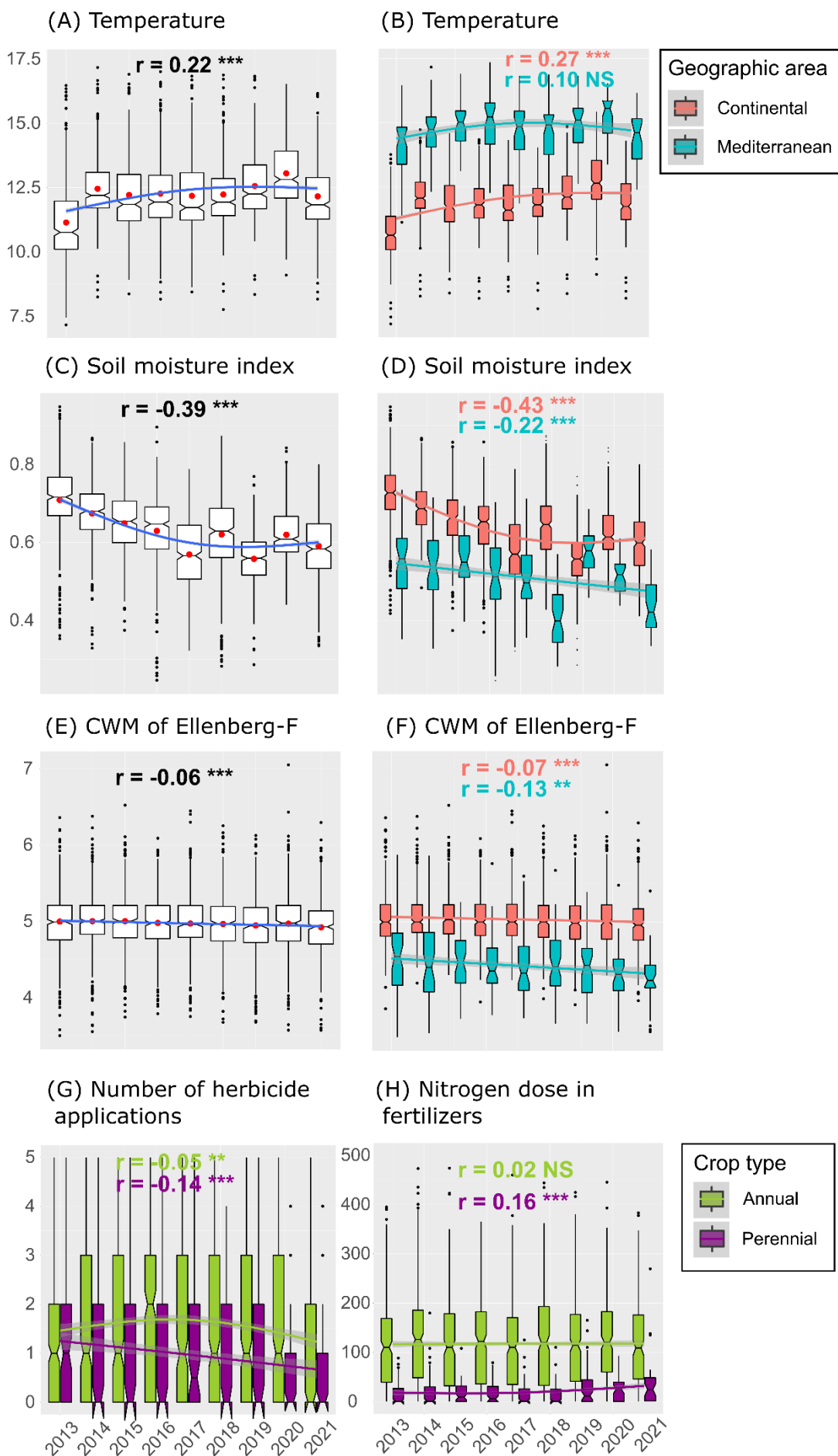
242 **Fig. 2**. Temporal changes in temperature, soil moisture, CWM of Ellenberg-F, number of herbicide and

243 nitrogen dose in fertilizers. Red dots represent mean values. The curves are from a GAM, with a smooth

244 term on the year restricted to three effective degrees of freedom. (A, C, E) National trend. (B, D, F)

245 Trend by geographic area: CZ and MZ. (G, H) Trend by crop type: annual (wheat, maize, lettuce) and

246 perennial (vineyard). Spearman coefficients are reported and significance of correlation coefficients is

247 referred as following: NS p ≥ 0.01; ** p < 0.01; *** p < 0.001.

248

249 *Spatial analyses of plant communities*

250 The first PCA axis (named thereafter stress-tolerance axis) explained 36.4% of the variation and

251 revealed a gradient from continental hygrophilous, ruderal and competitive species associated with

252 resource-rich environments, to Mediterranean xero-thermophilous stress-tolerant species adapted to

253 resource-poor and arid environments (**Fig. 3, Appendix G, Fig. SG.2**). Communities with continental

254 species were more nitrophilous, had a higher SLA and flowering duration, while Mediterranean

255 communities had a higher seed mass. The second PCA axis (named thereafter ruderal axis) explained

256 19.7% of the variation and contrasted competitive/conservative species adapted to low disturbance

257 (high stature, late and short flowering) with ruderal/acquisitive species adapted to high disturbance

258 (short stature, early and long flowering).

259 Spatial models revealed that climate had a predominant impact on functional composition and

260 particularly on Ellenberg values, opposing in a consistent way Mediterranean species to nitrophilous

261 continental ones along the stress-tolerance axis (**Fig. 4**). Temperature increased the CWM of seed mass

262 and decreased the CWM and CWV of SLA (convergence). High temperatures lead to divergence in all

263 Ellenberg values except the Ellenberg-L, while soil moisture brought convergence in the Ellenberg-T

264 and K. Field margin management was the agricultural practice with the strongest effect, favoring

265 ruderal species with higher SLA and/or lower seed mass (PCA Axis 1), shorter stature and longer

266 flowering duration (PCA Axis 2). Herbicide applications had no significant effect, while the average

267 annual nitrogen dose in fertilizers decreased the species richness and Ellenberg-R, but increased

268 Ellenberg-N, SLA and divergence in flowering duration (**Fig. 4**). The number of observers surveying a

269 site over the 9-year period was positively correlated with species richness (average increase of 1.68

270 species by observer) and with the CWM and CWV of flowering duration.

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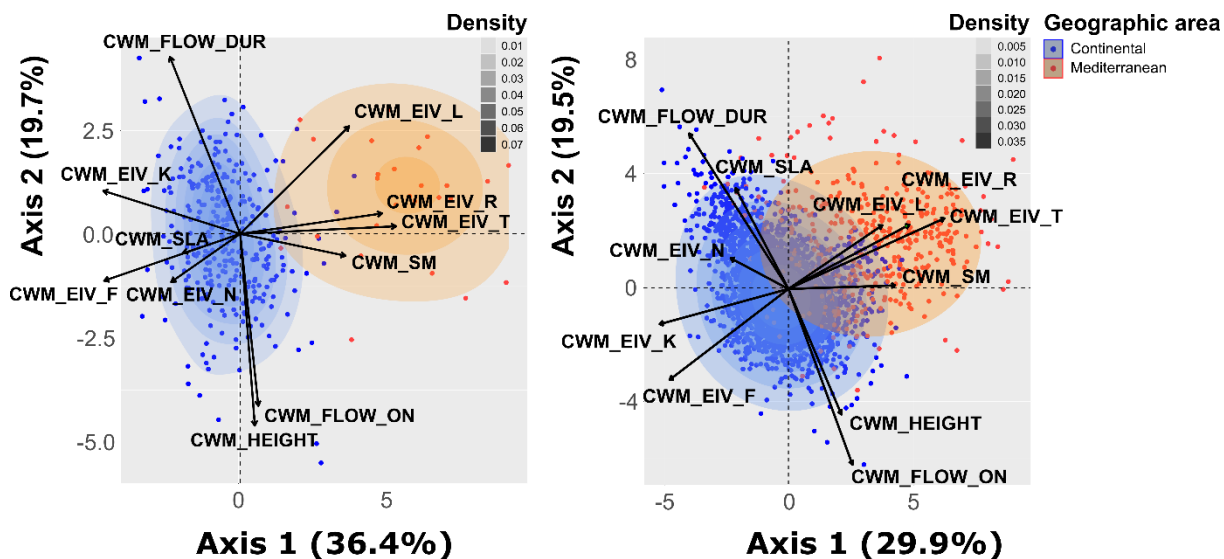
272

273 **Fig. 3**. Normed PCA on CWM (first two axes). (A) Scores of CWM of functional traits computed by site.

274 (B) Scores of CWM of functional traits computed by observation. The color of the dots indicates the

275 region to which they belong and the density curve highlights the concentration of data points in a given

276 area. The correlations of traits to the PCA axes are in **Appendix G**, **Fig. SG.1** and the PCA for annual and

277 perennial species in **Fig. SG. 3**. Abbreviations for CWM: CWM_SLA, specific leaf area; CWM_HEIGHT,

278 maximum plant height; CWM_SM, seed mass; CWM_FLOW_ON, flowering onset; CWM_FLOW_DUR,

279 flowering duration; CWM_EIV_L/T/K/F/R/N, Ellenberg-L/T/K/F/R/N.

280

281 *Temporal analyses of plant communities*

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

283 represented the same ecological strategies, explaining 29.9% and 19.5% of the variation, respectively.

19

284   However, one difference was that SLA was more correlated to the ruderal rather than the stress-

285   tolerance axis in the PCA based on observations.

286   Climatic factors were also the most influential in temporal models, with high R^2 for the CWM of

287   Ellenberg-T (R^2 = 0.33) and stress-tolerance axis (R^2 = 0.27, **Fig. 4**). Regressions between Ellenberg

288   values and climatic factors remained consistent across spatial and temporal models, with increasing

289   temperature leading to an increase and divergence in Ellenberg-T values. However, new patterns

290   emerged in temporal models, with increasing temperature and drought associated with shorter

291   flowering duration, and later flowering onset only for increasing temperature (**Fig. 4**). Here again,

292   margin management was the agricultural practice with the largest impact on community changes, with

293   an increase in its frequency associated with more ruderal species. The date of observation also

294   influenced community changes, with a later observation related to more conservative, competitive

295   and continental species, and to a decrease in species richness.
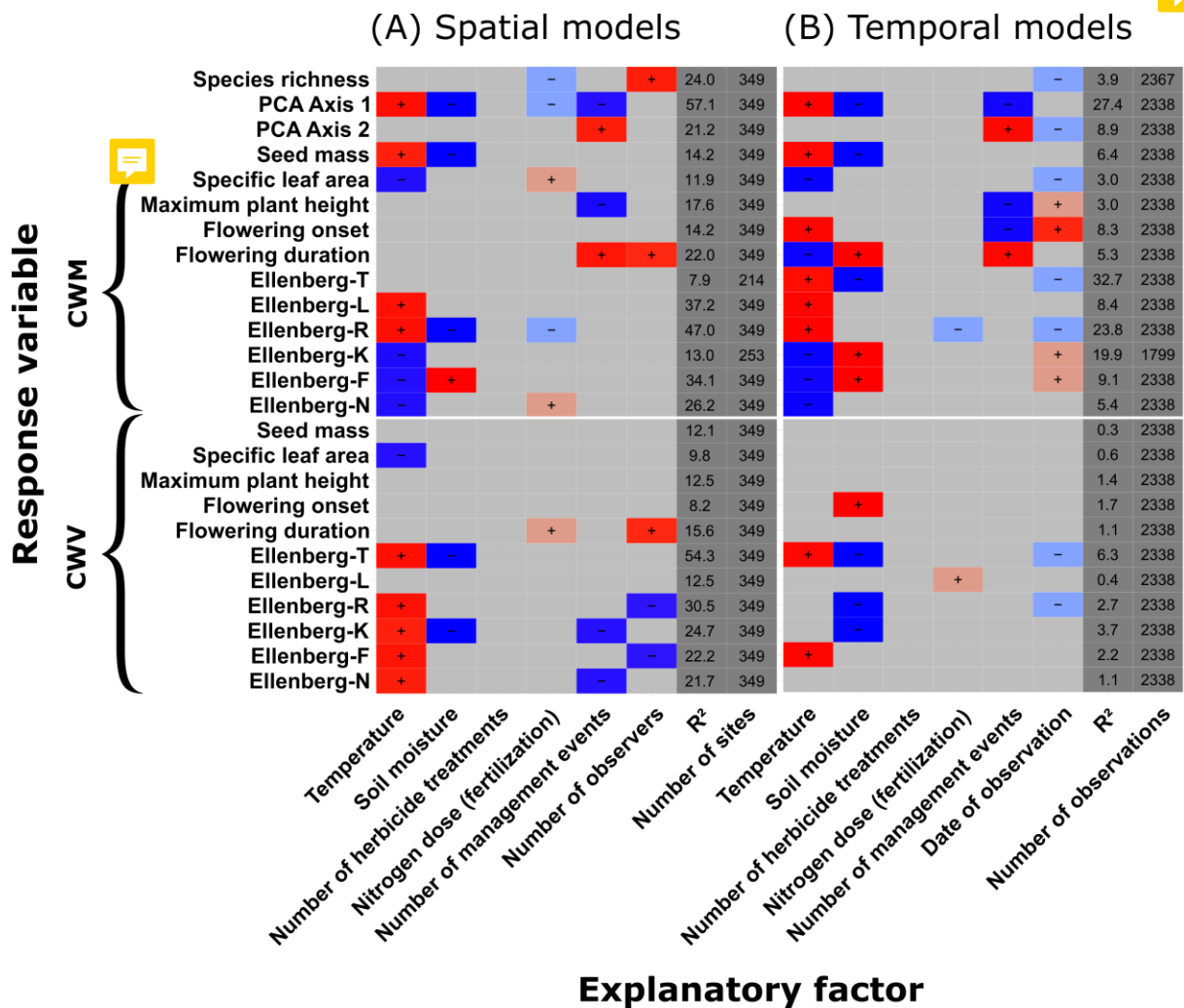
Fig. 4. Results of (A) spatial (SAR) and (B) temporal models (GAMM), with response variables in rows and explanatory factors in columns. The adjusted R², expressed as a percentage of variation, and the number of observations are reported. Significance is indicated by colored cells, with a p-value threshold of 0.01. Positive estimates are in red, negative estimates in blue, and the strength of the relationship (based on the estimates) is reflected by the lightness of the color (weaker when lighter). As response variables were standardized prior to the analysis, estimates can be compared (see **Appendix H** for raw values).

Results differed depending on the subset of data used (**Fig. 1**). In vineyards and the MZ, soil moisture did not have any influence on diversity or functional composition (**Appendix H**) and temperature only

307 increased the Ellenberg-T and decreased SLA in the MZ. In the MZ, Mediterranean species declined

308 (decrease of Ellenberg-T and convergence towards higher values of Ellenberg-K) in frequently managed

309 margins. Nitrogen dose tended to decrease the number of species in the MZ, an effect also found on

310 annual species. In vineyards, no agricultural effect was detected. The effect of the observation date

311 was opposite in the MZ compared to the national scale, with Ellenberg-L increasing and Ellenberg-R

312 and N decreasing across the season. Annuals were more impacted by climatic variations and seasonal

313 effects than perennials, with high R^2 for the Ellenberg-T (R^2 = 0.39) and F (R^2 = 0.32). Margin

314 management affected perennials and annuals differently. For perennials, only the height was reduced

315 with increasingly frequent management, while annuals flowered earlier and longer. Finally, fertilization

316 had a negative effect on species richness and caused a shift towards more continental and late-

317 flowering species in annuals.

318

319 **Discussion**

320

321 The changes observed in both spatial and temporal analyses can be interpreted through the lens of

322 Grime's competitor, stress-tolerant, ruderal (CSR) framework (**Fig. 5**; Grime, 1988). According to

323 Grime, stress (i.e. a shortage of resources such as nutrients, water and light) and disturbance (i.e. the

324 partial or total destruction of plant biomass) determine three main plant strategies representing

325 combinations of traits that are viable under conditions of low disturbances and high resources

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

327 resources (ruderal, R). Originally developed to classify individual plant species into strategies, Grime's

328 theory can be useful to interpret functional changes in plant communities, especially in the context of

329 global changes where vegetation is subject to harsher climatic conditions (more droughts) and various

330 levels of agricultural disturbances (**Fig. 5**). Below, we use this framework to contextualize our results.

331

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

333 Our analyses revealed a shift towards more stress-tolerant and less ruderal species, primarily driven

334 by climate (Díaz et al., 2016; Pakeman et al., 2009). Increasing temperature and drought favored more

335 xerophilous (Ellenberg-F) and thermophilous (Ellenberg-T) species, with higher seed mass and lower

336 nitrogen requirement, thus shifting the position of communities along the stress-tolerance axis. Our

337 results also indicated a functional convergence of Ellenberg values in wet and cold sites, while sites

338 increasingly or already warmer and drier allowed for coexistence of a wider functional variety of

339 species.

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

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

342 (see also Martin et al., 2019). The increase in mean thermal preference at the community-level with

23

343   rising temperatures was already documented, but mainly by studies covering entire floras (regional or

344   local species pool) and time scales of several decades to a century (Salinitro et al., 2019; Tamis et al.,

345   2005). We found that this trend is now detectable over a short-term period of only nine years (Martin

346   et al., 2019). Interestingly, as in other recent studies (Duchenne et al., 2021; Martin et al., 2019), this

347   trend was more pronounced in northern France, while Mediterranean communities responded less to

348   climate change (**Appendix H**). On top of the fact that climatic trends observed in the MZ were weaker

349   than in the CZ, Mediterranean species are already adapted to dry and heat stress, and might be more

350   resilient to extinction risks (Thuiller et al., 2005). Because of their geographic position north of the

351   Mediterranean Sea, they might also experience some competitive release due to the lack of

352   immigrants coming from the south, and the northward shift of more temperate species (Duchenne et

353   al. 2021).

354   Beyond the increase in mean thermal preference, our temporal models revealed additional trends that

355   align well with the existing literature, including a decrease in mean SLA and an increase in mean seed

356   mass (Alarcón Víllora et al., 2019; Kühn et al., 2021). These trait values (low SLA, high seed mass) are

357   also known to be linked to less intensive agriculture (Fried et al., 2020; Richner et al., 2015). All of this

358   suggests that climate change and the evolution towards more extensive agricultural practices will

359   select the same trait values towards more stress-tolerant and less ruderal strategies.

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

361   could increase the abundance of late-emerging and late-flowering species, i.e. species that have high

362   thermal requirements to complete their life cycle (Peters et al., 2014). Critically, such changes can

363   reduce the ability of species to escape field margin management, which typically favors early and long

364   flowering species, as expected with a ruderal strategy. As species will not be able to advance their

365   phenology indefinitely, this can ultimately result in species losses in the long-term, unless farmers may

366   also adapt the temporality of their practices to climate change.

367

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

369   Temporal variations in agricultural practices over the short-term had a weaker influence on diversity

370   and species assembly than climatic variations (Alarcón Víllora et al., 2019; Fried et al., 2019). Field

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

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

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

374   agricultural fields, which can only have collateral effects. Maximum height was the only trait of the

375   ruderal axis that did not respond to climate, but only to the level of disturbance. Interestingly, this trait

376   tended to increase more in the MZ, where a decrease in the frequency of margin management was

377   observed. This potentially suggests a functional change in response to declining agricultural

378   intensification in the MZ, that would warrant further investigations. It is worth noting that the ruderal

379   axis partially partitions annual from perennial species (Lavorel & Garnier, 2002; also the PCA are not

380   exactly similar on these two sets of species, see **Appendix G**), consistent with studies showing that

381   agricultural disturbances benefit more annual species in field margins (Bassa et al., 2011; Hall et al.,

382   2020).

383   Fertilization had a weaker but very consistent impact on floristic communities, increasing the nutrient

384   requirement (Ellenberg-N) and acquisitive capacity (SLA), indicating higher levels of competition

385   among species (Andrade et al., 2021; Pellissier et al., 2014). This can reduce species richness (Kleijn &

386   Verbeek, 2000), an effect detected in the MZ and leading to the loss of some annual Mediterranean

387   species (Poinas et al., under review). Due to functional trade-offs, high nitrogen levels can favor

388   nitrophilous plant species, which are often less thermophilous and more acidiphilous, explaining that

389   nitrogen dose was related to affinity for acidic soils in our models. Nitrogen application levels have

390   only slightly increased over time, primarily in vineyards. This aligns with the weak change in global

391   nitrophily levels in plant communities over time, suggesting that eutrophication may no longer be the

392   primary driver of changes in vegetation (Alignier, 2018; Duchenne et al., 2021).
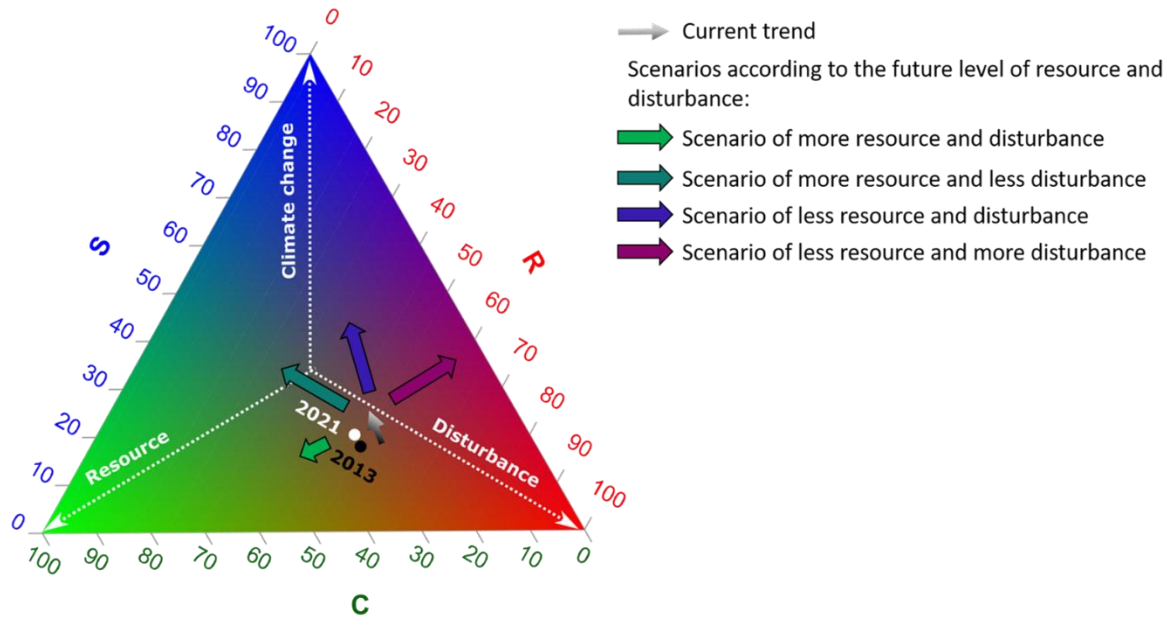
Fig. 5. Grime's CSR triangle depicting the temporal trajectory of community strategies between 2013 and 2021. The CSR scores for 119 out of 142 focal species were extracted from Pierce et al. (2017). We computed community-weighted means of CSR scores by observation, which were then averaged by year. The relative percentages of each strategy are depicted through the use of green, blue and red colors (C = competitor, S = stress-tolerant and R = ruderal). White arrows indicate expected impacts of climate change, disturbance, and resource levels. Colored arrows represent scenarios based on future agricultural intensification levels, assuming persistent or intensified climate change (thus ignoring the right corner scenario of declining stress-tolerant and increasing ruderal species). Increased resource and disturbance levels could lead to a collapse in functional diversity, represented by a shorter arrow.

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

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

26

409   and Díaz et al. (2016), but can also occurred within a narrower functional range (such as plants

410   colonizing agricultural field margins). As a result, agricultural intensification and climate change act in

411   opposite ways on the functional composition of communities. Climate change favors species that are

412   adapted to high temperatures and drought, but not to intensive agriculture. On the contrary,

413   agricultural disturbances select species more sensitive to current climatic trends.

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

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

416   al., 2009). Our results show little effect of agricultural practices, likely because of their limited temporal

417   trend and great range of spatial variability. Our findings allow us to distinguish main trends in

418   community trajectories according to four climatic and agricultural scenarios (**Fig. 5**). The most likely

419   scenario is accelerating climate change coupled with an agricultural abandonment and more extensive

420   practices in Europe (blue arrow in **Fig. 5**, Miller et al., 2022; Peeters et al., 2021), which will likely result

421   in an increase in xero-thermophilous and conservative species. However, a large part of these species

422   are specialized to their habitat (e.g. Mediterranean species as found in Munoz et al. (2017); Fried,

423   Chauvel, et al., 2009) and have a high affinity for calcareous soils, which will probably limit their

424   expansion towards the CZ. Areas where they are unable to colonize might suffer a decrease in species

425   richness, and this scenario could be worsen if current levels of agricultural intensification are

426   maintained or increased. Mediterranean species could face severe agricultural intensification in

427   northern France, that would likely limit their expansion, while at the same time ruderal species would

428   become less frequent mostly because of drought. This highlights the need to consider the conjunction

429   of climate change and intensive agriculture.

430

431   **Conclusion**

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

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

27

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

435   practices had a limited effect on diversity and species assembly at the national level, with field margin

436   management having the greatest impact. It is clear from our findings that the persistence of intensive

437   agricultural practices and accelerating climate change would have critical consequences for the

438   conservation of floristic diversity in agroecosystems, as species selected by climate change are poorly

439   adapted to intensive farming. To preserve biodiversity, future agricultural practices should prioritize

440   the creation of a favorable microclimate for species persistence while reducing local intensification.

441   Our findings suggest a likely reduction in ruderality and an increase in stress-tolerance according to

442   Grime's strategies, raising concerns about potential loss of plant diversity in intensively managed areas.

443   Considering the synergies between climate change and agricultural practices, even at a regional level,

444   is thus crucial for addressing future agriculture challenges.

452

453   **Conflict of interest disclosure**

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

455   this article.

456

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

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

29

References

Alarcón Víllora, R., Hernández Plaza, E., Navarrete, L., Sánchez, M. J., & Sánchez, A. M. (2019). Climate and tillage system drive weed communities' functional diversity in a Mediterranean cereal-legume rotation. *Agriculture, Ecosystems & Environment*, *283*, 106574. https://doi.org/10.1016/j.agee.2019.106574

Alignier, A. (2018). Two decades of change in a field margin vegetation metacommunity as a result of field margin structure and management practice changes. *Agriculture, Ecosystems & Environment*, *251*, 1–10. https://doi.org/10.1016/j.agee.2017.09.013

Andrade, C., Villers, A., Balent, G., Bar-Hen, A., Chadoeuf, J., Cylly, D., Cluzeau, D., Fried, G., Guillocheau, S., Pillon, O., Porcher, E., Tressou, J., Yamada, O., Lenne, N., Jullien, J., & Monestiez, P. (2021). A real-world implementation of a nationwide, long-term monitoring program to assess the impact of agrochemicals and agricultural practices on biodiversity. *Ecology and Evolution*, *11*(9), 3771–3793. https://doi.org/10.1002/ece3.6459

Bassa, M., Boutin, C., Chamorro, L., & Sans, F. X. (2011). Effects of farming management and landscape heterogeneity on plant species composition of Mediterranean field boundaries. *Agriculture, Ecosystems & Environment*, *141*(3–4), 455–460. https://doi.org/10.1016/j.agee.2011.04.012

Baude, M., Colin, A., Calipel, C., Duvernoy, J., & Foussard, A. (2022). *Chiffres clés du climat France, Europe et Monde—Édition 2022* [Rapport ministériel]. Service des données et études statistiques - Ministère de la Transition écologique. https://www.statistiques.developpement-durable.gouv.fr/edition-numerique/chiffres-cles-du-climat-2022/pdf/chiffres-cles-du-climat-2022-integral.pdf

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and

485   divergence in a Mediterranean rangeland. *Journal of Ecology*, *100*(6), 1422–1433.

486   https://doi.org/10.1111/1365-2745.12003

487   Bopp, M.-C., Kazakou, E., Metay, A., & Fried, G. (2022). Relative importance of region, seasonality and

488   weed management practice effects on the functional structure of weed communities in French

489   vineyards. *Agriculture, Ecosystems & Environment*, *330*, 107892.

490   https://doi.org/10.1016/j.agee.2022.107892

491   Box, G. E. P., Jenkins, G. M., Reinsel, G. C., & Ljung, G. M. (2015). *Time Series Analysis: Forecasting and*

492   *Control*. John Wiley & Sons.

493   Cressie, N. (2015). *Statistics for Spatial Data*. John Wiley & Sons.

494   Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C.,

495   Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T.,

496   Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form

497   and function. *Nature*, *529*(7585), Article 7585. https://doi.org/10.1038/nature16489

498   Duchenne, F., Martin, G., & Porcher, E. (2021). European plants lagging behind climate change pay a

499   climatic debt in the North, but are favoured in the South. *Ecology Letters*, *24*(6), 1178–1186.

500   https://doi.org/10.1111/ele.13730

501   Emmerson, M., Morales, M. B., Oñate, J. J., Batáry, P., Berendse, F., Liira, J., Aavik, T., Guerrero, I.,

502   Bommarco, R., Eggers, S., Pärt, T., Tscharntke, T., Weisser, W., Clement, L., & Bengtsson, J.

503   (2016). How Agricultural Intensification Affects Biodiversity and Ecosystem Services. In

504   *Advances in Ecological Research* (Vol. 55, pp. 43–97). Elsevier.

505   https://linkinghub.elsevier.com/retrieve/pii/S0065250416300204

506   Fitter, A. H., & Fitter, R. S. R. (2002). Rapid Changes in Flowering Time in British Plants. *Science*,

507   *296*(5573), 1689–1691. https://doi.org/10.1126/science.1071617

508   Fonty, E., Sarthou, C., Larpin, D., & Ponge, J.-F. (2009). A 10-year decrease in plant species richness on

509   a neotropical inselberg: Detrimental effects of global warming? *Global Change Biology*, *15*(10),

510   2360–2374. https://doi.org/10.1111/j.1365-2486.2009.01923.x

511   Fried, G., Armengot, L., Storkey, J., Bourgeois, B., Gaba, S., Violle, C., & Munoz, F. (2020). Do ecological
512   specialization and functional traits explain the abundance–frequency relationship? Arable
513   weeds as a case study. *Journal of Biogeography*, *48*(1), 37–50.
514   https://doi.org/10.1111/jbi.13980

515   Fried, G., Blanchet, C., Cazenave, L., Bopp, M.-C., Kazakou, E., Metay, A., Christen, M., Alard, D., &
516   Cordeau, S. (2022). Consistent response of weeds according to Grime's CSR strategies along
517   disturbance and resource gradients in Bordeaux vineyards. *Weed Research*, *62*(5), 347–359.
518   https://doi.org/10.1111/wre.12549

519   Fried, G., Chauvel, B., & Reboud, X. (2009). A functional analysis of large-scale temporal shifts from
520   1970 to 2000 in weed assemblages of sunflower crops in France. *Journal of Vegetation Science*,
521   *20*(1), 49–58. https://doi.org/10.1111/j.1654-1103.2009.05284.x

522   Fried, G., Cordeau, S., Metay, A., & Kazakou, E. (2019). Relative importance of environmental factors
523   and farming practices in shaping weed communities structure and composition in French
524   vineyards. *Agriculture, Ecosystems & Environment*, *275*, 1–13.
525   https://doi.org/10.1016/j.agee.2019.01.006

526   Fried, G., Kazakou, E., & Gaba, S. (2012). Trajectories of weed communities explained by traits
527   associated with species' response to management practices. *Agriculture, Ecosystems &*
528   *Environment*, *158*, 147–155. https://doi.org/10.1016/j.agee.2012.06.005

529   Gaba, S., Fried, G., Kazakou, E., Chauvel, B., & Navas, M.-L. (2014). Agroecological weed control using
530   a functional approach: A review of cropping systems diversity. *Agronomy for Sustainable*
531   *Development*, *34*(1), 103–119. https://doi.org/10.1007/s13593-013-0166-5

532   Garnier, E., & Navas, M.-L. (2012). A trait-based approach to comparative functional plant ecology:
533   Concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable*
534   *Development*, *32*(2), 365–399. https://doi.org/10.1007/s13593-011-0036-y

535   Garnier, E., Vile, D., Roumet, C., Lavorel, S., Grigulis, K., Navas, M.-L., & Lloret, F. (2019). Inter- and
536   intra-specific trait shifts among sites differing in drought conditions at the north western edge

537   of the Mediterranean Region. *Flora*, *254*, 147–160.

538   https://doi.org/10.1016/j.flora.2018.07.009

539 Grime, J. P. (1988). The C-S-R model of primary plant strategies—Origins, implications and tests. In L.

540   D. Gottlieb & S. K. Jain (Eds.), *Plant Evolutionary Biology* (pp. 371–393). Springer Netherlands.

541   https://doi.org/10.1007/978-94-009-1207-6_14

542 Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities:

543   Mechanisms and consequences. *Journal of Vegetation Science*, *17*(2), 255–260.

544   https://doi.org/10.1111/j.1654-1103.2006.tb02444.x

545 Guichard, L., Dedieu, F., Jeuffroy, M.-H., Meynard, J.-M., Reau, R., & Savini, I. (2017). Le plan Ecophyto

546   de réduction d'usage des pesticides en France: Décryptage d'un échec et raisons d'espérer.

547   *Cahiers Agricultures*, *26*(1), Article 1. https://doi.org/10.1051/cagri/2017004

548 Hall, R. M., Penke, N., Kriechbaum, M., Kratschmer, S., Jung, V., Chollet, S., Guernion, M., Nicolai, A.,

549   Burel, F., Fertil, A., Lora, Á., Sánchez-Cuesta, R., Guzmán, G., Gómez, J., Popescu, D., Hoble, A.,

550   Bunea, C.-I., Zaller, J. G., & Winter, S. (2020). Vegetation management intensity and landscape

551   diversity alter plant species richness, functional traits and community composition across

552   European vineyards. *Agricultural Systems*, *177*, 102706.

553   https://doi.org/10.1016/j.agsy.2019.102706

554 Kleijn, D., & Verbeek, M. (2000). Factors affecting the species composition of arable field boundary

555   vegetation. *Journal of Applied Ecology*, *37*(2), 256–266. https://doi.org/10.1046/j.1365-

556   2664.2000.00486.x

557 Kühn, N., Tovar, C., Carretero, J., Vandvik, V., Enquist, B. J., & Willis, K. J. (2021). Globally important

558   plant functional traits for coping with climate change. *Frontiers of Biogeography*, *13*(4).

559   https://doi.org/10.21425/F5FBG53774

560 Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem

561   functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556.

562   https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., & Bonis, A. (2008). Assessing functional diversity in the field – methodology matters! *Functional Ecology*, *22*(1), 134–147. https://doi.org/10.1111/j.1365-2435.2007.01339.x

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

Lososová, Z., Chytrý, M., Cimalová, S., Kropáč, Z., Otýpková, Z., Pyšek, P., & Tichý, L. (2004). Weed vegetation of arable land in Central Europe: Gradients of diversity and species composition. *Journal of Vegetation Science*, *15*(3), 415–422. https://doi.org/10.1111/j.1654-1103.2004.tb02279.x

Lovejoy, T. E. (2006). *Climate Change and Biodiversity* (Yale University Press). The Energy and Resources Institute (TERI).

MacLaren, C., Storkey, J., Menegat, A., Metcalfe, H., & Dehnen-Schmutz, K. (2020). An ecological future for weed science to sustain crop production and the environment. A review. *Agronomy for Sustainable Development*, *40*(4), 24. https://doi.org/10.1007/s13593-020-00631-6

Martin, G., Devictor, V., Motard, E., Machon, N., & Porcher, E. (2019). Short-term climate-induced change in French plant communities. *Biology Letters*, *15*(7), 20190280. https://doi.org/10.1098/rsbl.2019.0280

Metay, A., Garcia, L., Kazakou, E., & Fried, G. (2022). Effet des couverts sur la flore en viticulture. *Agronomie, Environnement & Sociétés*, *12*(1). https://hal-montpellier-supagro.archives-ouvertes.fr/hal-03776173

Miller, D., Legras, S., Barnes, A., Cazacu, M., Gava, O., Helin, J., Irvine, K., Kantelhardt, J., Landert, J., Latruffe, L., Mayer, A., Niedermayr, A., Povellato, A., Schaller, L., Schwarz, G., Smith, P., Vanni, F., Védrine, L., Viaggi, D., … Vlahos, G. (2022). Creating Conditions for Harnessing the Potential of Transitions to Agroecology in Europe and Requirements for Policy. *EuroChoices*, *21*(3), 72–79. https://doi.org/10.1111/1746-692X.12374

589 Munoz, F., Fried, G., Armengot, L., Bourgeois, B., Bretagnolle, V., Chadoeuf, J., Mahaut, L., Plumejeaud,

590   C., Storkey, J., Violle, C., & Gaba, S. (2017). *Database of weeds in cultivation fields of France*

591   *and UK, with ecological and biogeographical information* [Data set]. Zenodo.

592   https://doi.org/10.5281/zenodo.1112342

593 Murray, B. R., Brown, A. H. D., Dickman, C. R., & Crowther, M. S. (2004). Geographical gradients in seed

594   mass in relation to climate. *Journal of Biogeography*, *31*(3), 379–388.

595   https://doi.org/10.1046/j.0305-0270.2003.00993.x

596 Office français de la biodiversité. (2021). *Carte des régions d'origine—Référentiel technique de la*

597   *marque Végétal local—Version 2021*. www.vegetal-local.fr

598 Oliver, T. H., & Morecroft, M. D. (2014). Interactions between climate change and land use change on

599   biodiversity: Attribution problems, risks, and opportunities. *WIREs Climate Change*, *5*(3), 317–

600   335. https://doi.org/10.1002/wcc.271

601 Pakeman, R. J., Lepš, J., Kleyer, M., Lavorel, S., Garnier, E., & Consortium, the V. (2009). Relative

602   climatic, edaphic and management controls of plant functional trait signatures. *Journal of*

603   *Vegetation Science*, *20*(1), 148–159. https://doi.org/10.1111/j.1654-1103.2009.05548.x

604 Peeters, A., Lefebvre, O., & Balogh, L. (2020). A Green Deal for implementing agroecological systems:

605   Reforming the Common Agricultural Policy of the European Union. *Journal of Sustainable and*

606   *Organic Agricultural Systems*, *70*, 83–93. https://doi.org/10.3220/LBF1610123299000

607 Pellissier, L., Wisz, M. S., Strandberg, B., & Damgaard, C. (2014). Herbicide and fertilizers promote

608   analogous phylogenetic responses but opposite functional responses in plant communities.

609   *Environmental Research Letters*, *9*(2), 024016. https://doi.org/10.1088/1748-

610   9326/9/2/024016

611 Peters, K., Breitsameter, L., & Gerowitt, B. (2014). Impact of climate change on weeds in agriculture: A

612   review. *Agronomy for Sustainable Development*, *34*(4), 707–721.

613   https://doi.org/10.1007/s13593-014-0245-2

614 Pierce, S., Negreiros, D., Cerabolini, B. E. L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B., Wright, S. J.,

615 Soudzilovskaia, N. A., Onipchenko, V. G., van Bodegom, P. M., Frenette-Dussault, C., Weiher,

616 E., Pinho, B. X., Cornelissen, J. H. C., Grime, J. P., Thompson, K., Hunt, R., Wilson, P. J., …

617 Tampucci, D. (2017). A global method for calculating plant CSR ecological strategies applied

618 across biomes world-wide. *Functional Ecology*, *31*(2), 444–457. https://doi.org/10.1111/1365-

619 2435.12722

620 Poinas, I., Fried, G., Henckel, L., & Meynard, C. N. (2023). Scale dependence in agricultural drivers of

621 field margin plant communities: Influence of spatial resolution and extent. *bioRxiv.*

622 https://doi.org/10.1101/2023.03.02.530797

623 Richner, N., Holderegger, R., Linder, H. P., & Walter, T. (2015). Reviewing change in the arable flora of

624 Europe: A meta-analysis. *Weed Research*, *55*(1), 1–13. https://doi.org/10.1111/wre.12123

625 Salinitro, M., Alessandrini, A., Zappi, A., & Tassoni, A. (2019). Impact of climate change and urban

626 development on the flora of a southern European city: Analysis of biodiversity change over a

627 120-year period. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-46005-

628 1

629 Sonnier, G., Shipley, B., & Navas, M.-L. (2010). Quantifying relationships between traits and explicitly

630 measured gradients of stress and disturbance in early successional plant communities. *Journal

631 of Vegetation Science*, *21*(6), 1014–1024. https://doi.org/10.1111/j.1654-1103.2010.01210.x

632 Tamis, W. L. M., Zelfde, M. V., Der Meijden, R. V., & De Haes, H. A. U. (2005). Changes in Vascular Plant

633 Biodiversity in the Netherlands in the 20th Century Explained by their Climatic and other

634 Environmental Characteristics. *Climatic Change*, *72*(1), 37–56.

635 https://doi.org/10.1007/s10584-005-5287-7

636 Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to

637 plant diversity in Europe. *Proceedings of the National Academy of Sciences*, *102*(23), 8245–

638 8250. https://doi.org/10.1073/pnas.0409902102

639   Wheeler, G. R., Brassil, C. E., & Knops, J. M. H. (2023). Functional traits' annual variation exceeds

640   nitrogen-driven variation in grassland plant species. *Ecology*, *104*(2), e3886.

641   https://doi.org/10.1002/ecy.3886

642   Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin,

643   T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K.,

644   Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics

645   spectrum. *Nature*, *428*(6985), Article 6985. https://doi.org/10.1038/nature02403

646