Montpellier, August 1st 2023

Dear editors and reviewers,

We are grateful for the many helpful comments you provided to improve our manuscript. In our new version, we have focused on clarifying some aspects of our analyses and justifications, all the while including the Grime triangle earlier in the manuscript and including it in our material and methods. We also expand, as suggested by the reviewers, on some of the perspectives of future analyses using this long-term / large-scale dataset.

Below we provide detailed responses to the reviewer comments, including some new analyses, some of which we decided to leave out of the manuscript but that help address the reviewers’ comments.

We hope you find these modifications useful. Looking forward to reading your further comments or decision.

All the best,
Isis Poinas, on behalf of all co-authors

Below, the original comments from reviewers are in black, while our responses are in blue.

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:
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 Ellenberg 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
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.

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<tr>
<th>Number of years of flora data</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of sites</td>
<td>20</td>
<td>20</td>
<td>14</td>
<td>16</td>
<td>21</td>
<td>29</td>
<td>47</td>
<td>94</td>
<td>294</td>
</tr>
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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:

“Our 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
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 covarations 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.”


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 revisited 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
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.

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

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Authorship statement: I.P., G.F. and C.N.M. planned and designed the research; I.P. analyzed the data and wrote the first draft of the manuscript; G.F. and C.N.M. contributed substantially to revisions. All authors gave final approval for publication.

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

Number of cited references: 55

Number of tables: 1

Number of figures: 5
Abstract

Over the past decades, agricultural intensification and climate change have led to vegetation shifts in Europe. However, these impacts are often studied using meta-analyses at large scales, or using taxonomic diversity. Functional trade-offs linking traits responding to climate and farming practices are rarely analyzed, especially on large-scale empirical studies. Here we used a standardized yearly monitoring effort of agricultural field margin flora at the national scale to assess the spatio-temporal response of diversity and functional traits to climatic and agricultural variations. We examined temporal trends in climate, agricultural practices, plant species richness, and trait community-weighted means and variances across 555 sites in France between 2013 and 2021. We found that temperatures have increased while soil moisture has decreased, reflecting current climate change, whereas the intensity of agricultural practices did not show clear temporal trends over the past decade. Changes in plant communities were noticeable, especially as they relate to climate change, while the impact of agricultural practices was limited and mainly exerted through field margin management and to a lesser extent, fertilization. Mediterranean, vineyards and perennial species demonstrated reduced response to climatic variations. Our findings suggest that species adapted to climate change (including Mediterranean species) have increased in proportion and are spreading northward. Importantly, we identified functional trade-offs suggesting that these species are also the most vulnerable to intensive agricultural practices. We put these results into the conceptual framework of Grime’s CSR triangle and suggest that the convergence of climate change and the maintenance of a highly intensive agriculture could carry a risk of abrupt declines in floristic diversity of field margins, a concern that merits further attention.

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

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

Changes in plant communities cannot be discerned solely by taxonomic diversity due to the differing traits affected by resource availability and disturbance levels (Garnier & Navas, 2012); therefore, a functional dimension is required to accurately understand these changes. This is particularly important in an agroecological context, where both resource (fertilization) and disturbance (herbicides, field management) gradients play crucial roles (Saba et al., 2014; MacLaren et al., 2020). For instance, weeds with a ruderal strategy are better adapted to agricultural disturbances, such as tillage, herbicides or frequent margin management (Grime, 2006; Fried et al., 2022). At the same time, traits responding to agricultural practices can co-vary with other traits that are linked to resources, competitive ability, or climate. For example, seed mass, which is often used as a proxy for competitive
ability, increases along soil fertility, temperature and solar radiation gradients (Fried et al., 2022; Murray et al., 2004). Furthermore, correlations among different traits may represent trade-offs that impact community adaptation (Diaz et al., 2016; Wright et al., 2004). In this context, Grime (1988) proposed a framework called the CSR triangle, which defines three axes of variation - competitive, stress-tolerance, and ruderal adaptations - that are correlated to multiple traits and have proven useful to understand plant community dynamics (Fried et al., 2022). As traits responding to climate and agricultural practices may co-vary (Garnier & Navas, 2012), it can be difficult to identify the main drivers behind community changes.

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

In this study, we aimed at deciphering how spatio-temporal variations of climate and agricultural practices in France structure the diversity and trait composition of field margin plant communities. We studied the herbaceous field margin, which represents the uncultivated vegetated area located between the cultivated strip and the adjacent habitat. Using a standardized national monitoring effort spanning 9 years (2013-2021) in 555 agricultural field margins covering continental France, we aimed to determine temporal trends in agricultural practices and climate, and explore the spatial and
temporal drivers of species diversity and functional traits. We hypothesized that plant traits sensitive to temperature and soil moisture will co-vary with both spatial climatic gradients and temporal warming trends while agricultural practices would have a greater spatial than temporal influence on plant communities, as we did not expect clear temporal trends in these practices. On top of the national analyses, and because this dataset includes the Mediterranean flora, which has been shown to respond more strongly to some agricultural filters (Poinas et al., under review), we included analyses separating this region from the others. We also separated vineyards from annual crops, because vineyards include very different management practices and no crop rotation (Metay et al., 2022). Finally, we also analyzed annual plant species separately, as they may respond more rapidly to environmental changes (Martin et al., 2019; Fitter & Fitter, 2002).
Materials and methods

Vegetation survey

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

Climatic and agricultural variables

We gathered two types of explanatory variables: the first came directly from the 500-ENI network and reflects agricultural practices assessed directly on the monitoring sites; the second one included meteorological data from an external database (see below).
Agricultural practices were reported yearly from interviews of farmers into a standardized online database. Data collected relate to fertilization, herbicide use and field margin management. Daily meteorological data were extracted from the SAFRAN climate model of Météo France, with a resolution of 8 km (Le Moigne, 2002). Meteorological data were averaged over a one-year window prior to each floristic observation, while agricultural data were summed over the same period (Table 1). We selected variables that were weakly correlated (Spearman correlation < 0.65, Appendix B) and have been shown to influence plant communities in previous studies (Table 1, see Appendix C for the choice of variables).
Table 1. List of explanatory factors (blue), functional traits (green) and response variables (red) with their abbreviations, units and calculation. The variables only used in temporal models are underlined, while those only used in spatial ones are in italic. We noted the expected link of each factor and trait to the agricultural resource and disturbance gradient, and to climate change. A left-pointing triangle indicates an increase in relation to the corresponding factor of the same color. An hourglass symbol was used for relationships with contradictory findings in the literature (see Appendix C for the references).

<table>
<thead>
<tr>
<th>Factors</th>
<th>Abbreviations</th>
<th>Units</th>
<th>Index used</th>
<th>Hypothesis of response to the Agricultural gradient: Disturbance (Di) and Resource (R)</th>
<th>Hypothesis of response to the Climatic gradient: Drought (Dr) and Increasing temperature (T)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>TEMP</td>
<td>°C</td>
<td>Annual mean of daily values</td>
<td></td>
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<tr>
<td>Soil moisture</td>
<td>MOI</td>
<td>%</td>
<td>Annual mean of daily values</td>
<td></td>
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<tr>
<td>Dose of nitrogen (fertilization)</td>
<td>N_DOSE</td>
<td>kg/ha</td>
<td>For each application: Dose = ( \frac{\text{Quantity} \times N \text{ of the formulation}}{100} ) Doses were summed one year before observation</td>
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<tr>
<td>Number of herbicide treatments</td>
<td>HERB</td>
<td></td>
<td>Treatments were summed one year before observation</td>
<td></td>
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<tr>
<td>Number of management events</td>
<td>MAN</td>
<td></td>
<td>All types of management (mowing, grazing...). Number of management events were summed one year before observation.</td>
<td></td>
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</tr>
<tr>
<td><strong>Date of observation</strong></td>
<td>DATE</td>
<td>Julian days</td>
<td></td>
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<tr>
<td><strong>Number of observers</strong></td>
<td>OBS</td>
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<tr>
<td>Specific leaf area</td>
<td>SLA</td>
<td>m² kg⁻¹</td>
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<tr>
<td>Maximum plant height</td>
<td>HEIGHT</td>
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<tr>
<td>Seed mass</td>
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<td>g</td>
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<tr>
<td>Flowering onset</td>
<td>FLOW_ON</td>
<td>months</td>
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<td>Flowering duration</td>
<td>FLOW_DUR</td>
<td>Months</td>
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<tr>
<td>Trait</td>
<td>Abbreviation</td>
<td>Description</td>
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<tr>
<td>Ellenberg indicator for light, temperature, continentality, moisture, pH and nutrients</td>
<td>EIV_L, EIV_T, EIV_K, EIV_F, EIV_R, EIV_N</td>
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<tr>
<td>Species richness</td>
<td>$S$</td>
<td>Number of species</td>
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<tr>
<td>Functional composition</td>
<td>See abbreviations above for each trait preceded by “CWM_”</td>
<td>Community weighted means (CWM) : community trait values weighted by species abundance (Lavorel et al., 2008)</td>
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<tr>
<td>Functional divergence</td>
<td>See abbreviations above for each trait preceded by “CWV_”</td>
<td>Community weighted variances (CWV) : community trait variability around the average value (Sonnier et al., 2010)</td>
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<tr>
<td>PCA traits - axis</td>
<td>PCA_1</td>
<td>Scores of sites or observations on the 1st axis of the PCA including CWM of all traits</td>
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<tr>
<td>PCA traits - axis</td>
<td>PCA_2</td>
<td>Scores of sites or observations on the 2nd axis of the PCA including CWM of all traits</td>
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</tbody>
</table>
Plant functional traits

We extracted from external databases five functional traits and six species-level indices of ecological requirements, assumed to respond to agricultural or climatic factors (Table 1, Appendix B-C).

Functional traits were missing for four species, two of which could be imputed from an average over other species of the same genus. The remaining two species were removed from the analysis (representing 0.01% of the total abundances among the 142 species considered). In the following analyses, maximal height and seed mass were log-transformed to ensure normality and reduce the weight of extreme values.

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

$$\text{CWM} = \sum_{i=0}^{n} P_i \times \text{trait}_i \quad \text{(Eq. 1)}$$

$$\text{CWV} = \sum_{i=0}^{n} P_i \times (\text{trait}_i - \text{CWM})^2 \quad \text{(Eq. 2)}$$

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

The species pool was defined by the biogeographic region in the spatial analyses, and by site in the temporal analyses (see below), to focus on the relevant axes of variation we were most interested in.

We extracted biogeographic regions from the VégétalLocal map (Office français de la biodiversité, 2021). To quantify the difference between observed and null CWV, we computed effect sizes...
A positive effect size denotes a divergence in trait values within the community (convergence for negative effect size). We performed a normed PCA on the CWM of traits (by site for spatial analyses, by observation for temporal analyses) and we took the first two axes, representing different combinations of traits.

Temporal trends in climate, agricultural practices and plant communities

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

Spatial analyses of plant communities

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

Temporal analyses of plant communities

To disentangle temporal effects on plant communities, we used generalized additive mixed models (GAMM) to account for repeated measures at a site, with a Gaussian distribution in most cases (but see Appendix F, Table SF.2). We included the site identity as a random effect, and a first-order
temporal autocorrelation structure within sites (Box et al., 2015). Observer bias was accounted for by including the observer identity as a random term nested within sites. We removed observations with missing values in climatic and agricultural factors (1805 out of 4172 observations), and a few observations that distorted trait distributions (Appendix F), resulting in varying observation numbers across models (see Fig. 4).

Results

Temporal trends in climate, agricultural practices and plant communities

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

Plant species richness has slightly increased over time at the national scale ($r = 0.07, p < 0.001, 1.3$ species per decade), even more in the MZ ($r = 0.20, p < 0.001, 4.2$ species by decade) and vineyards ($r = 0.17, p < 0.001, 3.3$ species by decade). In France, we saw an increase in the CWM of maximal height ($r = 0.08, p < 0.001$), seed mass ($r = 0.10, p < 0.001$), flowering onset ($r = 0.07, p < 0.001, 3.12$ days by
decade) and a decrease of flowering duration ($r = -0.10$, $p < 0.001, -7.83$ days by decade) (Appendix E).

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

\[ r = 0.22^{***} \]

Geographic area
- Continental
- Mediterranean

(C) Soil moisture index

\[ r = -0.39^{***} \]

(E) CWM of Ellenberg-F

\[ r = -0.06^{***} \]

(G) Number of herbicide applications

\[ r = -0.05^{**} \]
\[ r = -0.14^{***} \]

(H) Nitrogen dose in fertilizers

\[ r = 0.02 \text{ NS} \]
\[ r = 0.16^{***} \]

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

Spatial analyses of plant communities

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

Spatial models revealed that climate had a predominant impact on functional composition and particularly on Ellenberg values, opposing in a consistent way Mediterranean species to nitrophilous continental ones along the stress-tolerance axis (Fig. 4). Temperature increased the CWM of seed mass and decreased the CWM and CWV of SLA (convergence). High temperatures lead to divergence in all Ellenberg values except the Ellenberg-L, while soil moisture brought convergence in the Ellenberg-T and K. Field margin management was the agricultural practice with the strongest effect, favoring ruderal species with higher SLA and/or lower seed mass (PCA Axis 1), shorter stature and longer flowering duration (PCA Axis 2). Herbicide applications had no significant effect, while the average
annual nitrogen dose in fertilizers decreased the species richness and Ellenberg-R, but increased Ellenberg-N, SLA and divergence in flowering duration (Fig. 4). The number of observers surveying a site over the 9-year period was positively correlated with species richness (average increase of 1.68 species by observer) and with the CWM and CWV of flowering duration.

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

Temporal analyses of plant communities

PCA on CWM by observation closely mirrored PCA on CWM by site (Fig. 3). The first two axes represented the same ecological strategies, explaining 29.9% and 19.5% of the variation, respectively.
However, one difference was that SLA was more correlated to the ruderal rather than the stress-tolerance axis in the PCA based on observations.

Climatic factors were also the most influential in temporal models, with high $R^2$ for the CWM of Ellenberg-T ($R^2 = 0.33$) and stress-tolerance axis ($R^2 = 0.27$, Fig. 4). Regressions between Ellenberg values and climatic factors remained consistent across spatial and temporal models, with increasing temperature leading to an increase and divergence in Ellenberg-T values. However, new patterns emerged in temporal models, with increasing temperature and drought associated with shorter flowering duration, and later flowering onset only for increasing temperature (Fig. 4). Here again, margin management was the agricultural practice with the largest impact on community changes, with an increase in its frequency associated with more ruderal species. The date of observation also influenced community changes, with a later observation related to more conservative, competitive and continental species, and to a decrease in species richness.
Fig. 4. Results of (A) spatial (SAR) and (B) temporal models (GAMM), with response variables in rows and explanatory factors in columns. The adjusted 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...
increased the Ellenberg-T and decreased SLA in the MZ. In the MZ, Mediterranean species declined (decrease of Ellenberg-T and convergence towards higher values of Ellenberg-K) in frequently managed margins. Nitrogen dose tended to decrease the number of species in the MZ, an effect also found on annual species. In vineyards, no agricultural effect was detected. The effect of the observation date was opposite in the MZ compared to the national scale, with Ellenberg-L increasing and Ellenberg-R and N decreasing across the season. Annuals were more impacted by climatic variations and seasonal effects than perennials, with high $R^2$ for the Ellenberg-T ($R^2 = 0.39$) and $F$ ($R^2 = 0.32$). Margin management affected perennials and annuals differently. For perennials, only the height was reduced with increasingly frequent management, while annuals flowered earlier and longer. Finally, fertilization had a negative effect on species richness and caused a shift towards more continental and late-flowering species in annuals.
Discussion

The changes observed in both spatial and temporal analyses can be interpreted through the lens of Grime's competitor, stress-tolerant, ruderal (CSR) framework (Fig. 5; Grime, 1988). According to Grime, stress (i.e. a shortage of resources such as nutrients, water and light) and disturbance (i.e. the partial or total destruction of plant biomass) determine three main plant strategies representing combinations of traits that are viable under conditions of low disturbances and high resources (competitor, C), low disturbances and low resources (stress-tolerant, S) or high disturbances and high resources (ruderal, R). Originally developed to classify individual plant species into strategies, Grime's theory can be useful to interpret functional changes in plant communities, especially in the context of global changes where vegetation is subject to harsher climatic conditions (more droughts) and various levels of agricultural disturbances (Fig. 5). Below, we use this framework to contextualize our results.

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

Our analyses revealed a shift towards more stress-tolerant and less ruderal species, primarily driven by climate (Díaz et al., 2016; Pakeman et al., 2009). Increasing temperature and drought favored more xerophilous (Ellenberg-F) and thermophilous (Ellenberg-T) species, with higher seed mass and lower nitrogen requirement, thus shifting the position of communities along the stress-tolerance axis. Our results also indicated a functional convergence of Ellenberg values in wet and cold sites, while sites increasingly or already warmer and drier allowed for coexistence of a wider functional variety of species.

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

Beyond the increase in mean thermal preference, our temporal models revealed additional trends that align well with the existing literature, including a decrease in mean SLA and an increase in mean seed mass (Alarcón Villora et al., 2019; Kühn et al., 2021). These trait values (low SLA, high seed mass) are also known to be linked to less intensive agriculture (Fried et al., 2020; Richner et al., 2015). All of this suggests that climate change and the evolution towards more extensive agricultural practices will select the same trait values towards more stress-tolerant and less ruderal strategies.

Finally, temporal analyses showed additional phenological changes, suggesting that climate change could increase the abundance of late-emerging and late-flowering species, i.e. species that have high thermal requirements to complete their life cycle (Peters et al., 2014). Critically, such changes can reduce the ability of species to escape field margin management, which typically favors early and long flowering species, as expected with a ruderal strategy. As species will not be able to advance their phenology indefinitely, this can ultimately result in species losses in the long-term, unless farmers may also adapt the temporality of their practices to climate change.
Agricultural practices have a weaker impact on diversity and species assembly

Temporal variations in agricultural practices over the short-term had a weaker influence on diversity and species assembly than climatic variations (Alarcón Víllora et al., 2019; Fried et al., 2019). Field margin management was the most impactful practice, affecting traits related to the ruderal syndrome in a consistent way. This supports the idea that field margin management, as the only practice applied directly in the margin, has a greater impact than herbicides and fertilization applied in the adjacent agricultural fields, which can only have collateral effects. Maximum height was the only trait of the ruderal axis that did not respond to climate, but only to the level of disturbance. Interestingly, this trait tended to increase more in the MZ, where a decrease in the frequency of margin management was observed. This potentially suggests a functional change in response to declining agricultural intensification in the MZ, that would warrant further investigations. It is worth noting that the ruderal axis partially partitions annual from perennial species (Lavorel & Garnier, 2002; also the PCA are not exactly similar on these two sets of species, see Appendix G), consistent with studies showing that agricultural disturbances benefit more annual species in field margins (Bassa et al., 2011; Hall et al., 2020).

Fertilization had a weaker but very consistent impact on floristic communities, increasing the nutrient requirement (Ellenberg-N) and acquisitive capacity (SLA), indicating higher levels of competition among species (Andrade et al., 2021; Pellissier et al., 2014). This can reduce species richness (Kleijn & Verbeek, 2000), an effect detected in the MZ and leading to the loss of some annual Mediterranean species (Poinas et al., under review). Due to functional trade-offs, high nitrogen levels can favor nitrophilous plant species, which are often less thermophilous and more acidiphilous, explaining that nitrogen dose was related to affinity for acidic soils in our models. Nitrogen application levels have only slightly increased over time, primarily in vineyards. This aligns with the weak change in global nitrophily levels in plant communities over time, suggesting that eutrophication may no longer be the primary driver of changes in vegetation (Alignier, 2018; Duchenne et al., 2021).
Fig. 5. Grime’s CSR triangle depicting the temporal trajectory of community strategies between 2013 and 2021. The CSR scores for 119 out of 142 focal species were extracted from Pierce et al. (2017). We computed community-weighted means of CSR scores by observation, which were then averaged by year. The relative percentages of each strategy are depicted through the use of green, blue and red colors (C = competitor, S = stress-tolerant and R = ruderal). White arrows indicate expected impacts of climate change, disturbance, and resource levels. Colored arrows represent scenarios based on future agricultural intensification levels, assuming persistent or intensified climate change (thus ignoring the right corner scenario of declining stress-tolerant and increasing ruderal species). Increased resource and disturbance levels could lead to a collapse in functional diversity, represented by a shorter arrow.

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

Our findings revealed that resource level (driven by fertilization) and climate vary the position of communities along the stress-tolerance axis, while disturbance level (driven by field margin management) and climate varies the position of communities along the ruderal axis. This supports the view that functional trade-offs are not only evident on a global scale as found by Wright et al. (2004)
and Díaz et al. (2016), but can also occurred within a narrower functional range (such as plants colonizing agricultural field margins). As a result, agricultural intensification and climate change act in opposite ways on the functional composition of communities. Climate change favors species that are adapted to high temperatures and drought, but not to intensive agriculture. On the contrary, agricultural disturbances select species more sensitive to current climatic trends. These trade-offs emphasize the need to consider the existing interactions between climate and agricultural practices when predicting future community trajectories (Garnier et al., 2019; Pakeman et al., 2009). Our results show little effect of agricultural practices, likely because of their limited temporal trend and great range of spatial variability. Our findings allow us to distinguish main trends in community trajectories according to four climatic and agricultural scenarios (Fig. 5). The most likely scenario is accelerating climate change coupled with an agricultural abandonment and more extensive practices in Europe (blue arrow in Fig. 5, Miller et al., 2022; Peeters et al., 2021), which will likely result in an increase in xero-thermophilous and conservative species. However, a large part of these species are specialized to their habitat (e.g. Mediterranean species as found in Munoz et al. (2017); Fried, Chauvel, et al., 2009) and have a high affinity for calcareous soils, which will probably limit their expansion towards the CZ. Areas where they are unable to colonize might suffer a decrease in species richness, and this scenario could be worsen if current levels of agricultural intensification are maintained or increased. Mediterranean species could face severe agricultural intensification in northern France, that would likely limit their expansion, while at the same time ruderal species would become less frequent mostly because of drought. This highlights the need to consider the conjunction of climate change and intensive agriculture.

Conclusion

Our study highlights climate as the primary factor affecting field margin plant communities in France, with increasing temperatures and decreasing soil moisture fostering Mediterranean, stress-tolerant
and conservative species, while negatively affecting ruderal species. In comparison, agricultural practices had a limited effect on diversity and species assembly at the national level, with field margin management having the greatest impact. It is clear from our findings that the persistence of intensive agricultural practices and accelerating climate change would have critical consequences for the conservation of floristic diversity in agroecosystems, as species selected by climate change are poorly adapted to intensive farming. To preserve biodiversity, future agricultural practices should prioritize the creation of a favorable microclimate for species persistence while reducing local intensification.

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. Considering the synergies between climate change and agricultural practices, even at a regional level, is thus crucial for addressing future agriculture challenges.
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Conflict of interest disclosure

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

Appendix A-H. Supplementary data

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