# Scale dependence in agricultural drivers of field margin plant communities: influence of spatial resolution and extent

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**Abstract**

In recent decades, agricultural intensification has led to a strong decline in biodiversity. Agricultural field margins, defined as the uncultivated herbaceous vegetation located between the cultivated strip and an adjacent habitat, usually constitute an important refuge for biodiversity in highly disturbed landscapes, and are critical to the preservation of ecosystem services. However, field margins are also strongly impacted by agricultural practices in their immediate vicinity. Agricultural impacts are often studied at local to landscape scales, and rarely include national or larger spatial extents, where one of the challenges is the lack of availability of standardized monitoring efforts including both biodiversity and agricultural practices. Here, we take advantage of one such monitoring effort to assess the effects of agricultural practices on field margin flora at different extents and resolutions in continental France. We used spatial simultaneous autoregressive and generalized dissimilarity models to assess the response of species richness and community composition to climatic, soil, landscape, agricultural (fertilization, herbicides) and margin management factors. Analyses were repeated at the plot-level, as well as at 25, 40, 60 and 75 km resolutions, and at regional and national extents. We found that species richness is better explained by agricultural practices at the plot-level, and by climate and crop diversity at coarse resolutions, whereas composition responds more strongly to climate at the plot-level, and to fertilization and crop diversity at coarse resolutions. There was a strong variation in the explanatory percentage among regions, but climate effects tended to be weaker within biogeographic units compared to the national level. This allows a better understanding of landscape and management effects, and reveals interactions between local and regional effects. We suggest that providing an agricultural regulatory framework at the scale of biogeographic subdivisions could help provide pertinent measures to conserve biodiversity that are better adapted to the regional context.

**Keywords:** field margin, arable plants, plant assembly, agroecosystem, spatial scale, spatial resolution, spatial extent, species pool, crop diversity, agricultural practices

## Introduction

Since the second half of the 20th century, agricultural intensification has resulted in steady declines in biodiversity across a wide range of taxa and habitats (Emmerson et al., 2016). The mechanization of agriculture and the resulting aggregation of cropped fields has contributed to the loss of semi-natural areas, such as herbaceous field margins, defined here as uncultivated vegetated areas located between the cultivated strip and the adjacent habitat. Despite their modest area in France (less than 1%), field margins play an important ecological role in agroecosystems, as refuge islands and food sources supporting endangered species (Storkey et al., 2011), pollinators (Zamorano et al., 2020) and pest predators (Woodcock et al., 2016). Within landscapes, they act as natural corridors linking habitats and supporting the maintenance of populations of plants, insects, mammals and birds (Haddaway et al., 2018). Locally, they buffer pesticide and fertilizer drift into adjacent terrestrial and aquatic habitats (Haddaway et al., 2018). Their importance has been increasingly recognized in recent European agricultural policies, for example through the conditioning of a green payment provided that margin strips are preserved (Matthews, 2013). Field margins are ecotones and, as such, reflect a mixture of weed ruderal species well adapted to agricultural disturbances, with species that are typical of grasslands and forests (Aavik & Liira, 2009). Many of these species are not directly targeted by agricultural practices, but their habitat is the most directly exposed. Therefore, they are of great interest for studying the unintended impacts of agriculture on biodiversity.

At the local scale, agricultural practices play a key role in shaping the species distribution and diversity of plants from field margins (Marshall & Moonen, 2002). Each crop type has its own characteristic combination of practices (e.g., sowing date, fertilization level, herbicide use), that shapes the floristic community structure within agricultural fields (Bourgeois et al., 2020), and may have spillover effects into the field margins. Chemical inputs (e.g., pesticides and fertilizers) drift to the margins and directly affect plant composition and richness (Fried et al., 2018). Finally, direct management of margins further selects for species adapted to these disturbances (Bassa et al., 2011). Agricultural practices also

aggregate at larger spatial scales and impact landscape dispersal dynamics (Tscharntke et al., 2005). At the landscape scale, habitat composition is an important driver of community structure. The proportion and diversity of non-crop habitats in the landscape generally has a positive effect on field margin biodiversity (Rader et al., 2014), along with crop diversity (Sirami et al., 2019). At the regional and national scale, cropping systems are defined by the sequence of crop successions along with the cultural practices associated to each crop (Leenhardt et al., 2010); they form stable uniform agricultural units which are called agricultural regions in France (Richard-Schott, 2009). However, the influence of these agricultural regions on regional species pools remains to be clarified. While it is well established that soil and climate shape the distribution of species across regions forming cohesive pools of species (Cornell & Harrison, 2014), the challenge remains to characterize how these wide assemblages respond to large-scale structured agricultural practices.

In ecology, spatial scale is usually defined by two attributes: resolution (or grain) and extent, both of them having a strong importance on the processes unveiled. Spatial grain is the size of the unit of analysis. It is often assumed that coarser resolutions allow ignoring local stochasticity to focus on the main patterns structuring communities (Chase, 2014). For example, landscape is expected to have the greatest influence when the grain size is closest to the average area of the different habitats. However, using excessively coarse resolutions may lead to uninformative patterns (Viana & Chase, 2019). Spatial extent is the total area covered by the sampling. It determines the range of variability in environmental gradients, as well as the potential of inclusion of dispersal processes (Viana & Chase, 2019). Naturally, local filtering effects are easier to detect at small extents, and within biogeographic regions, where different study sites are more likely to represent homogeneous conditions for other predictors (e.g. climate) (Viana et al., 2016).

Very few studies have explored issues related to the integration of several spatial scales in agroecosystems. Some suggest that agricultural effects could prevail at fine spatial grains. For example, weed species' richness within winter wheat crops in Spain was found to decrease linearly with field-

level intensification, while remaining constant at the landscape-level (Guerrero et al., 2014). However, field margin communities may be subjected to a greater influence of landscape than agricultural practices (as found by Berquer et al. (2021) at a scale lower than 1 km), in contrast to what happens within agricultural fields. Concepción et al. (2012) revealed that extensive farming has a weaker positive impact on weed diversity in field center and inner field edge when the landscape is too simple within a 500 m radius. This suggests that landscape-scale simplification or intensification may result in a depletion of the regional species pool, which then becomes primarily composed of species adapted to agricultural disturbances, therefore altering the diversity and composition of local assemblages in the long term. We can thus assume that, in some instances, the structure of agricultural communities could be better explained at a landscape or regional spatial grain. Regarding spatial extent, although some studies have addressed national (Rader et al., 2014), continental (Billeter et al., 2008) or regional scales (Nascimbene et al., 2012), these usually included a small sample size, several proxies instead of direct measures of the targeted agricultural practices, and a lack of standard survey procedures across plots. The development of larger-scale studies with standardized sampling efforts is required to thoroughly address the issue of spatial scale on agricultural impacts.

Here we aim at teasing out the effects of spatial resolution and extent, for a better understanding of agricultural practices on plant diversity and composition in field margins. To this end, we rely on a standardized national monitoring effort in 462 agricultural field margins covering France, including monitoring of plant communities as well as agricultural practices. Initial analyses of this dataset at a plot-level showed that vegetation composition is primarily structured along a landscape and soil gradient, and secondarily, along an agricultural intensification gradient (Andrade et al., 2021; Fried et al., 2018). Composition is driven by margin management and fertilization, while species richness responds to the level of intensification (herbicide applications). Building on these first findings, we investigate further by varying the spatial extent and resolution of analysis. Regarding spatial resolution, our first hypothesis is that local agricultural practices will be easier to detect at finer grains because field margin flora is primarily affected by local factors. Our second hypothesis is that landscape and

regional aggregation effects, which influence species filtering at larger spatial grains, will predominate over local practices at broader resolutions. Regarding spatial extent, our hypothesis is that soil and climate will dominate at the national extent and become less important within biogeographic regions, providing a clearer picture of the influence of agricultural practices at the regional extent.

## Materials and methods

### *Vegetation survey*

We used vegetation data from a national monitoring effort, the 500-ENI network, which is funded by the French Ministry of Agriculture (see details in Andrade et al., 2021). Agricultural field margins covering continental France, were surveyed yearly since 2013, representing a total of 543 unique plots between 2013 and 2019 (including some plot turnover between years, see **Fig. SA.1**). These survey plots are located in field margins representing four main crop types: annual crops (with winter wheat or maize as the main crop production, but including other crops in the rotation), market gardening crops (mainly lettuce) and vineyards. The proportion of plots under organic farming is roughly 20%, but agricultural practices cover a wide range of pesticide application, fertilizers and soil management. We selected a subset of plots that had at least five years of botanical data between 2013 and 2019, leaving a total of 462 field margins. Within each survey plot, plant species were identified in ten 1 $m^2$ quadrats along the field margin: the ten quadrats were divided into two sets of five contiguous quadrats of 0.25 x 2 $m^2$ separated by 30 m (**Fig. SA.2**). The transect line was equidistant from the cultivated strip and the adjacent habitat, and the presence-absence of each species was recorded for each quadrat. 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 3079 observations (year x plot), leading to the identification of 689 species. Since we were interested in spatial rather than temporal variations, we summarized plant surveys by averaging the presence-absence of the species detected across years, resulting in one data point per field margin, therefore representing a frequency

of occurrence varying continuously from 0 to 1 (0 = was never detected in that plot; 1 = was detected throughout all years).

*Explanatory 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 plots; the second one was retrieved from external open access databases. These include soil, climate and landscape data.

Agricultural practices were reported yearly from interviews of farmers into an online database according to a national standardized acquisition protocol. Data collected mainly relate to fertilization, pesticide use, tillage and boundary management (**Fig. SA.3**). Soil characteristics (in the layer 0-5 cm) were downloaded from SoilGrids at a 250 m resolution (Hengl et al., 2014), while climatic data (means and variability by year and season for the period 1979-2013) were downloaded from Chelsa Climate database at a 1 km resolution (Karger et al., 2017). We extracted landscape descriptors from OSO land cover maps at a 10 m resolution for 2016 (Inglada et al., 2017). This is a median year with respect to the temporal period covered by our sampling, and we assumed that landscape cover did not change dramatically between 2013 and 2019. We considered percent cover of eight landscape classes (**Fig. SA.3**) within buffers of 1 km radius, and used Shannon diversity index (SHDI) (Turner & Gardner, 2015) to characterize compositional landscape heterogeneity from these landscape metrics. A Shannon's diversity index was also estimated for crop landscape diversity within a buffer of 1 km, considering 17 types of crops (**Fig. SA.3**) retrieved from external databases (OSO, Graphical Parcel Register and the database TOPO).

Our dataset contained missing values on some of the predictors (from 0 to 21.5% missing values at the level of observations), which were completed with a multivariate imputation method, according to a random forest algorithm (package MICE of R v.4.0.0, Buuren & Groothuis-Oudshoorn, 2011). As for biodiversity data, we used mean values over the analysis period for all predictors for each plot; these means by plot were not substantially changed by the imputation method (**Appendix B**).

171 For compositional analyses, all explanatory variables were standardized to have equal mean and
172 standard deviation. We limited the number of explanatory variables to seven (**Table 1**) so that we could
173 include the same ones at different resolutions (see section on data analysis below). We aimed to
174 represent the essential variables in different categories (climate, soil, landscape and practices) and
175 ensure they were not highly correlated (Pearson correlation coefficient < 0.6). We retained mean
176 annual temperature and soil pH, since they are tightly related to floristic composition and richness in
177 agroecosystems (Fried et al., 2008). Landscape and crop diversity were selected as indicators of
178 landscape heterogeneity (Rader et al., 2014; Sirami et al., 2019). Finally, we included the herbicide
179 treatment frequency index, the nitrogen dose applied in fertilizers (within adjacent agricultural fields)
180 and the number of margin management events. These variables have consistently been reported to
181 have a significant effect on field margin communities (Aavik & Liira, 2009; Bassa et al., 2011; Fried et
182 al., 2018).

183 *Data analysis*

184 To analyze the relationships between floristic species richness, composition and environment
185 (including agricultural practices) in relation to spatial scale, we built on two statistical methods, each
186 repeated at the national extent using different resolutions, and then at different spatial extents using
187 the plot resolution. We used Gaussian spatial simultaneous autoregressive models (SAR) with species
188 richness as response variable, to take into account spatial autocorrelation, and used generalized
189 dissimilarity models (GDM) to study species composition while dealing with nonlinear relationships
190 between environmental distance and species turnover (Ferrier et al., 2007).

191 SARs were implemented (package SPDEP, function *errorsarlm*) using a correlated spatial error term,
192 which is added as a predictor and is a function of the spatial neighborhood of the response variable
193 (**Appendix C**) (Cressie, 2015). We can thus model linear relationships that take into account spatial
194 autocorrelation in the data, i.e. the tendency of nearby points to have more similar values than
195 expected by chance. Hereafter, we will refer to spatial structuring as spatial autocorrelation, that can

196 result from an effect of the spatially structured environment or from an internal process of the
197 community (Borcard et al., 2018). Species richness was transformed with a square root to comply with
198 normality. We assessed the residual autocorrelation of each model with a Moran's I test (with a p-
199 value threshold of 0.05) (Thioulouse et al., 2018), based on the same spatial weight matrix included in
200 the models. None of the models displayed significant residual autocorrelation. In order to quantify the
201 importance of each variable and the spatial component, we computed partial regression using the
202 Nagelkerke pseudo-$R^2$ (Lichstein et al., 2002; **Appendix C**).

203 The use of GDMs (R package $_{GDM}$, function *gdm*) to model species composition is appropriate when
204 species turnover rate varies along the environmental gradients and hence when the response is non-
205 linear. The Bray-Curtis dissimilarity among all pairs of plots was modeled as a function of
206 environmental pairwise distance (computed for each factor) and geographical distance (Ferrier et al.,
207 2007). The geographical distances account for the spatial structuring into communities. Since the same
208 plots are used multiple times in the calculation of biological and environmental distances, the
209 environmental table was permuted 500 times to assess variable significance. We then evaluated the
210 importance of each variable in the model with the same procedure as above (partial regressions based
211 on the explained deviance; Maestri et al., 2017).

212 The different analyses detailed in the above sections were reiterated at different spatial scales. The
213 first approach was to increase the study resolution by aggregating data into grid cells. We opted for
214 the following spatial resolutions: 25, 40, 60 and 75 km (**Fig. 1A, Fig SD.1**). Only cells containing at least
215 two plots were retained. Cells for which all plots were less than 5 km apart were also removed to avoid
216 autocorrelation issues that may lead to extreme values, as were cells in the land - sea borders with
217 more than half of their surface covered by water. Overall, this led to some analyses at finer resolutions
218 that contained less grid cells than coarser analyses. Since not all scales have the same number of grid
219 cells or plots by cell (**Table 2**), the potential influence of these variations was investigated by
220 resampling (**Appendix D**). Whenever possible, explanatory data were directly extracted at the scale of

interest (climate, soil and landscape). All other factors were averaged by cell, including the frequency of occurrence by plot. Species richness in each grid cell was obtained by aggregating plot-level species lists. The coordinates of the grid cell centers were used in all spatial analyses. In order to take into consideration the arbitrary position of the grid on the map, we replicated analyses by shifting the grid position three times to check for consistency in analyses.

Lastly, we proceeded with the same analysis at two different extents: national and regional. For this purpose, plots were grouped within ten biogeographical regions standing for the wide pedo-climatic and floristic gradients in France (**Fig. 1B**, based on the VégétalLocal map; Office français de la biodiversité, 2021). The following four regions were dropped because the number of plots was too low (<40): Alps, Corsica, Massif Central and Rhone-Saone-Jura basin.

## Results

### *Influence of agricultural and environmental variables on community structure at different spatial resolutions*

At the plot-level resolution, the predictors explained 27.8% of the variance in species richness. Herbicides and nitrogen dose were the main drivers and explained respectively 1.5 and 1.3% of the total variance in species richness, both having a slight negative effect on richness. With respect to plant community composition, the GDM explained 29.5% of deviance, the main drivers being mean annual temperature (6.9%) and soil pH (1.2%).

With increasing spatial resolution, the relative importance of farming practices decreased in favor of an increased influence of climate and landscape on richness (except at intermediate resolution, **Fig. 2A-E**). Temperature had a positive effect on richness, while soil pH had no significant influence. Crop diversity was the predominant landscape factor at all aggregated scales, showing a consistent positive influence on richness, but only significant at the coarsest resolutions (60-75 km, **Table 3A**). On the

contrary, landscape diversity did not seem to have any impact (**Table 3A**). Both herbicides and nitrogen dose reduced the number of species at the plot-level, but these effects were not robust to the grid and resolution studied (**Table 3A**). Similarly, the weak positive effect of margin management on species richness was mainly apparent at the plot-resolution (**Table 3A**). Richness variation attributed to spatial structure was higher at the plot resolution (11.4%) compared to coarser resolutions where it was non-significant (**Fig. 2A-E**).

With regard to composition, the explanatory power of the models increased at coarser spatial grains (**Fig. SE.1**). Climate and landscape (mainly through crop diversity) together contributed to overall differences in species composition among plots, much more strongly than farming practices and soil at all scales (**Fig. 2F-J**). In contrast to richness, climate had less influence on composition at coarser resolutions while the influence of landscape increased. Fertilization structured the species distribution more strongly at the coarsest resolution (4.3%) than at the finest, for which it was not significant (**Fig. 2F-J, Table 3B**). While herbicides decreased species richness, they did not influence species composition. Also, we observed that the importance of spatial structure was relatively high at all aggregated scales (**Fig. 2F-J**).

*Influence of agricultural and environmental variables on community structure at different spatial extents*

The influence of environmental filters on species richness and composition varied greatly among regions (**Fig. 3**). For example, the high explanatory power of the SAR for the Mediterranean zone (ZM) (approximately 38.8%) contrasted with the lower one for the Armorican Massif (MA) (15.1%).

Some landscape effects emerged as more significant than at the national extent. For example, landscape diversity had an important influence (6.5%) on richness of the northern Paris Basin (BPN), an effect that was not visible at the national extent with all regions confounded (**Table 4A**). Agricultural effects on richness were often more predominant at the regional extent (**Fig. 3A**). The effects of nitrogen fertilization, herbicides and margin management were more clearly revealed at this scale. The

direction of the relationships between richness and predictors remained consistent with analyses at the national level (except for the south-western France (ZSO), which depicted a negative relationship of species richness with temperature, **Table 4A**).

With regard to composition, climatic conditions appeared to have a stronger influence at a national rather than regional extent (**Fig. 3B**). As with richness, new impacts of landscape and practices were highlighted within regions, such as the influence of landscape diversity on composition in ZM (2.2%), and the number of margin management events in ZM (5.6%) and MA (6.9%) (**Fig. 3B**, **Table 4B**).

## Discussion

In line with our initial hypotheses, the effects of agricultural practices on field margin flora, although detected at all resolutions, were more prominent within biogeographic regions. In general terms, herbicides and fertilization were important to explain species richness at the plot-level, whereas fertilization stood out in explaining species composition at coarse resolutions. Conversely, climate and landscape variables always predominated when data were aggregated at coarser resolutions and large (i.e. national) extent. Climate also explained a large percentage of variation in species composition at the plot-level. As the botanical diversity of field margins is currently declining, these results are of great interest to protect these habitats, which sometimes represent the last reservoirs in the most intensive landscapes (Marshall & Moonen, 2002).

### *Influence of agricultural and environmental variables on community structure at different spatial resolutions*

Our results provided evidence that composition was better explained by large-scale agricultural effects, while richness was mostly impacted by local land use intensification. This is consistent with some studies reporting that the effects of agricultural practices on field margin plant communities are at least as important to landscape effects (Bassa et al., 2011; Gabriel et al., 2006; but see Martin et al.,

294 2020). The negative impacts of herbicides and nitrogen on local richness of field margins have already
295 been reported many times (Aavik & Liira, 2009; Fried et al., 2018). Here, nitrogen fertilization affected
296 both richness and composition, while herbicides only had an impact on richness. This is in agreement
297 with Fried et al. (2018), who reported that herbicides decreased species richness, but had no effect on
298 functional composition, as opposed to fertilization. Our results revealed a large-scale effect of nitrogen
299 use, previously evidenced on species richness of natural, semi-natural and agricultural habitats (Billeter
300 et al., 2008; Kleijn et al., 2009). Storkey et al. (2011) demonstrated that large-scale eutrophication is a
301 major explanatory factor of the threat status of arable species in Europe and even more than herbicide
302 use, although the two factors are difficult to disentangle and likely in interaction. However, the
303 importance of this effect on composition and not on richness contrasted with studies conducted so
304 far.

305 The fact that composition was better explained at coarser resolutions, while richness was not (**Fig.**
306 **SE.1**) may be explained by a distinct effect of the aggregation of plots in the grid cells. Composition can
307 be better explained at coarser resolutions because rare species, specialists of particular conditions, can
308 easily be missing at the plot-level but have higher probabilities to be present in larger grid cells that
309 combine several plots. Coarser resolutions also buffer stochastic effects related to the dispersal of
310 generalist species that can attenuate the weight of explanatory variables at the plot-level. However,
311 at the scale of coarser grid cells, richness may depend more on the variability (complementarity) of the
312 practices of each plot included in the cell than on their average values as computed here. While
313 considering only local agricultural effects may be sufficient to explain species richness of field margins,
314 a full understanding of community assembly will only be achieved by including the influence of species
315 pools and their responses to regional intensification.

316 Regarding landscape variables, crop diversity was the best predictive factor of richness and
317 composition and was particularly determinant at large-scales. While the response of plant species
318 richness to Shannon crop diversity is inconsistent among studies and dependent on the level of

intensification (Martin et al., 2020; Sirami et al., 2019), we found here a consistently positive effect regardless of the scale. This can be viewed as landscape complementation for species that are specialists of a single crop and not encountered in any other type of habitat (Storkey et al., 2011). Another explanation would be that crop diversity is negatively related to field size (Martin et al., 2020), and this latter might have an additional effect on richness (Fahrig et al., 2015). In contrast, our analysis did not reveal any effects of habitat diversity in the landscape on richness, but an effect on composition and only at the plot-level. Although a diverse landscape does not necessarily support more species, it may favor functionally more diverse communities (dispersing from different neighboring habitats), supporting the idea that species richness alone cannot capture all aspects of biodiversity (Aavik et al., 2008; Fried et al., 2018). The effect of crop diversity on composition increased with resolution, while this was not the case for landscape diversity, likely because landscapes became more homogeneous in terms of habitat diversity, while they still remained different in terms of crops (**Fig. SF.1**).

*Influence of agricultural and environmental variables on community structure at different spatial extents*

Our results pointed to strong regional specificities, underlining complex interactions between local and regional scales. For example, the influence of landscape diversity on richness was very high in the BPN, a region mainly composed of large cereal open-fields (**Fig. SF.2-3**). The direction of this effect was unexpected, since landscape diversity decreased the number of species in field margins. It is possible that diverse landscapes have fewer croplands and more natural habitats, so that species adapted to agricultural disturbances are less prevalent in the landscape species pool. Given the high level of intensification in this region, the species from natural habitats are too vulnerable to establish locally. The discrepancy between the low level of landscape disturbance and the high level of local disturbance ultimately results in a local loss of species. This apparently counter-intuitive finding could thus be explained by interactions between the regional pool and local conditions (Cornell & Harrison, 2014; Myers & Harms, 2009). Likewise, the detrimental effect of nitrogen fertilization on richness was only

344 significant in the Mediterranean Zone (ZM). In this region, soils had low nitrogen content (**Fig. SF.3**),
345 and the species pool is mostly composed of stress-tolerant species adapted to nutrient-poor soil
346 conditions. Due to its regional composition, Mediterranean flora would thus be more sensitive to soil
347 enrichment. This supports the results of Kleijn et al. (2009) who concluded that the impact of nitrogen
348 is greater in less intensive regions. Biogeographic regions differed not only in their agricultural impacts
349 but also in the diversity of their regional pools. ZM and ZSO were slightly more diverse than MA (**Fig.**
350 **SF.3**), which reflected in their percentages of total explained richness. When species richness is higher,
351 species turnover between plots also has the potential to be higher, thereby providing new insights into
352 some agricultural effects. Clarifying regional specificities should thus be a strong priority for future
353 agroecological studies, as it paves the way for a deeper comprehension of interactions among scales,
354 environmental and agricultural factors.

355 *Limits and implications for upcoming studies and management in agricultural context*

356 Our study presented a number of shortcomings that needed to be considered. First, at coarser
357 resolutions and at the regional extent, the number of units available for analysis decreased with
358 respect to the plot-level at the national scale. This constrained our analysis to a limited number of
359 variables, forcing us to prioritize over other factors that are also recognized to have an influence on
360 field margin vegetation (e.g. rainfall, soil texture, Fried et al., 2008). Nevertheless, our purpose was
361 not to determine the most influential descriptors at all scales, but rather to assess the congruence of
362 the results by considering the same set of variables at different spatial scales. Furthermore, we tested
363 the bias that emerged from averaging over coarser scales on different number of plots by cell by
364 bootstrapping and observed that it caused little variation of the model parameters (**Fig. SD.2**). We are
365 therefore fairly confident that our results are robust in this respect. Another potential shortcoming
366 was that the means computed within aggregated grid cells might not fully represent the regional pool
367 or agricultural region. Indeed, the monitoring plots were stratified to represent the main crops and
368 practices at the national level and not at the landscape or regional level. Checking the

representativeness of the plots with the regional context is thus key to assess the relevance of the results.

Our results have not only methodological but also practical implications for crop management. It turned out that crop diversity had a major positive impact on plant diversity in field margins, whose importance in public policies has just begun to be recognized (Galán-Martín et al., 2015). Promoting a wide range of crops at the landscape level could slow the decline of some highly specialized arable plant species, particularly in landscapes with large semi-natural cover including field margins (Sirami et al., 2019). In this respect, the obligation of crop rotation as part of the enhanced conditionality of subsidies in the new CAP in Europe can be seen as very beneficial for field margins. Fertilization significantly altered floristic assemblages and is more impactful on a large scale than herbicides, which is of major interest for national agricultural policies. Finally, measures should also be adapted to each region. Indeed, our findings suggest that some decisions could be very costly in some regions and provide little benefit, while less effort would yield better outcomes in another region (Kleijn et al., 2009). For instance, a drastic reduction of fertilizers in highly intensive regions mainly composed of nitrophilous species will have little impact on plant communities of field margins if this action is not coupled with landscape restoration. In contrast, diversified areas will be more susceptible to respond to less costly mitigation measures and are of higher conservation concern (Stevens et al., 2010). In conclusion, we encourage agricultural stakeholders and scientists involved in monitoring programs to further evaluate the changes in field margin flora and its protection measures across different spatial scales, and implement regulatory measures that incorporate landscape-level management planning adapted to each biogeographic / agricultural region.

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**Appendix A-F. Supplementary data**

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

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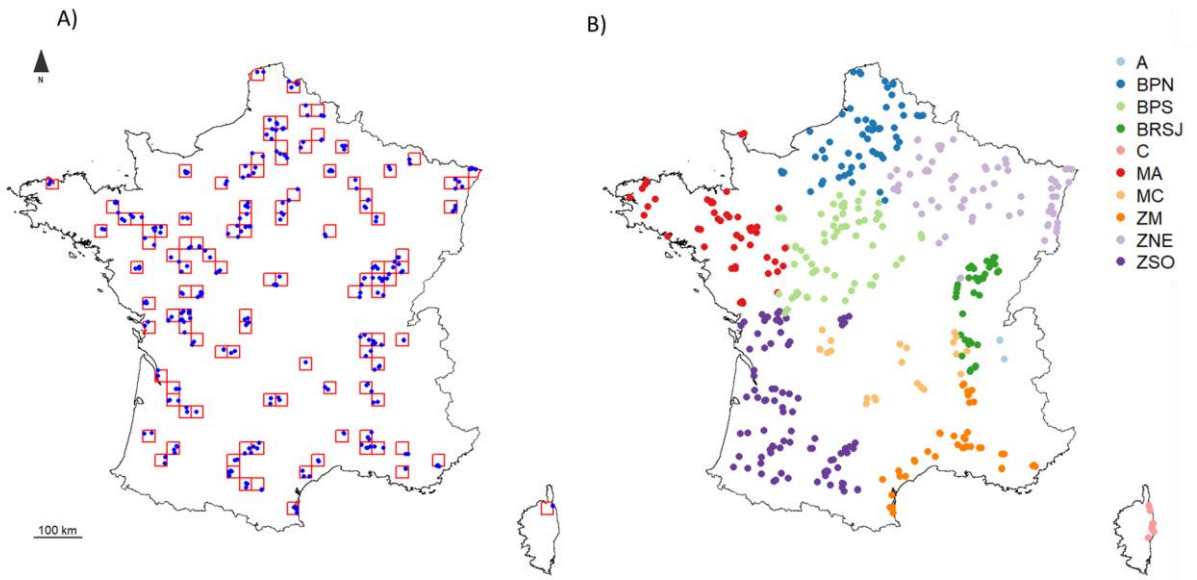
558 **Figures**




559

560 **Fig. 1.** Distribution maps of the field margins (colored points) surveyed in France distributed in (A) a
561 grid of 25 km and (B) in different biogeographic regions. Only cells selected for analyses are presented
562 in A). A = « Alps », BPN = « Northern Paris Basin », BPS = « Southern Paris Basin », BRSJ = « Rhone-
563 Saone-Jura Basin », C = « Corsica », MA = « Armorican Massif », MC = « Massif Central », ZM =
564 « Mediterranean Zone », ZNE = « North-Eastern France » and ZSO = « South-Western France ». The
565 regions C, A, MC and BRSJ have been removed because of their small number of plots.

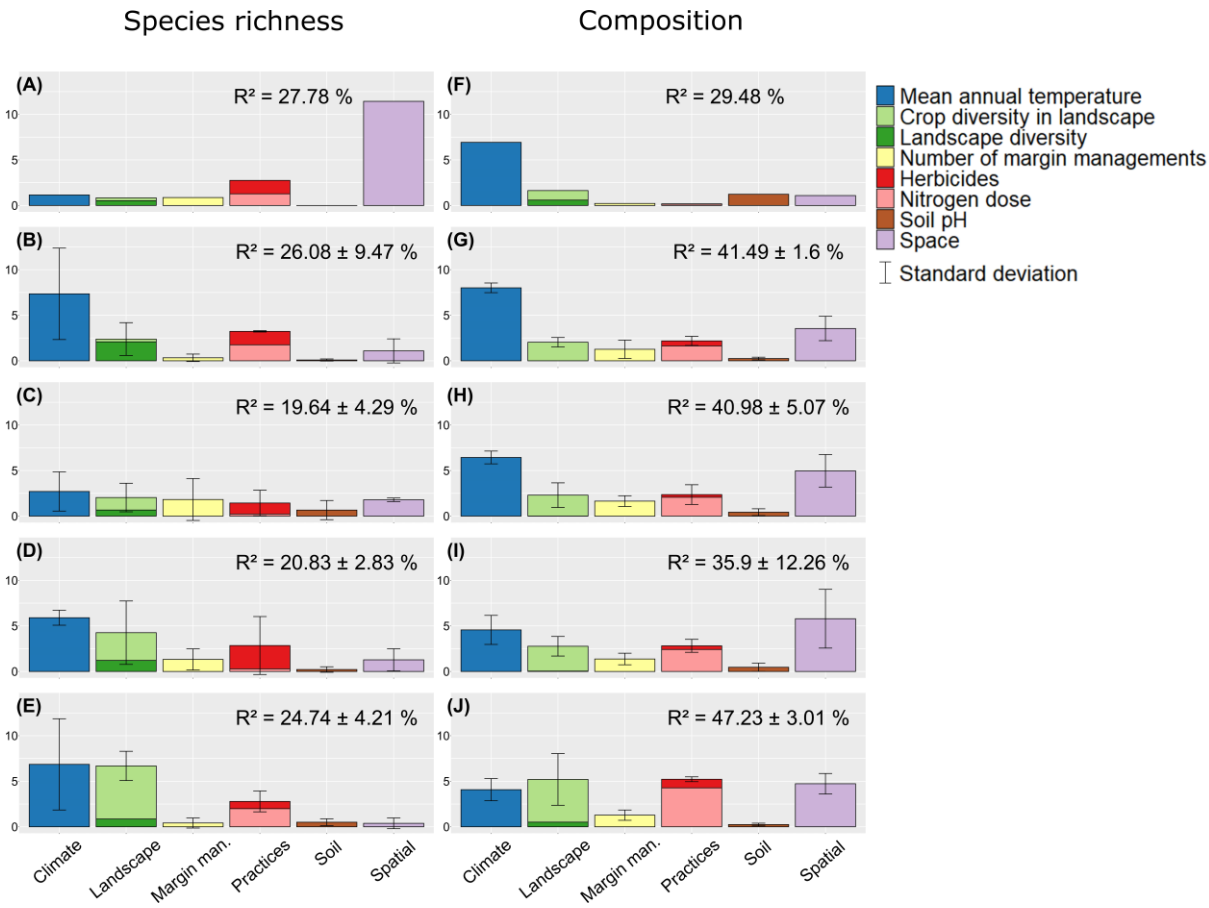



**Fig. 2.** Percentage of explained variance of species richness (SAR) and composition (GDM) by each factor for each spatial resolution. (A, F) 0 km; (B, G) 25 km; (C, H) 40 km; (D, I) 60 km; (E, J) 75 km. Standard deviations are computed from the three resamplings of grids. Percentages of explained variance are reported in **Table SE.1**.

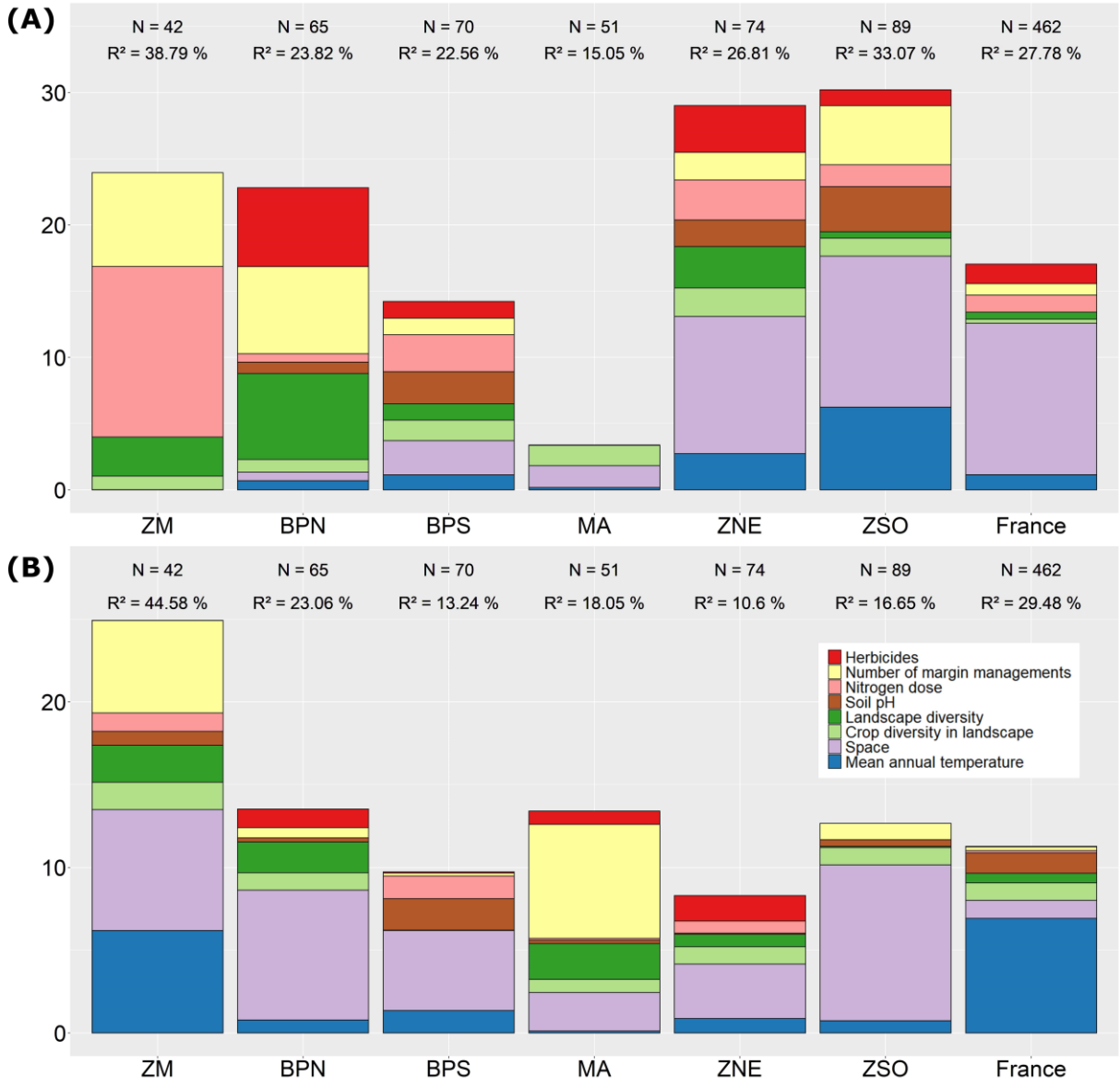



**Fig. 3.** Percentage of explained variance for (A) richness (SAR) and (B) composition (GDM) for each biogeographic region and national extent. Regions are ordered by area from left to right. Percentages of explained variance are reported in **Table SE.2**.

575 **Tables**

576 **Table 1.** Description of explanatory factors used in analyses, with their abbreviations and scale of

577 computation. The variables computed by observation and then averaged by plot are underlined.

| Factors | Abbreviations | Units | Calculation | Type of factor | Data source | Scale of computation |
|---|---|---|---|---|---|---|
| **Mean annual temperature** | TEMP | °C x 10 | | Climate | Chelsa Climate | 1 km |
| **Soil pH (water)** | PH | pH x 10 | | Soil | SoilGrids | 250 m |
| **Shannon's habitat diversity index** | SHDI | | $-\sum_{i=1}^{n} p_i \ln p_i$ With $p_i$ the proportion of the habitat i in the landscape | Landscape | OSO | 1 km |
| **<u>Shannon's crop diversity index</u>** | SHDI_C | | $-\sum_{i=1}^{n} p_i \ln p_i$ With $p_i$ the proportion of crop i in the agricultural area | Landscape | RPG | 1 km |
| **<u>Dose of nitrogen (fertilization and amendments)</u>** | N_DOSE | kg/ha | $\frac{Quantity \times N\ of\ the\ formulation}{100}$ | Agricultural practices | 500-ENI | Plot |
| **<u>Treatment Frequency Index of herbicides</u>** | HERB | | $\frac{Applied\ dose\ of\ used\ products \times treated\ area}{certified\ dose \times plot\ area}$ For herbicides in vineyards, the treated area accounts for one third of the plot area if the treatment is done on the rows and two thirds if it is done on the inter-rows. In case of missing information, the treatment is supposed to involves only the rows (i.e. the most frequent practice). | Agricultural practices | 500-ENI | Plot |
| **<u>Number of management events</u>** | MAN | | All types of management (mowing, grazing…) | Margin management | 500-ENI | Field margin |
| **Spatial structure** | SPAT | m (Lambert 93) | Based on geographical coordinates, see **Appendix C** for more details | Spatial | 500-ENI | Plot |

578

**Table 2.** Details concerning the sampling for each resolution. Means and standard deviations were computed based on the three positions of grids at each resolution.

| **Spatial resolution (km)** | **0** | **25** | **40** | **60** | **75** |
|---|---|---|---|---|---|
| **Mean number of plots by cell** (rounded to the hundredth) | | 2,68 ± 0,07 | 3,30 ± 0,09 | 4,63 ± 0,09 | 5,78 ± 0,07 |
| **Mean number of plots** (rounded to the unit) | 462 | 306 ± 10 | 387 ± 9 | 418 ± 12 | 428 ± 1 |
| **Mean number of cells** (rounded to the unit) | | 87 ± 7 | 105 ± 3 | 86± 2 | 71 ± 2 |

**Table 3.** Significance of each predictor (in row) for each spatial resolution (in column, in km). For species richness in A), the direction of the relationship is indicated by +/-. The color gradient indicates the number of times the predictor was significant over the three grid shifts.

**A) Species richness**

| | 0 | 25 | 40 | 60 | 75 |
|---|---|---|---|---|---|
| **Temperature** | + | + | + | + | + |
| **Ph** | + | - | - | - | - |
| **Landscape diversity** | - | - | - | - | - |
| **Crop diversity** | + | + | + | + | + |
| **Herbicides** | - | - | - | - | - |
| **Nitrogen dose** | - | - | - | + | - |
| **Margin management** | + | + | + | + | + |
| **Spatial structure** | | | | | |

Significant in all grids
Significant in 2 grids
Significant in 1 grid
Never significant

**B) Composition**

| | 0 | 25 | 40 | 60 | 75 |
|---|---|---|---|---|---|
| **Temperature** | | | | | |
| **Ph** | | | | | |
| **Landscape diversity** | | | | | |
| **Crop diversity** | | | | | |
| **Herbicides** | | | | | |
| **Nitrogen dose** | | | | | |
| **Margin management** | | | | | |
| **Spatial structure** | | | | | |

**Table 4.** Significance of each predictor (in row) for each biogeographic region and for national extent (in column, see **Fig. 1** for abbreviations of region names). For species richness in A), the direction of the relationship is indicated by +/-. Cells are colored in green when the relationship is significant.

**A) Species richness**

| | BPN | BPS | MA | ZM | ZNE | ZSO | France |
|---|---|---|---|---|---|---|---|
| **Temperature** | + | + | + | - | + | - | + |
| **Ph** | - | + | - | + | + | - | + |
| **Landscape diversity** | - | - | - | - | + | + | - |
| **Crop diversity** | + | + | + | + | + | + | + |
| **Herbicides** | - | - | - | - | - | - | - |
| **Nitrogen dose** | - | - | - | - | - | - | - |
| **Margin management** | + | + | - | + | + | + | + |
| **Spatial structure** | | | | | | | |

**B) Composition**

| | BPN | BPS | MA | ZM | ZNE | ZSO | France |
|---|---|---|---|---|---|---|---|
| **Temperature** | | | | | | | |
| **Ph** | | | | | | | |
| **Landscape diversity** | | | | | | | |
| **Crop diversity** | | | | | | | |
| **Herbicides** | | | | | | | |
| **Nitrogen dose** | | | | | | | |
| **Margin management** | | | | | | | |
| **Spatial structure** | | | | | | | |