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Abstract

Understanding the relative importance of spatial, temporal variables, environmental conditions and management practices as filters for weed assemblages is essential to promote biodiversity in agrosystems. In this study, we used a unique data set covering 46 vineyard plots in France (Champagne, Beaujolais and Languedoc winegrowing areas) with 883 flora surveys performed between 2006 and 2012. The three objectives of the present study were: (1) to characterize weed communities composition and structure (richness and abundance) in vineyards from three traditional winegrowing areas in France; (2) to evaluate the relative importance of spatial, temporal variables, environmental conditions and management practices on weed species composition and structure; (3) to determine whether or not weed composition and structure are affected by the same factors. The results of the study revealed that *season* (including timing of management practices) was the most important filter for weed communities in vineyards, opposing in each plot a spring community and a summer-autumn community. Furthermore, spatial variations between regions (latitude), soil types (pH) and inter-annual variations (2006 to 2012) were also seen to have a strong effect on species turnover. Farming practices explained an overall low variation in composition of weed communities but some species showed a high and consistent fit to contrasting practices. For example, herbicide applications (mostly glyphosate) promoted some species such as *Malva sylvestris* and *Sorghum halepense* whereas tillage in inter-rows selected typical annual weeds such as *Cerastium glomeratum* and *Galium aparine*. Farming practices had a much higher influence on species richness and abundance with equal effect of both herbicides and soil tillage for controlling weed species richness and abundance in inter-rows, but stronger effects of herbicides were observed on species abundance in the rows. Tillage along the rows and a combination of mowing and tillage along the inter-rows were associated to the highest level of weed richness and abundance. Our study suggests that grapevine growers have a limited ability to influence species composition (mostly determined by abiotic factors) but their choice of management can modulate the level of weed richness and abundance. Our results will contribute to guide farmers towards more integrated management practices, ensuring both an optimal management

of the spontaneous vegetation in vineyards and allowing this vegetation to provide various ecosystem services.

Key words: weed community; French vineyards; pedoclimate; herbicides; tillage; season.

1. Introduction

Promoting biodiversity in agrosystems, combined with a reduced dependence on pesticides has become a key issue in agriculture over recent years (Altieri, 1999; Feledyn-Szewczyk *et al.*, 2016). Among taxa associated with cultivated land, weed species may play an important role in maintaining biodiversity, as long as their adverse effects on crop production are limited (Marshall *et al.*, 2003; Storkey, 2006). In order to achieve this goal, a thorough understanding of the relative importance of biotic, abiotic and anthropogenic factors, acting as filters for species assemblages in weed communities is needed (Belyea and Lancaster, 1999). Specifically, improving the knowledge about how environmental factors and management practices influence the variations of weed community composition and structure is an essential first stage in developing alternative weed control management practices at both the field and the landscape scales (Michez and Guillerm, 1984). Vineyards are an ideal study model as flora management practices have become more diversified in recent years (Gago *et al.*, 2007). Before the 1970s, vegetation in- and between vine rows was traditionally managed by soil tillage (Barralis *et al.*, 1983; Maillet, 1992). The generalized use of chemical weed control then induced important changes in composition and richness of weed communities between the 1970s and the 1990s (Barralis *et al.*, 1983; Maillet, 1992; Monteiro *et al.*, 2008). Herbicide application has caused shifts in weed flora composition due to the progressive removal of herbicide sensitive species that has led to an overall reduced species richness and to the progressive increase of some tolerant species (physiologically) or species able to escape (temporally) the treatments (Dastgheib and Frampton, 2000; Baumgartner *et al.*, 2007; Gago *et al.*, 2007; Sanguankeo *et al.*, 2009). Besides the effect of herbicides per se, the timing of their application can also shift the weed community, especially if applied when weeds are less susceptible to chemical control (Baumgartner *et al.*, 2007). Nowadays, herbicide treatments in vineyards are usually restricted to the vine rows (which represents from 10 to 15% of the total vineyard surface area), and can involve pre-emergence and/or post-emergence herbicides (Dastgheib and Frampton, 2000). Frequently tilled rows and inter-rows represent highly disturbed habitats which often harbour communities with a small number of species but with a large variability in species abundance (Wilmanns, 1989, 1993; Kazakou *et al.*, 2016). More recently, weed control in vineyards is being provided by establishing a cover crop (Baumgartner *et al.*, 2008). Besides their effect on weeds, cover-crops in vineyards are primarily used as leverage to confront various agronomic issues such as poor soil organic carbon levels, erosion and fertility losses (Salome et al., 2016, Garcia et al., 2018). Sometimes, spontaneous vegetation can be preferred as it provides a low cost intercropping option and may offer interesting trade-offs between ecosystem services (Kazakou et al., 2016). Whatever the case (spontaneous vegetation or cover crop), the vegetation is then mown. In conclusion, three main weed management methods co-exist in vineyards: soil tillage, herbicide applications and mowing. In addition to farming practices, the weed composition of vineyards can be affected by environmental factors such as soil or climate, related to species ecological preferences. Weed flora is also characterized by a seasonal dynamic, related to the differences in species requirements for temperature and precipitation to germinate and complete their life cycle.

A study of vineyards in Central Europe showed that management practices were the most important factor affecting weed species composition in a vineyard, nevertheless, seasonal dynamics of the weed community were also remarkable (Lososová *et al.*, 2003). Most of the previous studies have identified management practices as the main factor affecting weed community variation but it should be noted that so far, data concerning vineyard weed community variation exist only at local scales without taking into account both spatial and temporal variations. In annual crops this kind of large-scale analysis was realized by Fried *et al.* (2008) using data from approximately 700 fields in France in order to determine the respective importance of environmental factors *versus* management practices on weed species richness and composition. The authors found that major variations in species composition were mainly associated with the current crop type and the preceding crop type followed by large-scale environmental gradients of soil pH and rainfall which explained more variations than soil tillage practices.

It is essential to develop similar large-scale analyses in vineyards as selection of the most appropriate soil management practices for each vineyard must consider factors like soil type, climatic conditions and temporal complementarity between vines and weeds for resource acquisition in order to avoid potential competition (Celette *et al.*, 2008; Ripoche *et al.*, 2010; Guerra and Steenwerth, 2011). In the present study we used a unique data set from a large number of vineyards in France (Champagne, Beaujolais and Languedoc) in order to analyze temporal (seasonal and inter-annual), spatial (row and inter-row) and environmental variations of weed richness and composition.

The objectives of the present study are: (1) to characterize weed communities composition and structure (richness and abundance) in vineyards from three traditional winegrowing areas in France; (2) to evaluate the relative importance of different factors (spatial, temporal variables, environmental conditions and management practices) on weed species composition and structure; (3) to analyze if weed composition and structure are affected by the same environmental factors and farming practices, despite the different profiles of winegrowing area.

2. Material and methods

2.1. Study regions

As part of the Biovigilance Flore national arable weed survey conducted in France, mainly on annual crops (see Fried *et al.* (2008)), specific surveys were also performed in vineyards between 2006 and 2012. The vineyard vegetation surveys covered three main wine production regions: i) Languedoc, ii) Beaujolais and northern Rhône valley and iii) Champagne, covering a diversity of pedo-climatic conditions and management practices from the south to the north of France (Figure 1). Languedoc has a Mediterranean climate with a mean annual temperature of 14.1°C, and 686 mm annual rainfall in the surveyed plots, based on WorldClim database (Hijmans *et al.*, 2005). The Treatment Frequency Index (TFI) for herbicides, i.e. the cumulative ratio of the dose applied to the recommended dose, for all treatments applied during the growing season (Halberg, 1999), ranged between 0.4 in 2006 to 0.5 in 2013 (Pujol, 2017) with a mean of 0.48 in our surveyed plots. Permanent or temporary sown or spontaneous cover crops in the inter-rows are only observed in 29% of the Languedoc vineyards (Agreste, 2009) but in only 10.2% of our surveyed plots in this region. Beaujolais and northern Rhone valley have a semi-continental climate with temperate influences, with a mean annual temperature of 11.4°C and 776 mm annual rainfall in the surveyed plots. The TFI for herbicides ranged between 1.1 in 2006 to 1.2 in 2010 (Pujol, 2017), with a mean of 1.38 in our surveyed plots. In this region, 42% of the vineyards display a cover crop in the inter-rows (Agreste, 2009) with 40.6% of the surveyed plots with cover crops. Finally Champagne has a continental climate with oceanic influences, with a mean annual temperature of 10.1°C and 657 mm annual rainfall. The TFI for herbicides ranged between 1.2 in 2010 to 1.4 in 2013 (Pujol, 2017) with 1.24 on the rows of our surveyed plots. Only 26% of the vineyards have cover crops in this region (Agreste, 2009) but 62.5% in our surveyed plots. The Biovigilance sampling represented the mean level of herbicide treatments well in each region, however in terms of cover crops, Biovigilance was only representative in Beaujolais and the northern Rhone valley while cover crops were under-represented in Languedoc (10.2% against 29%) and over-represented in Champagne (62.5% against 26%).

2.2. Vegetation surveys

Forty-six vineyard plots were surveyed among which 18 plots were located in Languedoc, 18 plots in the Beaujolais and northern Rhone Valley and 10 plots in Champagne (Table 1). In each of the 46 vineyard plots, from 1 to 36 surveys were performed between 2006 and 2012 (Table 1). In each vineyard plot, a quadrat of 2000 m² was surveyed. Two different areas, rows (R) and inter-rows (IR), were distinguished within the 2000 m² quadrat due to the usually different management practices applied in these areas (Table 2). Each of these two areas was surveyed at two or three different periods of the year: in early winter, in spring, in summer and/or in autumn, in order to integrate the seasonal variability of the flora (except for the first year of the survey where only autumnal surveys were done, see Table 1). In the present study, we used 883 samplings out of 1060, including 449 samplings on the grapevine row and 434 samplings on the grapevine inter-row (Table 1), we discarded 16 samplings without indication of sampling area (rows or inter-rows) and 161 samplings in control plots with no herbicide applications (only in the Champagne area).

The abundance of each species was estimated using five abundance classes as developed in (Barralis, 1976). This method takes into account the number of individuals per m^2, using the following scale intervals: ‘1’ less than 1 individual/m^2 ; ‘2’ 1–2 individuals/m^2 ; ‘3’ 3–20 individuals/m^2 ; ‘4’ 21–50 individuals/m^2 ; ‘5’ more than 50 individuals/m^2. At the community-level, we calculated species richness (S), the number of species in a sampling unit, and total abundance that we defined as the sum of the abundance of each species present in a sampling unit. For this purpose, we transformed the abundance class into a quantitative scale using the median of the range of density associated with each abundance class (“1”: 0.5 ind/m^2; “2: 1.5 ind/m^2; “3”: 11.5 ind/m^2; “4”: 35.5 ind/m^2 and “5”: 75 ind/m^2).

2.3. Explanatory variables

Explanatory variables can be grouped into four types: i) spatial variables, ii) environmental conditions, iii) management practices and iv) temporal variables. To account for the spatial component of variability (see Borcard *et al*. (1992)), spatial variables were constructed by using longitudinal x and latitudinal y coordinates of the studied vineyards. First (x, y), second (x^2, y^2) and third (x^3,y^3) order terms of the spatial coordinates were created for the analyses, along with interaction terms (xy^2, x^2y). Second and third order terms were included in order to account for more complex, patchy spatial patterns in community composition or diversity to be detected (Legendre and Legendre, 1998). Detailed soil analyses were only available for 14 plots (30% of the plots). Therefore, we retrieved 8 factors from the Soilgrids dataset at 250m resolution (Hengl *et al.*, 2017) based on the coordinates of the vineyard plots. There was a high correlation between available soil parameters and those estimated from the Soilgrids dataset (e.g. pH, r=0.86). We performed a principal component analysis (PCA) on the 7 soil variables (which included : soil organic carbon content, pH index measured in water solution, bulk density (fine earth) in kg per cubic meter, CEC (Cation Exchange Capacity of soil), weight percentage of the sand particles (0.05–2 mm), weight percentage of the silt particles (0.0002–0.05 mm), weight percentage of the clay particles (<0.0002 mm), volumetric percentage of coarse fragments (>2 mm)) and extracted the three first axes, which represented 82% of total inertia and were associated to a gradient of soil pH on axis 1 and to soil texture gradient on axis 2 and 3, opposing sandy soils to silty soils on axis 2 and clay soils to sandy soils on axis 3, respectively (see Appendix S1 for the detail outputs of the PCA). Winegrowers were asked about vegetation management along the rows (R) and the inter-rows (IR) for the years covered by the survey. Three main types of management practices can be distinguished: mowing (including crushing), soil tillage and chemical treatments with herbicides. The main types of soil tillage implemented in our survey included “rasette” (25%), rotary inter-vine hoes (15%) and mouldboard plough (8%), with a typical working depth between 5-15 cm. Glyphosate represented the main herbicide used (61.2%) followed by aminotriazole (13.3%) and glufosinate (8.5%). Table 2 summarizes the main trend in the management practices in each region. Different management practices or combinations are employed on the R and the IR and management practices differ also on the same vineyard plot over the years. Thus, to summarize management practices of each year in each vineyard, we used the number of mowings, of soil tillings and of herbicide treatments per year. We also distinguished management practice types and the different combinations of management practices applied to the rows and to the inter-rows: 1- herbicides only (H), 2- soil tillage only (T), 3-mix of herbicides and soil tillage (HT), 4- mix of soil tillage and mowing (TM). Temporal variations in vineyard flora were assessed with two variables: the date of the vegetation sampling (Julian Day) that account for seasonal variation in weed flora (hereafter called ‘Season’) and the year which could account for particular weather conditions. Table 3 gives the units and ranges of the raw variables used in the study.

2.4. Data analysis

Frequency of occurrence of species was compared between the rows and the inter-rows using a fidelity measurement, which reflects the concentration of species occurrence in different habitats (Chytrý *et al.*, 2002). We used the phi coefficient of association $\Phi = \frac{N.n_p - n.N_p}{\sqrt{n.N_p.(N-n).(N-N_p)}}$

with N the total number of samples used (883), Np, the number of samples in the rows (449), n, the number of occurrences of the species in the whole dataset and np the number of occurrences of the species in the rows. This index ranged from -1 (species associated to inter-rows) to +1 (species associated to rows). For the three different regions, we also computed species ranking based on their frequency of occurrence in the vineyard plots. In this latter case, for the sake of simplicity we did not distinguish between rows and inter-rows (i.e., a species is considered to occur in a vineyard plot as long as it is present in either the row or the inter-row).

To analyze the relationship between explanatory variables and vegetation composition, we used a constrained ordination method that was applied separately on the two areas (rows and inter-rows). Before analysis, species abundance data were square-rooted. An indirect model (Detrended Correspondence Analysis, DCA) was first used to decide whether to use a linear or a unimodal approximation (Ter Braak and Smilauer, 2002; Lepš and Šmilauer, 2003). These DCA revealed that the rate of turnover of plant taxa across the sites on the first axis of variation was such that a unimodal model assumption would be more appropriate than a linear model assumption (DCA axis 1 length = 4.43 in the inter-rows, DCA axis 1 length = 4.43 in the rows). Therefore, Canonical Correspondence Analysis (CCA) was undertaken between the vegetation assemblage data and the 16 explanatory variables. Collinearity issues were checked with a variation inflation factor (VIF) with an initial CCA including all 16 explanatory variables. VIF values of 10 or higher are usually interpreted as revealing severe multicollinearity issues (Hair *et al.*, 2006). At this step, three variables with VIF > 10 were removed (x^3, y^2, y^3) for both row and inter-row datasets. Correlation among the 13 remaining variables can be visualized in Appendix S2. We further reduced the number of explanatory variables by performing a backward and a forward selection of explanatory variables based on *P*-value using function ordistep of package vegan (Oksanen *et al.*, 2017).

We then compared the gross and net effects of each explanatory variable, following the methodology described in Lososová *et al.* (2004). The gross effects represented the variation explained by a ’univariate’ CCA containing the predictor of interest as the only explanatory variable. The net effect of each particular variable after partitioning out the effect shared with the other explanatory variables (also called conditionals) was tested with a partial CCA (pCCA). We extracted the explained variance and the adjusted R-squared for models of both gross and net effects of each variable retained in the reduced models. In models of net effects, model fit was also assessed by the F-value for which a type I error rate was estimated using 999 permutation tests of the constrained axis. The importance of each explanatory variable was ranked using the values of the pCCA (i.e. net effect) models. Subsequently, we identified the 10 species with the highest fit for the best explanatory variable of each group of variables (i.e., spatial, temporal, soil and management). Species fit on the constrained ordination axes was calculated using the 'goodness' function of the vegan package.

We first compared species richness and total abundance on the rows and on the inter-rows according to the nature of the management practices applied (1-herbicides only, 2- soil tillage only, 3- mix of herbicides and soil tillage, 4- mix of mowing and soil tillage) using Kruskal-Wallis tests and dedicated post-hoc tests to determine pairwise differences among treatments. Then, in order to achieve a more general understanding of the variation in plant species richness and in the total abundance of plant per plot, we developed linear mixed-models. To deal with the non-independence of the residuals for each plot due to the repeated surveys on the same plots, we consider the identity of the plots as a random effect on the intercept. All other variables were considered as fixed factors. All explanatory variables were standardized before analysis. We performed a backward elimination of non-significant terms of linear mixed effects models using the function step of the lmerTest package (Kuznetsova *et al.*, 2015). Residuals of the reduced models were checked with Shapiro-Wilk test and visually inspected to detect trends that could bias estimates. Species richness was therefore square-rooted for both the row and the inter-row datasets, while we used the fourth and the sixth root of total abundance for inter-rows and rows, respectively. Collinearity issues were checked with VIF. Standardized effect size were computed with function sjp.lmer of package sjPlot (Lüdecke, 2017). All statistical analyses were performed using R 3.4.2 (R Development Core Team, 2017).

3. Results

Across the 883 surveys from 46 vineyard plots (in both rows and inter-rows), a total of 234 species were recorded of which 56 were found in the three winegrowing regions. The ten most frequent species (based on the 883 samples) included: *Convolvulus arvensis* (45.3%), *Cirsium arvense* (38.5%), *Senecio vulgaris* (37.0%), *Diplotaxis erucoides* (30.4%), *Geranium rotundifolium* (27.7%), *Erigeron canadensis* (25.4%), *Taraxacum officinale* (24.5%), *Crepis sancta* (24.5%), *Lactuca serriola* (21.3%) and *Sonchus oleraceus* (20.8%). Appendix S3 gives the 30 most frequent species with their detailed frequency in the rows and the inter-rows, as well as their frequency and rank in the three regions and their status (native/alien). Some species such as *Convolvulus arvensis*, *Senecio vulgaris*, *Cirsium arvense* and *Geranium rotundifolium* were widespread in all three regions while the top ranked species (based on frequency) in each regions differed sometimes markedly with *Diplotaxis erucoides* and *Sonchus oleraceus* in Languedoc, *Erigeron canadensis* and *Veronica persica* in the Rhone valley and *Taraxacum officinale* and *Poa annua* in Champagne (Appendix S3). The vineyard flora was composed of 85% native species, 6% archaeophytes (*i.e.* alien species introduced before 1500) and 8% neophytes (i.e. alien species introduced after 1500). The most frequent neophytes included *Erigeron canadensis*, *Crepis sancta* and *Veronica persica* while *Papaver rhoeas* was the most frequent archaeophyte. The mean relative abundance of alien species (archaeophytes + neophytes) at the 2000m² quadrat scale varied from 8% in Champagne to 24% in Rhone valley and 14% in Languedoc.

Most species (79%) are found in both rows and inter-rows with only 20 (9%) and 29 (12%) species only present in the rows or in the inter-rows, respectively. The fidelity index to the rows ranged between 0.197 for *Rubia peregrina* (the species most associated to the rows) and -0.160 for *Trifolium repens* (the species most associated to the inter-rows). Among common species, *Diplotaxis erucoides* (-0.129), *Poa annua* (-0.101), *Plantago lanceolata* (-0.076) and *Taraxacum officinale* (-0.073) were more frequent in the inter-rows while *Convolvulus arvensis* was more frequent in the rows (0.080). Globally the range of values of fidelity to the rows (-0.160, 0.197) compared to maximal potential values (-1, 1) showed that species are mostly present in both areas.

3.1. Factors affecting weed community composition

For the grapevine inter-rows, the selection procedure removed two variables: number of mowings and x^2y. The reduced model with 11 variables explained 16.69% of total inertia against 17.32% for the full model. The amount of variation in species composition explained by the net effects of particular variables, as detected by partial CCAs (Table 4), was highest for season and decreased first through latitudinal (y) and longitudinal (x^2) spatial variables, second through soil pH and year, and was lowest for management variables, with the number of soil tillings explaining the highest variations among management practices. The first two CCA axes explained 6.04% and 2.97% respectively. On CCA axis 1, weed species composition was mainly discriminated according to latitude (-0.977) and soil pH (0.728) and secondly according to longitude (-0.639), interaction between longitude and latitude (xy^2, -0.480), and the proportion of silt (-0.608, Figure 2a). Species negatively associated with axis 1 (*Malva sylvestris*, *Calendula arvensis* or *Diplotaxis erucoides*) were associated to the plots located in southern France in the Languedoc vineyard, on basic clay soils while species characteristics of Champagne, on more silty and neutral soils were positively associated to CCA axis 1, e.g. *Poa annua*, *Taraxacum officinale*, or *Mercurialis annua* (Figure 2a). The second axis was to a very large degree dependent on sampling date (-0.813, with early samplings on the positive loadings) and to a lesser extent to longitude (0.316), soil pH (-0.297), percent of silt (-0.293) and the number of soil tillings (-0.249). Species with early life cycles, typical to early spring are on positive loadings (*Crepis sancta*, *Cardamine hirsuta*, *Capsella bursa pastoris*) while summer therophytes are on positive loadings (*Digitaria sanguinalis*, *Heliotropium europaeum*, *Portulaca olearacea*, Figure 2a).

For the grapevine rows, the selection procedure kept all 12 initial variables and 16.07% of the total inertia was explained. As for the inter-rows, the amount of variation in species composition in grapevine row vegetation which was explained by the net effects of particular variables is highest for season and decreased first through latitude, second through longitude and soil texture (sand versus clay) and management variables, and is lowest for year (Table 4). The first two CCA axes showed 5.06% and 2.91% respectively. Similarly to the CCA analysis for inter-row vegetation, the row vegetation was discriminated on CCA axis 1 according to the spatial variables (latitude (-0.934), longitude (-0.794) and their interactions) as well as soil pH (0.817, Figure 3b). This first axis was also constrained by the number of herbicide treatments (-0.531). *Diplotaxis erucoides*, *Avena sterilis* and *Sonchus oleraceus* were associated to Languedoc region on basic clay soils with no or few herbicide treatments on the rows, while *Poa annua*, *Lamium purpureum* and *Anisantha sterilis* were associated to more acidic, silt loam or sandy loam soils with a higher number of chemical treatments on the rows. The second CCA axis opposed vineyard rows according to sampling date (-0.876) and number of soil tillings (-0.409). *Arenaria serpyllifolia*, *Crepis sancta*, *Fumaria officinalis* were associated to early sampled rows with little soil tillage while *Convolvulus arvensis*, *Amaranthus retroflexus* or *Equisetum* *ramosissimum* where associated with late sampled rows with several soil tillings (Figure 3a). Species ranks along the main gradients identified by partial CCA on the rows and the inter-rows are summarized in Table 5a and 5b.

3.2. Factors affecting weed communities structure (richness and abundance)

The mean number of species per plot was 9.4±5.4 (min=1, max=27) in the row and 10.1±5.5 in the inter-row (min=1, max=28). Species richness differed according to management practices in the inter-rows (Kruskal-Wallis test, $P<0.001$): there were no significant differences of species richness between inter-rows were herbicides were applied (7.55±4.73), inter-rows that were tilled (9.00±5.84) or inter-rows that were both treated with herbicides and tilled (8.80±6.28), while inter-rows that were mown and tilled showed the highest level of richness (12.45±5.66, Figure 4a). Total abundance showed similar variations between the management practices (Kruskal-Wallis test, $P<0.001$) with highest species density for mown/tilled inter-rows and lowest for chemical and/or mechanical control methods (Figure 4b).

The model selection procedure kept 5 variables to explain the species richness in inter-rows (see Appendix S4 for detailed output of the model). The marginal R^2 of the final model (for fixed factors) was 0.248 and the conditional R^2 (including the fixed factors and the random effect of plot identity) was 0.369 (against 0.264 and 0.378 for the full model). The standardized effect size was highest for soil pH, followed by percentage of silt, year, number of herbicide treatments and number of soil tillings (Figure 5a). These two management variables were only slightly negatively correlated (-0.3) for the inter-rows, showing a tendency to use one or the other practice, even if winegrowers could implement both practices in the same field the same year.

To explain species abundance in inter-rows, the model selection procedure kept 5 variables (see Appendix S5 for detailed output of the model). The marginal R^2 of the final model (for fixed factors) was 0.194 and the conditional R^2 (including the fixed factors and the random effect of plot identity) was 0.377 (against 0.210 and 0.382 for the full model). The standardized effect size was highest for percentage of silt and year, followed by the number of herbicide treatments, season and the number of soil tillage (Figure 5b). In summary, species richness and abundance in the inter-rows increased with the percentage of silt and decreased with year and the number of herbicide treatments applied per year and to a lesser degree with the number of soil tillings implemented each year. Species richness also increased with decreasing pH and abundance decreased with growing season (higher in spring, lower in autumn).

On the grapevine rows, species richness and total abundance differed according to soil management practices (Kruskal-Wallis tests, $P<0.001$). Species richness and total abundance were highest in tilled rows (10.42±4.79 species, 23.75±31.41 ind./m²) and showed lowest values in rows with herbicide treatments (8.92±5.67 species, 13.98±17.54 ind./m²), and in rows with a combination of herbicide treatments and soil tillage (7.27±4.17 species, 9.70±12.24 ind./m², Figure 4c,d).

On the grapevine rows, the model selection procedure for explaining species richness kept six variables (see Appendix S6 for detailed output of the model). The marginal R^2 (for fixed factors) was 0.215 and the conditional R^2 (including the fixed factors and the random effect of plot identity) was 0.372 (against 0.247 and 0.380 for the full model). The standardized effect size was highest for latitude, followed by longitude square rooted terms, number of herbicide treatments, year, season and number of soil tillings (Figure 6a). To explain species abundance in rows, the model selection procedure kept 5 variables (see Appendix S7 for detailed output of the model). The marginal R^2 of the final model (for fixed factors) was 0.210 and the conditional R^2 (including the fixed factors and the random effect of plot identity) was 0.298 (against 0.219 and 0.308 for the full model). The standardized effect size was highest for year, followed by x^2, and then by the season, percentage of silt and the number of herbicide treatments (Figure 6b).

In summary, species richness and abundance decreased with year, growing season and with the number of herbicide treatments and increased with x^2. Species richness increased with increasing latitude and decreased with an increasing number of soil tillings, while species abundance decreased with percentage of silt. VIF was < 10 for all explanatory variables of the full models, and < 2 in the reduced models, indicating no serious collinearity.

4. Discussion

With a total of 234 species recorded in our study, we covered about 25% of the plant species diversity found in French vineyards which is estimated at 900 species (Maillet, 2006). Such coverage was expected due to the extent of the survey limited to three regions and above all to the classical log-normal distribution of plant species with a few common species and a lot of rare species with a narrow distribution. However, our survey was representative of the distribution and the responses of the main weed species of the French vineyard including the 44 species considered as potentially noxious (Maillet *et al.*, 2001). The total explained variation in plant composition is about 16-17%. This percentage of explained variance is consistent with previous studies on plant community in arable fields (Fried *et al.*, 2008) or field margins (Cordeau *et al.*, 2010). The proportion of explained variation is a consequence of the large data set (883 samples x 234 species), resulting in a high amount of noise (Lososová *et al.*, 2004). Although this represents a relatively low amount of explanation, it allowed us to measure the relative contribution of individual variables that helped shaping the plant community and to assess the relative effect of management and environmental factors (Nagy *et al.*, 2018).

4.1 Contribution to plant assemblages of temporal and spatial characteristics of the plots

Season was the strongest driver of the plant assemblages in French vineyards. The succession of different species assemblages during the growing season, with the succession of spring communities (*Cardamine hirsuta*, *Crepis sancta*, *Veronica* spp.) followed by summer communities (*Amaranthus* spp., *Chenopodium album*, *Setaria* spp.) is well known in cultivated fields (Kropáč *et al.*, 1971; Lososová *et al.*, 2006; Šilc and Čarni, 2007). This is mainly a consequence of variation in species time of emergence (Roberts and Feast, 1970) related to different physiological requirements of temperature and humidity for seed germination (Jauzein, 1986). In vineyards, which are characterized by large spaces between rows and most generally with no cover crops in the inter-rows, such seasonal dynamics was expected to be higher compared to annual crops where the shade of crop canopy prevents new germinations in the course of the growing season (Andrade *et al.*, 2017). In addition, in our analysis the season not only covers the variation of weather over the year but probably also includes the differences of vegetation before and after management (mowing, herbicides, tillage), as soil management practices are usually applied between the first census in spring and the following censuses in summer/autumn. This could be important, all the more that certain practices such as tillage are known to stimulate new germination (Cordeau *et al.*, 2017a) and because tillage operations are more spread over the season in vineyards than in annual crops (concentrated in fallow period).

Latitude was the second strongest driver of plant composition after partialling out its shared effect with other variables (i.e. see gross effect, Table 2). It represents mainly the differences between the three regions based on their climatic conditions and the related specific species pool that formed at evolutionary temporal scale in Mediterranean versus continental regions. In the Languedoc, vineyard weed communities includes typical (sub)Mediterranean species such as *Equisetum ramosissimum* or *Heliotropium europaeum* while in Champagne, communities are often dominated by more cosmopolitan weed species such as *Poa annua* or *Mercurialis annua* (Rhône-Alpes vineyards being intermediary). Soil parameters (pH and texture) were also good descriptors of large-scale variations in plant composition (i.e. see net effect, Table 2). Results were consistent with previous knowledge on indicator species (Ellenberg *et al.*, 1992) with *Diplotaxis erucoides* and *Calendula arvensis* being indicative of basic soils (mainly in Languedoc vineyards), while *Cynodon dactylon* and *Epilobium tetragonum* were more associated with slightly acidic soils, more frequent in the Rhone valley. Among other dominant species, *Rumex crispus* and *Elytrigia repens* were associated with clay soils while *Erigeron sumatrensis* and *Sorghum halepense* were more abundant on sandy soils.

4.2 Contribution of management practices of the plots to plant assemblages

In our study, farming practices explained a low variation of plant composition. This is not in accordance with previous studies in vineyards where, species composition varied more by management (i.e. 49.5%) than by seasonal changes (i.e. 22.6%) (Lososová *et al.*, 2003). However, it is important to mention that in the study of Lososová *et al.* (2003), the observed plant composition shifts where associated with the transition from intensive agricultural management with frequent tilling and herbicide use, to a more environment- friendly management by mulching. This was not the case in our study, where farming practices were more homogeneous (herbicides were largely used, see Table 2) and considered to be consistent over the 7 years in the surveyed plot.

Despite a low explanatory power, our results concerning the number of herbicide treatments or the number of soil tillings are consistent with the knowledge of species biology and behaviour. *Sorghum halepense* and *Malva sylvestris* seems to be associated with fields where rows received high amounts of herbicide. This is in accordance with the fact that glyphosate (the most frequently used herbicide in the survey) was reported to show reduced efficacy against these species, e.g. in Greece (Travlos *et al.*, 2014). *Malva* spp. are considered to be naturally tolerant to glyphosate (Michael *et al.*, 2009), while the extensive underground rhizome of *Sorghum halepense* make it difficult to control even with such systemic herbicides. At the opposite side of the herbicide intensity gradient, rows that received no or very few herbicide treatments harbour species such as *Calendula arvensis* or *Muscari comosum* that were typically considered as decreasing since the large adoption of systemic herbicides in vineyards (Barralis *et al.*, 1983). Inter-rows that are poorly or not tilled are associated with higher abundance of perennial species such as *Trifolium repens*, *Lepidium draba* or *Rumex pulcher*, while regular soil tillage typically favours annual species such as *Cerastium glomeratum* or *Galium aparine* subsp. *aparine*. Globally our results are consistent with the idea that herbicide and tillage are strong filters of plant communities favouring mostly therophytes, or some perennials with high vegetative reproduction capacity through cuttings (tillage, e.g. *Convolvulus arvensis*) or deep and extensive root systems (herbicide e.g. *Sorghum halepense*). Whereas mowing appears to be a weaker management filter that allows the presence of a greater diversity of species (Kazakou et al., 2016).

The fact that season better explained community composition than the number of management operations per year suggests that rather than the number of treatments, their timing of application might determine species composition more importantly (Cordeau *et al.*, 2017b). In rotated annual crop fields, timing of tillage (in relation to the plant phenology and seed production for example) was identified as a strong assembly “filter” that can either constrain or advance the membership of species within the subsequent weed community (Smith, 2006; Cordeau *et al.*, 2017b).

4.3. Importance of environmental and management practice filters

One important finding of our study is that in French vineyards, seasonal and environmental factors shape plant assemblages while farming practices affect species richness and abundance. This result can be replaced in a conceptual framework commonly used in community assembly theory which assumes that local assemblages are shaped by a hierarchical series of environmental and anthropogenic filters (Ackerly and Cornwell, 2007). For French vineyards, our results suggest that there are different regional species pools (latitudinal effect), each of which is further differentiated according to soil conditions (acidic sandy soils versus basic clay soils). For a given species composition determined by these large-scale abiotic gradients, local management practices will then poorly modify the composition, but the number of soil tillings or herbicide treatments will limit the number of species or individuals of a given potential assemblage. In this respect, the importance of the effect of management practices on species richness between row and inter-row was quite different, particularly regarding the chemical or mechanical weed control strategies. Indeed, according to our results, a large number of chemical weed control or tillage methods reduced richness with a stronger effect on the rows than on the inter-rows, while the number of mowings has no effect on the richness in the row spacing. This latter result is not contradictory with the literature since it is reported that the height of mowing matters more than the number of mowings for filtering spontaneous flora (Abu-Dieyeh and Watson, 2005).

4.4. Management implications

Species richness has been recently proposed as a good indicator of diversified and sustainable cropping systems less prone to dominance by highly adapted resistant weed species (Storkey and Neve, 2018). In this regard, our study showed that herbicides were the less sustainable management practices with lower species richness and a strong decrease with increasing number of treatments. Whereas mechanical control (in rows) and combination of mowing and soil tillage (in the inter-rows, i.e. usually this corresponds to a temporary spontaneous cover) showed the highest species richness. As already reported by Storkey and Neve (2018), the plots with the higher number of herbicide treatments are also those with the most troublesome weeds such as *Sorghum halepense* or *Malva* *sylvestris*. Finally, managing rows and inter-rows with different tactics may create different habitats at the field level and select species with different response traits, enhancing the overall weed species richness at the vineyard plot scale.

One limitation of this survey is the absence of data on grape yield in order to try to relate it to weed abundance and diversity (Sanguankeo *et al.*, 2009). Depending on the objectives of the grapevine growers, different levels of weed abundance can be tolerated. Herbicides showed the highest level of control of weed abundance but soil tillage appeared as an effective alternative at least for the inter-rows where a similar level of control is obtained with this method. Maybe due to less intense tillage on the rows in order to limit possible unintended effects on the vines, weed abundance remained higher in tilled rows compared to rows sprayed with herbicides and the number of soil tillings did not reduce weed abundance on the rows. However, the lowest abundance was observed in rows that combined herbicides and soil tillage. This shows that, in vineyards using only chemical control, the number of herbicide treatments can be potentially reduced and, depending on seasonal soil moisture conditions, some herbicide treatments could be replaced by soil tillage without increased weed abundance.

Combinations of mowing and tillage appear as the strategy which leads to the highest level of species richness and abundance in comparison with herbicide use (Steenwerth *et al.*, 2016). These practices usually imply the development and the management of a spontaneous cover in the inter-rows with possible provision of ecosystem services to the agrosystem (Garcia *et al.*, 2018), such as runoff control and erosion mitigation during winter for example (Novara *et al.*, 2011). Moreover, temporary spontaneous cover is often seen as less competitive and easier to manage than sown cover crops because it may provide ecosystem services to the agrosystem and allows the grapevine grower to control the weeds mechanically or chemically if needed, depending on the climatic conditions of the year (Ripoche *et al.*, 2010), without dedicating time and money to sowing a cover crop. This practice seems all the more relevant in wine-growing regions subject to high water stress risks (Languedoc-Roussillon for example, Delpuech and Metay (2018)) or for which the valuation per hectare of grape production is high (Pujol, 2017).

4.5. Conclusions

Large-scale surveys are useful for understanding the rules governing the assembly of weed communities. Our results suggest that weed species composition vary more during a season than between different regions and soil types, although these factors are the second and third most important, respectively. Management practices have only a weak effect on species composition whereas they control more importantly species richness and abundance, and have more effect on the rows than on the inter-rows. Combination of soil tillage and mowing appear as the more environmental-friendly practice with higher species richness and abundance. Our study is a first step permitting to identify the factors to take into account in order to ensure an optimal management of the spontaneous vegetation in vineyards while allowing this vegetation to provide various ecosystem services to the agrosystems.

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References

Abu-Dieyeh, M., Watson, A., 2005. Impact of mowing and weed control on broadleaf weed population dynamics in turf. Journal of Plant Interactions 1, 239-252.

Ackerly, D.D., Cornwell, W.K., 2007. A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. Ecology Letters 10, 135-145.

Agreste, 2009. De la place pour l'herbe dans les vignes. Agreste Primeurs 221, 1-4.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74, 19-31.

Andrade, J., Satorre, E., Ermácora, C., Poggio, S., 2017. Weed communities respond to changes in the diversity of crop sequence composition and double cropping. Weed Research 57, 148-158.

Barralis, G., 1976. Méthode d'étude des groupements adventices des cultures annuelles : application à la Côte d'Or., Colloque Int. Ecol. Biol. Mauvaises Herbes, Dijon, France, pp. 59-68.

Barralis, G., Cloquemin, G., Guérin, A., 1983. Evolution de la flore adventice du vignoble de Côte-d'Or sous la pression des techniques d'entretien des cultures. Agronomie 3, 585-594.

Baumgartner, K., Steenwerth, K.L., Veilleux, L., 2007. Effects of organic and conventional practices on weed control in a perennial cropping system. Weed Science 55, 352-358.

Baumgartner, K., Steenwerth, K.L., Veilleux, L., 2008. Cover-crop systems affect weed communities in a California vineyard. Weed Science 56, 596-605.

Belyea, L.R., Lancaster, J., 1999. Assembly rules within a contingent ecology. Oikos 86, 402-416.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045-1055.

Celette, F., Gaudin, R., Gary, C., 2008. Spatial and temporal changes to the water regime of a Mediterranean vineyard due to the adoption of cover cropping. European Journal of Agronomy 29, 153-162.

Chytrý, M., Tichý, L., Holt, J., Botta-Dukát, Z., 2002. Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13, 79-90.

Cordeau, S., Reboud, X., Chauvel, B., 2010. Relative importance of farming practices and landscape context on the weed flora of sown grass strips. Agriculture Ecosystems & Environment 139, 595-602.

Cordeau, S., Smith, R.G., Gallandt, E.R., Brown, B., Salon, P., DiTommaso, A., Ryan, M.R., 2017a. Disentangling the effects of tillage timing and weather on weed community assembly. Agriculture 7, 66.

Cordeau, S., Smith, R.G., Gallandt, E.R., Brown, B., Salon, P., DiTommaso, A., Ryan, M.R., 2017b. Timing of tillage as a driver of weed communities. Weed Science 65, 504-514.

Dastgheib, F., Frampton, C., 2000. Weed management practices in apple orchards and vineyards in the South Island of New Zealand. New Zealand Journal of Crop and Horticultural Science 28, 53-58.

Delpuech, X., Metay, A., 2018. Adapting cover crop soil coverage to soil depth to limit competition for water in a Mediterranean vineyard. European Journal of Agronomy 97, 60-69.

Ellenberg, H., Weber, H., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1992. Indicator values of central European plants. Scripta Geobotanica 18, 1-258.

Feledyn-Szewczyk, B., Kuś, J., Stalenga, J., Berbeć, A.K., Radzikowski, P., 2016. The Role of Biological Diversity in Agroecosystems and Organic Farming. Organic Farming-A Promising Way of Food Production. InTech.

Fried, G., Norton, L.R., Reboud, X., 2008. Environmental and management factors determining weed species composition and diversity in France. Agriculture Ecosystems & Environment 128, 68-76.

Gago, P., Cabaleiro, C., Garcia, J., 2007. Preliminary study of the effect of soil management systems on the adventitious flora of a vineyard in northwestern Spain. Crop Protection 26, 584-591.

Garcia, L., Celette, F., Gary, C., Ripoche, A., Valdés-Gómez, H., Metay, A., 2018. Management of service crops for the provision of ecosystem services in vineyards: A review. Agriculture, Ecosystems & Environment 251, 158-170.

Guerra, B., Steenwerth, K., 2011. Influence of floor management technique on grapevine growth, disease pressure, and juice and wine composition: a review. American Journal of Enology and Viticulture, ajev. 2011.10001.

Hair, J.F., Black, W.C., Babin, B.J., Anderson, R.E., Tatham, R.L., 2006. Multivariate data analysis (Vol. 6). Upper Saddle River, NJ: Pearson Prentice Hall.

Halberg, N., 1999. Indicators of resource use and environmental impact for use in a decision aid for Danish livestock farmers. Agriculture, Ecosystems & Environment 76, 17-30.

Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E., Wheeler, I., Mantel, S., Kempen, B., 2017. SoilGrids250m: Global gridded soil information based on machine learning. PLOS ONE 12, e0169748.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965-1978.

Jauzein, P., 1986. Échelonnement et périodicité des levées de mauvaises herbes. Bulletin de la Société Botanique de France. Lettres Botaniques 133, 155-166.

Kazakou, E., Fried, G., Richarte, J., Gimenez, O., Violle, C., Metay, A., 2016. A plant trait-based response-and-effect framework to assess vineyard inter-row soil management. Botany Letters 163, 373-388.

Kropáč, Z., Hadač, E., Hejný, S., 1971. Some remarks on the synecological and syntaxonomic problems of weed plant communities. Preslia 43, 139-153.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2015. Package 'lmerTest'. R package version 2.

Legendre, P., Legendre, L., 1998. Numerical ecology: second English edition. Developments in environmental modelling 20.

Lepš, J., Šmilauer, P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University press.

Lososová, Z., Chytrý, M., Cimalová, S., Kropáč, Z., Otýpková, Z., Pyšek, P., Tichý, L., 2004. Weed vegetation of arable land in Central Europe: Gradients of diversity and species composition. Journal of Vegetation Science 15, 415-422.

Lososová, Z., Chytrý, M., Cimalová, Š., Otýpková, Z., Pyšek, P., Tichý, L., 2006. Classification of weed vegetation of arable land in the Czech Republic and Slovakia. Folia Geobotanica 41, 259-273.

Lososová, Z., Danihelka, J., Chytrý, M., 2003. Seasonal dynamics and diversity of weed vegetation in tilled and mulched vineyards. Biologia 58, 49-57.

Lüdecke, D., 2017. sjPlot: Data Visualization for Statistics in Social Science. . R package version 2.4.0, https://CRAN.R-project.org/package=sjPlot.

Maillet, J., 1992. Constitution et dynamique des communautés de mauvaises herbes des vignes de France et des rizières de Camargue. USTL, Montpellier, p. 179.

Maillet, J., 2006. Flore des vignobles: Biologie et écologie des mauvaises herbes. Phytoma-La Défense des Végétaux 590, 43-45.

Maillet, J., Arcuset, P., Carsoulle, J., 2001. Connaître les mauvaises herbes des vignobles français: Lutte contre les mauvaises herbes. Phytoma-La Défense des Végétaux 544, 36-38.

Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R., Ward, L.K., 2003. The role of weeds in supporting biological diversity within crop fields. Weed Research 43, 77-89.

Michael, P.J., Steadman, K.J., Plummer, J.A., 2009. The Biology of Australian Weeds 52. Malva parviflora L. Plant Protection Quarterly 24, 2.

Michez, M., Guillerm, J., 1984. Signalement écologique et degré d'infestation des adventices des cultures d'été en Lauragais. Proc. 7ème Coll. Int. Ecol. Biol. Mauvaises Herbes 1, 155-162.

Monteiro, A., Lopes, C., Machado, J., Fernandes, N., Araújo, A., 2008. Cover cropping in a sloping, non-irrigated vineyard: 1-Effects on weed composition and dynamics. Ciência e Técnica Vitivinícola 23, 29-36

Nagy, K., Lengyel, A., Kovács, A., Türei, D., Csergő, A., Pinke, G., 2018. Weed species composition of small□scale farmlands bears a strong crop□related and environmental signature. Weed Research 58, 46-56.

Novara, A., Gristina, L., Saladino, S., Santoro, A., Cerdà, A., 2011. Soil erosion assessment on tillage and alternative soil managements in a Sicilian vineyard. Soil and Tillage Research 117, 140-147.

Oksanen, J., F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs, Wagner, H., 2017. vegan: Community Ecology Package. R package version 2.4-4. https://CRAN.R-project.org/package=vegan.

Pujol, J., 2017. Apports de produits phytosanitaires en viticulture et climat. Une analyse à partir des enquêtes pratiques culturales. Agreste Les Dossiers 39, 1-30.

R Development Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ripoche, A., Celette, F., Cinna, J.-P., Gary, C., 2010. Design of intercrop management plans to fulfil production and environmental objectives in vineyards. European Journal of Agronomy 32, 30-39.

Roberts, H.A., Feast, P.M., 1970. Seasonal ditribution of emergence in some annual weeds. Experimental Horticulture 21, 36-41.

Salomé, C., Coll, P., Lardo, E., Metay, A., Villenave, C., Marsden, C., Blanchart, E.,Hinsinger, P., Le Cadre, E. (2016). The soil quality concept as a framework to assess management practices in vulnerable agroecosystems: A case study in Mediterranean vineyards. Ecological indicators 61, 456-465.

Sanguankeo, P.P., Leon, R.G., Malone, J., 2009. Impact of weed management practices on grapevine growth and yield components. Weed Science 57, 103-107.

Šilc, U., Čarni, A., 2007. Formalized classification of the weed vegetation of arable land in Slovenia. Preslia 79, 283-302.

Smith, R.G., 2006. Timing of tillage is an important filter on the assembly of weed communities. Weed Science 54, 705-712.

Steenwerth, K.L., Orellana-Calderón, A., Hanifin, R.C., Storm, C., McElrone, A.J., 2016. Effects of various vineyard floor management techniques on weed community shifts and grapevine water relations. American Journal of Enology and Viticulture, ajev. 2015.15050.

Storkey, J., 2006. A functional group approach to the management of UK arable weeds to support biological diversity. Weed Research 46, 513-522.

Storkey, J., Neve, P., 2018. What good is weed diversity? Weed Research 58, 239-243.

Ter Braak, C.J., Smilauer, P., 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). www. canoco. com.

Travlos, I., Lysandrou, M., Apostolidis, V., 2014. Efficacy of the herbicide GF-2581 (penoxsulam+ florasulam) against broadleaf weeds in olives. Plant, Soil & Environment 12, 574-579.

Wilmanns, O., 1989. Communities and strategy types of plants of central European vineyards. Phytocoenologia 18, 83-128.

Wilmanns, O., 1993. Plant strategy types and vegetation development reflecting different forms of vineyard management 1. Journal of Vegetation Science 4, 235-240.

Figure captions

Figure 1. Distribution of the 46 vineyard plots across France and at the scale of the three vine production regions. The black lines represent the limit of the department, a French administrative unit dividing metropolitan France into 95 units.

Figure 2. Ordination diagrams of the reduced CCA model containingn a) the species (names coded with EPPO codes https://gd.eppo.int/) and b) the 11 significant explanatory variables. Only the species with the highest fit on the first two CCA axes are presented.

Figure 3. Ordination diagrams of the reduced CCA model containingn a) the species (names coded with EPPO codes https://gd.eppo.int/) and b) the 11 significant explanatory variables. Only the species with the highest fit on the first two CCA axes are presented.

Figure 4. Mean species richness (S) and mean density of vineyard plots in the inter- rows and the rows according to the main management practices : H = herbicides only, HT = combination of herbicides and soil tillage, T = soil tillage only, TM = combination of soil tillage and mowing (management practices or their combination that were represented in less than 20 surveys were discarded). Error bars represents confidence intervals. Different letters indicate significant differences according to Dunn test.

Figure 5. Standardized effects of the fixed variables of the reduced model explaining a) species richness and b) species abundance on the vine's inter-rows

Figure 6. Standardized effects of the fixed variables of the reduced model explaining a) species richness and b) species abundance on the vine's rows

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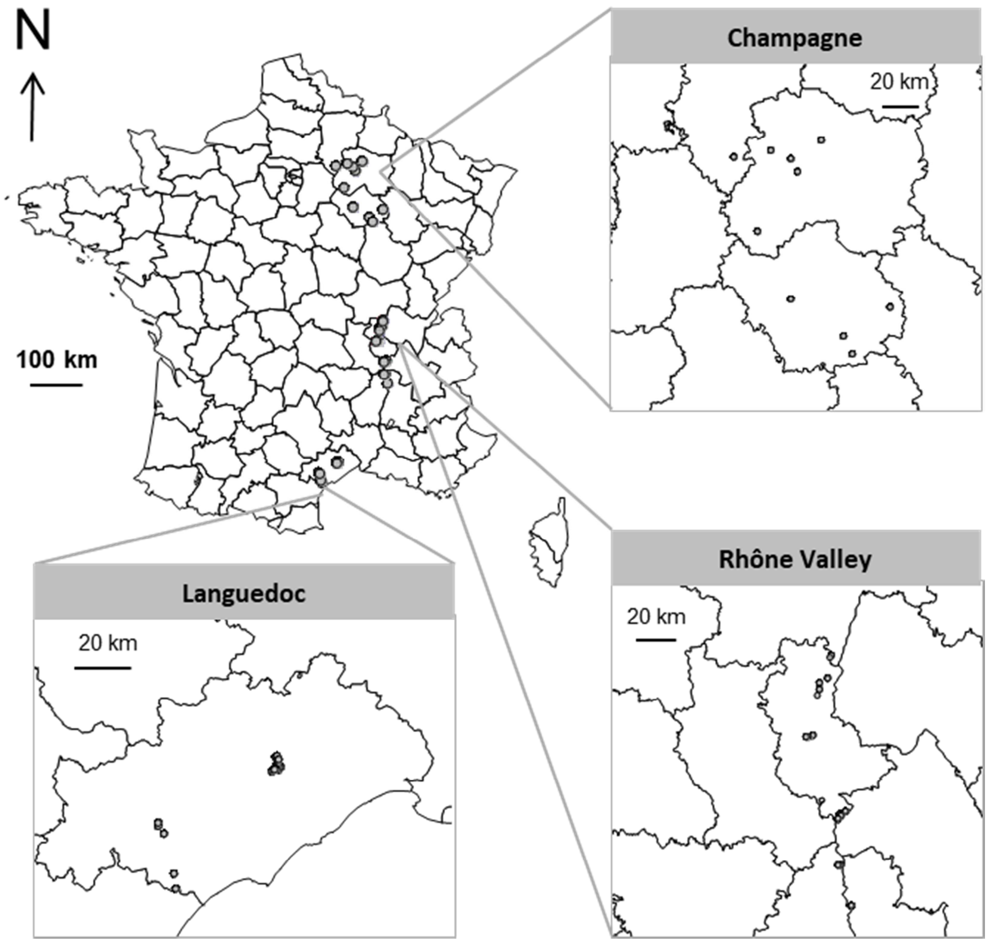

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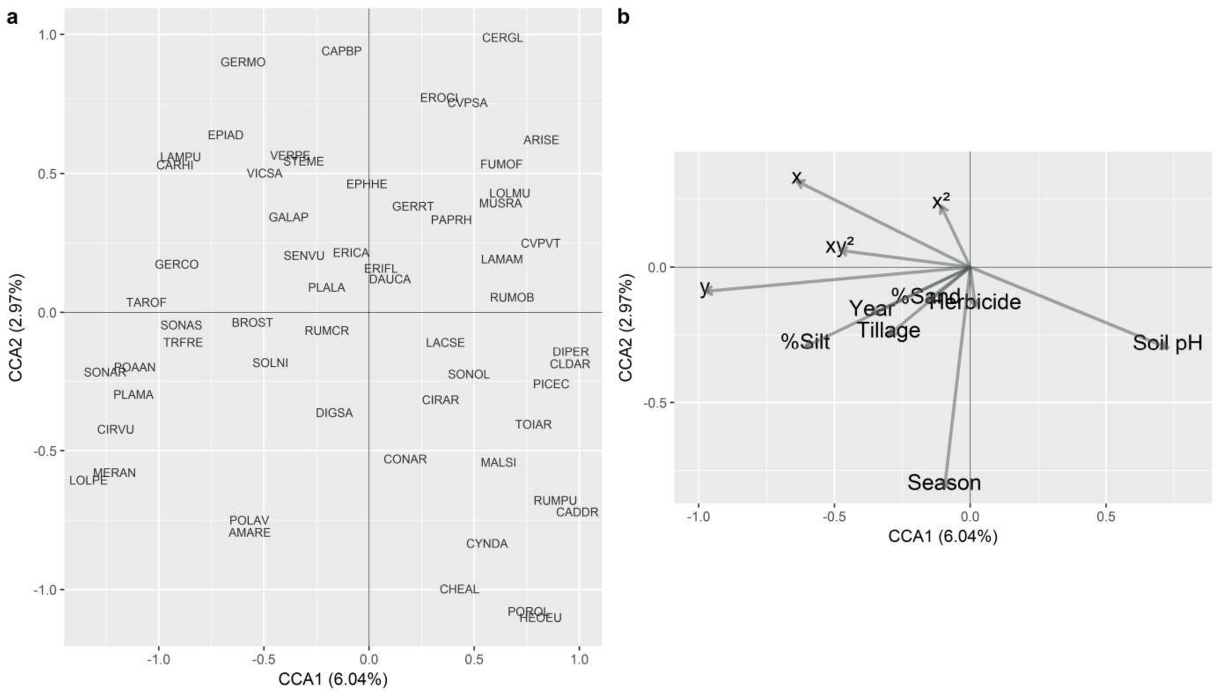

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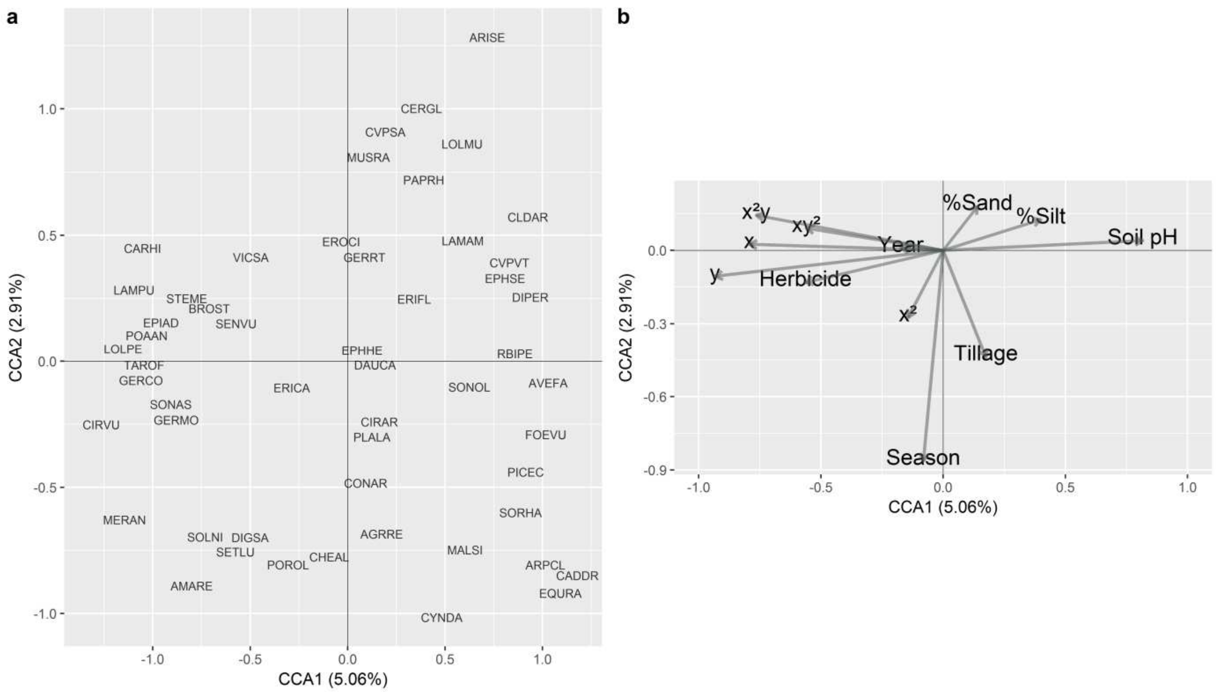

Figure 4. Mean species richness (S) and total abundance of vineyard plots in the inter- rows and the rows according to the main management practices : H = herbicides only, HT = combination of herbicides and soil tillage, T = soil tillage only, TM = combination of soil tillage and mowing (management practices or their combination that were represented in less than 20 surveys were discarded). Error bars represents confidence intervals. Different letters indicate significant differences according to Dunn test.

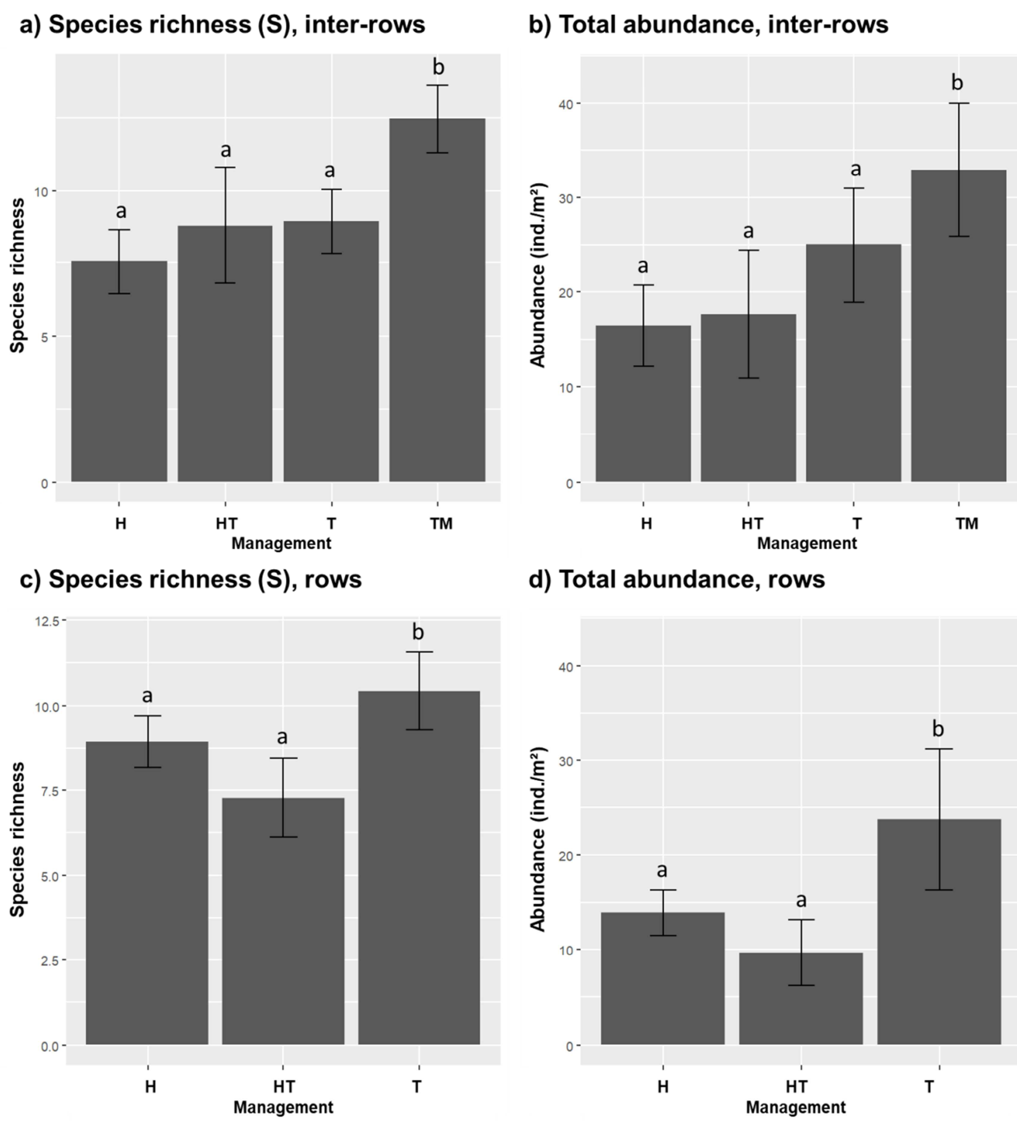

Figure 5. Standardized effects of the fixed variables of the reduced model explaining a) species richness and b) species abundance on the vine's inter-rows

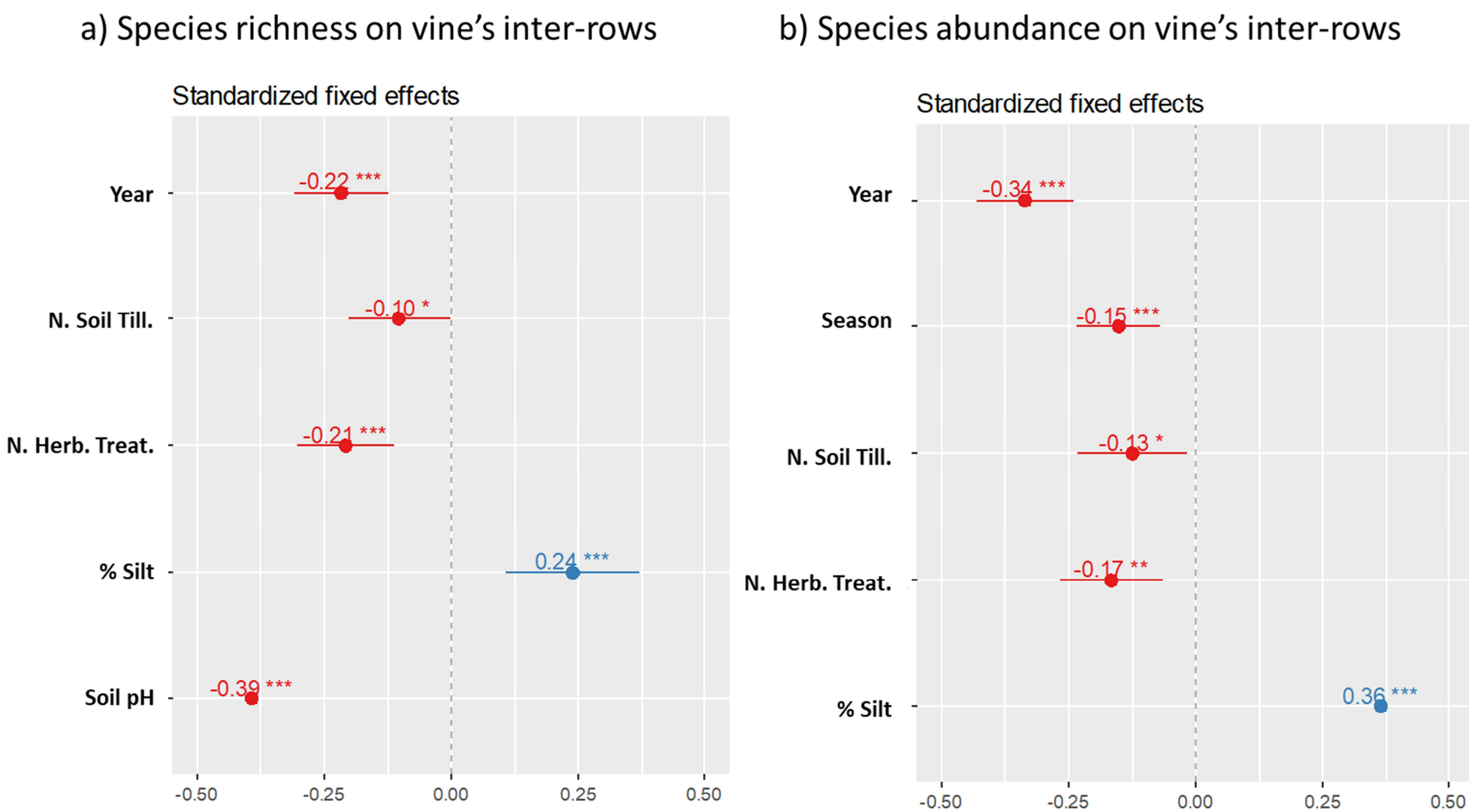

Figure 6. Standardized effects of the fixed variables of the reduced model explaining a) species richness and b) species abundance on the vine's rows

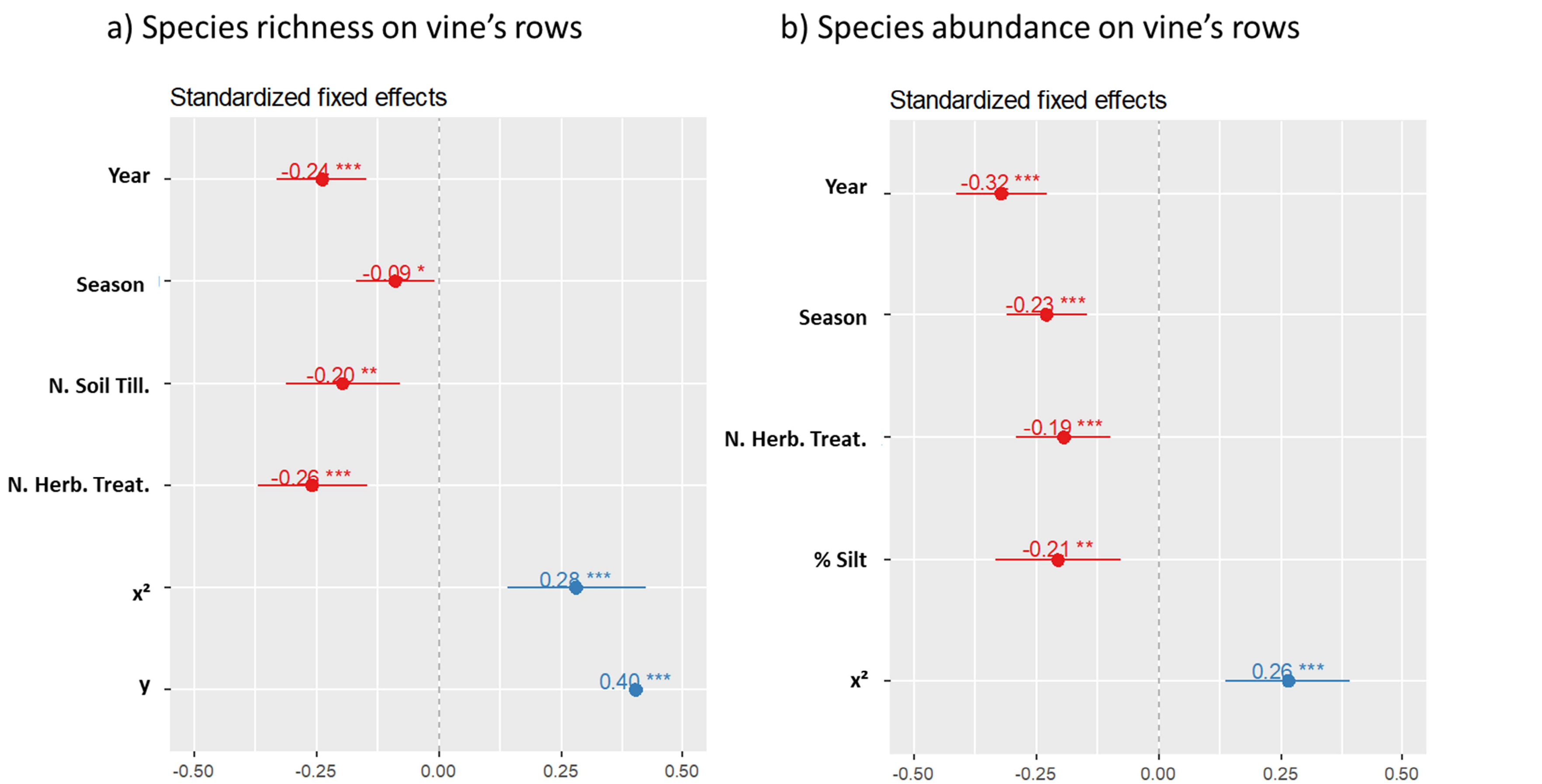

Table 1. Number of surveyed plots (#Plot) and floristic survey (#Surv.) by region and year. Season of floristic samples included late winter (W), spring (Sp), summer (Su) and autumn (A). Presence of a control plot (Cont.) without herbicide treatments is indicated.

Region	**Champagne**				**Languedoc**				**Rhône Valley**				**Total**
Year	#Plot	Seas.	Cont.	#Surv.	#Plot	Seas.	Cont.	#Surv.	#Plot	Seas.	Cont.	#Surv.	#Surv.
2006	0	-	-	0	10	A	No	20	14	A	No	21	41
2007	0	-	-	0	10	Sp/A	No	40	15	Sp/A	No	52	92
2008	0	-	-	0	18	W/Sp/A	No	108	15	Sp/A	No	52	160
2009	0	-	-	0	18	W/Sp/A	No	105	15	Sp/A	No	50	155
2010	10	Sp/Su/(A)	Yes	116	18	Sp/Su/A	No	106	14	Sp/Su/A	No	77	299
2011	10	Sp/Su	Yes	114	18	W/Su/A	No	105	0	-	-	0	219
2012	10	Sp/Su/(A)	Yes	94	0	-	-	0	0	-	-	0	94
Total	10	-	-	324	18	-	-	484	18	-	-	252	1060

Table 2. Main trends in management practices in the three regions and the two sampling area (rows and inter-rows). a) The first section gives the percentage of vineyard plots that received at least once, one of the three management practices (e.g. rows were never mowed, and in Champagne, the rows of all plots were at least once treated by herbicides). b) The second section gives the mean number of treatment per year for each management practices. c) The last section displays the proportion of surveys (plot x year) with a given management practice or a combination of management practices.

	Champagne		**Languedoc**		**Rhône valley**	
(a) % of field with this Management Practices during the survey period						
	R	IR	R	IR	R	IR
Mowing	0.0	80.0	0.0	11.1	0.0	66.7
Soil tillage	60.0	90.0	55.6	94.4	38.9	100
Herbicide	100	60.0	83.3	61.1	97.4	47.1
(b) Mean number of mowing, soil tillage or herbicides treatments per year[1]						
	R	IR	R	IR	R	IR
Number of mowing	0	**2**	0	0.29	0	1.01
Number of soil tillings	*1.43*	***2.39***	*1.21*	*1.78*	0.15	*1.32*
Number of herbicide treatments	**1.36**	0.57	1.03	0.85	*1.23*	0.39
(c) % of surveys (plot x year) with this (combination of) management practices[2]						
	R	IR	R	IR	R	IR
Mowing (M)	0.00	8.96	0.00	0.00	0.00	0.00
Soil tillage (T)	18.4	17.91	29.48	**45.90**	6.98	8.96
Herbicide (H)	**59.2**	22.39	**54.91**	27.32	**84.88**	16.42
Soil tillage + Mowing (TM)	0.00	**41.79**	0.00	10.93	0.00	**67.16**
Herbicide + Soil tillage (HT)	22.3	8.96	15.61	15.85	8.14	7.46

[1]Bold value are the highest of one line (e.g., the highest number of treatments are observed in Champagne for all three practices). Underlined figures represent the highest value between rows (R) and inter-rows (IR) for each region (e.g., herbicides are rather used on the rows and tillage and mowing on the inter-rows). Figures in italic represents the highest of one column, i.e. the highest value for the rows or the inter-rows for each region.
[2]Proportions are calculated for each area (R, IR) of each region (i.e., by column).

Table 3. Units and ranges of raw variables recorded on each surveyed vineyard plots. Abbreviations are given between brackets. Soil pH and soil texture values are derived from Soilgrids 250m (Hengl *et al.*, 2017).

Variable	**Unit**	**Ranges**
Spatial variables		
Latitude (y)	N, WGS84	43.25932- 49.13523
Longitude (x)	E, WGS84	3.05112- 4.861643
Temporal variables		
Date of sampling (Season)	Julian Day	32 (February, 1st) – 319 (November, 15th)
Year of sampling (Year)	Year	2006-2012
Soil variables		
Soil pH	-	6.286- 7.671
Soil texture, proportion of clay (% Clay)	%	20.571-32.000
Soil texture, proportion of silt (% Silt)	%	32.000- 51.429
Soil texture, proportion of sand (% Sand)	%	24.286- 44.571
Management variables		
Management intensity		
Number of soil tillings per year (N. Soil Till.)		0-8
Number of herbicide treatments per year (N. Herb. Treat.)		0-5
Number of mowing per year (N. Mowing)		0-8
Management type		
Herbicide (H)	-	yes-no
Soil tillage (T)	-	yes-no
Mowing (M)	-	yes-no
Herbicide + Soil tillage (HT)	-	yes-no
Soil tillage + Mowing (TM)	-	yes-no

Table 4. Gross and net effects of the explanatory variables on the vineyard species composition identified using (partial)CCA analyses with single explanatory variables. Bold figures correspond to the variable with highest % of explained variation for gross and net effects.

	Inter-row						**Row**					
	Gross effects		**Net effects**				**Gross effects**		**Net effects**			
	explained variation	**R^2_{adj}**	**explained variation**	**R^2_{adj}**	**F**	**P**	**explained variation**	**R^2_{adj}**	**explained variation**	**R^2_{adj}**	**F**	**P**
Spatial variables												
x	3.496	0.032	0.659	0.004	3.329	0.001	3.745	0.035	0.686	0.005	3.533	0.001
x^2	1.852	0.016	1.011	0.008	5.110	0.001	1.585	0.013	0.954	0.007	4.915	0.001
y	**5.864**	**0.056**	1.119	0.009	5.655	0.001	**4.668**	**0.044**	1.156	0.009	5.953	0.001
xy^2	2.022	0.017	0.735	0.005	3.714	0.001	2.190	0.019	0.515	0.003	2.652	0.001
x^2y	-	-	-	-	-	-	3.398	0.031	0.352	0.001	1.810	0.014
Temporal variables												
Season	2.723	0.024	**2.380**	**0.022**	**12.031**	**0.001**	2.708	0.024	**2.139**	**0.019**	**11.014**	**0.001**
Year	1.949	0.017	0.765	0.005	3.869	0.001	1.129	0.009	0.438	0.002	2.257	0.003
Soil variables												
Soil pH	4.170	0.039	0.746	0.005	3.772	0.001	3.903	0.036	0.687	0.005	3.538	0.001
Soil texture (silt, sand)	3.312	0.030	0.618	0.004	3.115	0.001	2.216	0.019	0.777	0.006	4.002	0.001
Soil texture (sand, clay)	0.666	0.004	0.471	0.002	2.372	0.001	0.882	0.006	0.968	0.007	4.984	0.001
Management variables												
N. Soil Till.	1.158	0.009	0.491	0.003	2.476	0.001	1.254	0.010	0.664	0.004	3.420	0.001
N. Herb. Treat.	0.412	0.001	0.329	0.001	1.659	0.049	2.064	0.018	0.456	0.002	2.346	0.001

Table 5. Names, score values and fit of the ten species giving the highest fit along the first constrained axis in the partial CCA models of the significant variables specified in Table 3 for a) inter-rows and b) rows.

a) inter-rows

Season(+spring, - summer)	**Axis 1 Score**	**Fit**	**Latitude (-high, +low)**	**Axis 1 Score**	**Fit**	**Soil pH**	**Axis 1 Score**	**Fit**	**N. Soil Till. (-low, +high)**	**Axis 1 Score**	**Fit**
Heliotropium europaeum	-1.294	0.057	*Poa annua*	-0.765	0.129	*Calendula arvensis*	-0.556	0.029	*Lepidium draba*	-0.558	0.011
Digitaria sanguinalis	-1.186	0.076	*Sonchus arvensis*	-0.622	0.023	*Malva sylvestris*	-0.468	0.027	*Rumex pulcher*	-0.307	0.013
Portulaca oleracea	-1.173	0.058	*Mercurialis annua*	-0.592	0.026	*Sonchus oleraceus*	-0.274	0.017	*Trifolium repens*	-0.175	0.022
Chenopodium album	-0.897	0.099	*Amaranthus retroflexus*	-0.587	0.022	*Diplotaxis erucoides*	-0.232	0.016	*Torilis arvensis*	-0.105	0.009
Convolvulus arvensis	-0.534	0.080	*Galium aparine*	-0.564	0.020	*Erigeron canadensis*	0.301	0.017	*Crepis sancta*	0.000	0.011
Erodium cicutarium	0.463	0.044	*Cardamine hirsuta*	-0.383	0.018	*Taraxacum officinale*	0.312	0.029	*Lactuca serriola*	0.030	0.015
Cerastium glomeratum	0.667	0.052	*Diplotaxis erucoides*	0.228	0.015	*Erodium cicutarium*	0.400	0.033	*Convolvulus arvensis*	0.048	0.015
Crepis sancta	0.689	0.132	*Erodium cicutarium*	0.360	0.026	*Geranium molle*	0.544	0.021	*Calendula arvensis*	0.169	0.008
Cardamine hirsuta	0.794	0.075	*Daucus carota*	0.485	0.017	*Portulaca oleracea*	0.721	0.022	*Galium aparine*	0.364	0.011
Capsella bursa-pastoris	0.833	0.059	*Euphorbia helioscopia*	0.507	0.017	*Vicia sativa*	0.871	0.052	*Cerastium glomeratum*	0.471	0.014

Table 5 coninued

b) rows

Season(+spring, - summer)	Axis 1 Score	Fit	Latitude (-high, +low)	Axis 1 Score	Fit	Soil texture (+clay,-sand)	Axis 1 Score	Fit	N. Herb. Treat. (-low, +high)	Axis 1 Score	Fit
Setaria pumila	-1.024	0.064	*Cirsium vulgare*	-1.159	0.060	*Polygonum aviculare*	-0.619	0.023	*Muscari comosum*	-0.512	0.037
Digitaria sanguinalis	-0.983	0.052	*Sonchus arvensis*	-1.020	0.040	*Erigeron sumatrensis*	-0.511	0.015	*Calendula arvensis*	-0.453	0.019
Chenopodium album	-0.874	0.062	*Mercurialis annua*	-1.003	0.072	*Daucus carota*	-0.468	0.027	*Mercurialis annua*	-0.410	0.015
Solanum nigrum	-0.766	0.054	*Geranium columbinum*	-0.556	0.029	*Galium aparine*	-0.450	0.021	*Polygonum aviculare*	-0.381	0.016
Convolvulus arvensis	-0.494	0.094	*Poa annua*	-0.547	0.039	*Cerastium glomeratum*	-0.432	0.022	*Setaria pumila*	-0.362	0.015
Fumaria officinalis	0.651	0.064	*Anisantha sterilis*	-0.500	0.026	*Plantago lanceolata*	0.467	0.037	*Lactuca serriola*	0.207	0.015
Lolium multiflorum	0.654	0.040	*Senecio vulgaris*	-0.287	0.033	*Avena fatua*	0.633	0.033	*Malva sylvestris*	0.284	0.017
Crepis sancta	0.664	0.099	*Helminthotheca echioides*	0.467	0.025	*Equisetum ramosissimum*	0.703	0.043	*Torilis arvensis*	0.518	0.024
Lamium purpureum	0.679	0.050	*Rumex crispus*	0.594	0.027	*Lepidium draba*	1.109	0.091	*Sonchus arvensis*	0.591	0.032
Cardamine hirsuta	0.849	0.082	*Equisetum ramosissimum*	0.698	0.043	*Rumex crispus*	1.166	0.106	*Sorghum halepense*	0.715	0.036